WILD
HERITAGE

February 20, 2025

Re: Tongass Land Management Plan Revision #64039 (submitted via https://cara.fs2c.usda.gov/Public/CommentInput?Project=64039)

Please accept these comments on the TLMP draft revision assessments as part of the public record. We submit these comments as feedback on the assessment drafts, note several places where factual corrections are needed, additional datasources, and published studies (hyperlinked herein) need to be included in the final integrated TLMP revision assessment.

Wild Heritage has been involved on the Tongass since our seminal breeding and winter bird studies (DellaSala et al. 1996), repeated by the US Fish & Wildlife Service in 2012 (Matsuoka et al. 2012). At the time, those studies underscored the importance of Tongass old-growth for bird communities and how thinning and canopy gap creation in second growth was not having much of a beneficial effect on old-growth associated bird species. Tongass old growth importance and its unique global significance via relative intactness and carbon density estimates have been updated and highlighted throughout our comments.

Notably, DellaSala (2011) published the first global assessment of temperate and boreal rainforests of the world that placed the Tongass in a global context of conservation importance as "*one of the world's last remaining relatively intact* temperate rainforests" (emphasis added). While Tongass intactness is globally significant, Canada's Great Bear rainforest, the Valdivia temperate rainforests of Chile/Argentina, and the temperate and hemi-boreal rainforests of Southern Siberia and the Russian Far East need to be also referenced in context as these rainforests eclipse the Tongass in total forested area and relative intactness, particularly given the amount of high-grade logging of Tongass high-volume old growth prior to the Tongass Timber Reform Act (Albert and Schoen 2013), which especially targeted Prince of Wales Island. This correction of proper context needs to be acknowledged in the terrestrial assessment along with the impact of high-grade logging that degraded high carbon dense, biodiverse old growth replacing it with impoverished plantations. While the total "productive" old growth on the Tongass is still impressive (~5 million acres, 89% of historic, DellaSala et al. 2022), most of the high-volume old growth was eliminated decades ago and this should be acknowledged for historical content (Albert and Schoen 2013). Further, the Tongass also contains low volume ("unproductive") old growth such as muskegs that should not be discounted in terms of their conservation significance as intact areas of high ecological integrity. Shoen and Albert (2007) conducted a conservation assessment of priority areas in southeast Alaska that included most of the

Tongass old growth and intact areas and this should be recognized in the terrestrial assessment.

Recent studies on the Tongass, not cited in the carbon assessment section, need proper recognition along with climate related studies that are published and peer reviewed (DellaSala et al 2015, Vynne et al. 2021). The reference to Halofsky as an unpublished "draft" should be referred to only when available to the public. Importantly, when Halofsky is published it will be a General Technical Report not subject to independent peer review and thus these other published studies take on important regional significance and should have been included.

Draft Carbon Stocks Assessment Misses Several Important Studies and Does Not Provide an Appropriate Carbon Life Cycle Analysis of Logging Related Carbon Losses

The Tongass has globally important carbon stocks representing up to 20% of the total stock on the national forests (DellaSala et al. 2022) and more than the 10% acknowledged in the draft carbon assessment. While we appreciate mention of our prior publication, there is a lot more in our study that should be referenced. For instance, most (96%) of the Tongass carbon is tied up in old growth and roadless areas (DellaSala et al. 2022) with very little (4%) stock in second growth. The 10% carbon stock cited in the draft carbon assessment is only for the live tree biomass component (see Law et al. 2023 cited in the assessment) and does not include dead biomass or below-ground carbon stocks that were reported in DellaSala's percentages as noted in their figure herein.

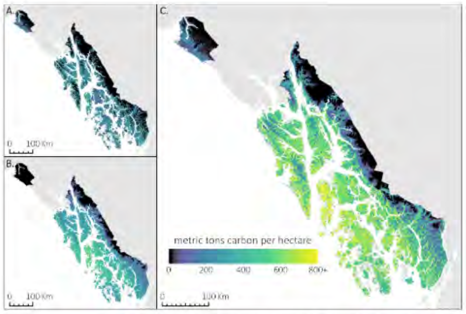


Figure 2. Spatial distribution of carbon (metric tons ha^{-1}) stored in (**A**) woody plant biomass (carbon pools include trees, roots, woody debris, seedlings/saplings, snags, and understory vegetation), (**B**) soil organic matter (top 1 m of mineral soil plus surface organic horizons), and (**C**)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

That omission needs to be corrected in the draft assessment. Further, your FIA based carbon assessment is missing wilderness areas (35% of the Tongass which includes old growth). DellaSala et al (2022) included all Tongass LUDs and their figures should be better cited. We request you include these data and related information in the carbon assessment from DellaSala et al. (2022) as noted herein from their published study.

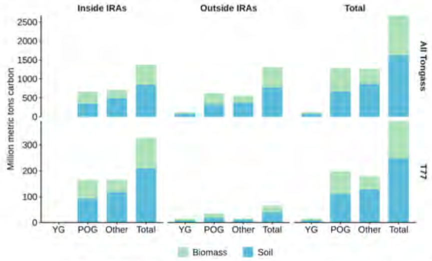
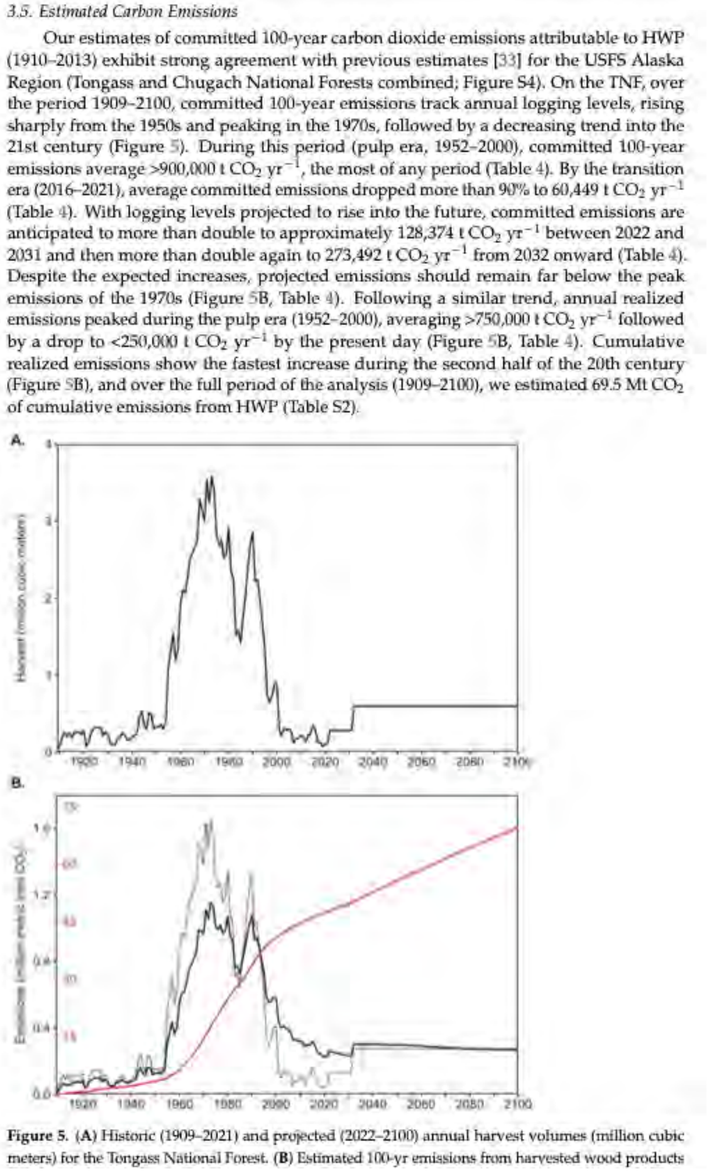


Figure 3. Carbon (million metric tons) stored in woody plant biomass and soil by forest age class (YG = young growth; POG = productive old growth) both inside and outside of Inventoried Roadless Areas (IRAs) and inside Tongass 77 watersheds (T77; bottom row) on the Tongass National Forest (top).

It cannot be overstated how import carbon stocks in old-growth forests and roadless areas are to the Tongass' globally important carbon sink properties. The stock change from logging that peaked in the 1980s has resulted in a great deal of atmospheric emissions that in no way are made up for by natural regeneration in young stands nor the minor amount of carbon tied up in much shorter-lived wood product pools. The harvested wood product pool pales in comparison to stocks retained for centuries in old-growth forests and they should never be compared to biogenic carbon in forests in a carbon assessment as harvest wood product pools come with a substantial cost to the climate because most of the carbon was released at some point post logging. Notably, on the Tongass, as much if not more than 50% of the biomass in an old-growth forest is left on site as slash, stumps, and tree trunks as “fall down” (DellaSala et al. 2022). That is a serious omission in the draft carbon assessment that lacks a proper life cycle analysis (Hudiburg et al. 2019) that needs to include all sector emissions from forest floor carbon losses to transport and distribution of wood products as emissions.

Here, we summarize the logging simulation analysis from DellaSala et al. (2022) that should be referenced in the draft carbon assessment in terms of emissions already released by historic logging and what would be released under alternative scenarios (the Forest Service should conduct an updated analysis based on TLMP alternatives using a similar approach).



3.5. Estimated Carbon Emissions

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

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

While the draft carbon assessment aptly notes that “harvest is the dominant disturbance,” it is incorrect to assume this has had “minimal impacts to carbon density.” This is an incorrect and highly subjective statement given that carbon density is highest in old-growth forests (DellaSala et al. 2022) and logging in these forests type converted them to low-carbon density second growth (~400,000 acres) at the expense of atmospheric emissions that you did not account for. While “on average, harvest affected 0.04 percent of the total forested area per year,” this is the wrong scale of analysis. What’s most important is how harvest targeted first and foremost the most carbon dense old-growth forests on the Tongass and then type converted them to diminished stocks that resulted in most of the carbon emitted.

Thus, in a nutshell, your carbon assessment is not based on best available science, needs to incorporate published studies that estimated stock reduction from logging (DellaSala et al. 2022), acknowledge how little is stored in wood product pools (Law et al. 2018, Hudiburg et al. 2019, Harmon 2019), and conduct a proper carbon life cycle analysis of the impacts of timber harvest (past, current, projected) on carbon stocks and how harvest targeted the most carbon dense forests on the Tongass. That is – the percentage of the land base logged on average is hiding the ball (trivializing) on how impactful logging has been aimed at the most productive, carbon dense old-growth forests. Harvest wood product pools are nearly always overestimated by the Forest Service and timber industry (Harmon et al. 2019) as is the case in the draft carbon assessment.

Terrestrial Assessment and Species of Conservation Concern

Ecological Integrity Problems are Incorrectly Portrayed as Primarily a Natural Disturbance Problem - the draft terrestrial assessment – as well as other Forest Service assessments like the national old growth threat assessment – inappropriately blames natural disturbances for declines in ecological integrity even though there are clearcut differences between logging-related forest disturbances vs. natural disturbances that are often associated with high levels of ecological integrity (DellaSala et al. 2025). We request that you specify clearly how ecosystems respond differently to cumulative logging and road building (degradation) vs. natural disturbances like blowdown, wildfires, insects and disease that in most cases are beneficial ecologically (DellaSala et al. 2022, 2025).

Species of Conservation Concern Draft List Is Missing Important Taxa - Yellow cedar is aptly noted in the draft terrestrial assessment for climate-change induced losses related to declining snowpack regionally. However, yellow cedar should have been selected as a species of conservation concern (SCC) in the SCC assessment given its widely documented decline. In addition, DellaSala et al. (1996) recommended the inclusion of the Pacific Slope Flycatcher (using difference criteria at the time) because of its tight association with old-growth forests and its lower abundance in second growth. We also appreciate the attention to bryophytes, fungi, and lichens as potential SCC mainly because these taxa tend to be very sensitive to subtle changes in forest microclimates that can be induced by edge effects from logging and road building. This is especially importance given the Tongass has world-class levels of lichen richness, for instance (DellaSala 2011). Additionally, we request that you query published datasets on endemic subspecies known to be distributed – and perhaps even isolated – across the Tongass archipelago, especially in karst areas (e.g., Androski et al. 2023).

Transition to Young/Second Growth Needs to Speed Up and Eliminated all Old Growth Harvesting aside from micro-site removals for Indigenous Uses - we fully support the Southeast Alaska Sustainability Strategy emphasis on transitioning the Tongass out of old-growth logging as demonstrated in our published studies (DellaSala and Furnish 2020, pdf attached). Tongass second growth can meet the Tongass timber targets entirely without the need for even 5 mm bd ft of old growth annually (DellaSala and Furnish 2020). The Forest Service's own analysis supports this request to transition fully into second growth.

Inadequate Climate Change Assessment – the draft terrestrial assessment refers to Halofsky et al. (draft) yet that is not provided to the public nor will it be subjected to independent peer review standards compared to the peer reviewed publications that were not cited and are available herein. There are several published reports and studies that need to be cited on the importance of the Tongass as potential climate refugia (DellaSala et al. 2015, 2022; Law et al. 2023, Vynne et al. 2023 – all hyperlinked above).

Conclusions (What's Needed in Revision)

The draft assessments overall need to be substantially improved based on the best available science pertaining to: (1) the Tongass' global significant ecosystem values by recognizing its global context compared to other temperate rainforest regions in DellaSala (2011); (2) its potential as climate refugia (DellaSala et al. 2015, Vynne et al. 2023, Law et al. 2023); (3) importance of Tongass old-growth forests and roadless areas for carbon and for climate refugia (DellaSala et al. 2022); (4) how historic logging targeted the most carbon dense forests (Albert and Schoen 2013); (5) the cumulative effects of logging and road building, including fragmentation of previously intact areas (DellaSala et al. 2022); emissions from logging and how little carbon is stored in wood product pools (Hudiburg et al. 2019, Harmon 2019, DellaSala et al. 2022); and (6) published climate projections of the region in relation to the Tongass' climate refugia properties (DellaSala et al. 2015, Vynne et al. 2023, Law et al. 2023). We request that you include a time series, spatially explicit analysis of old growth logging and road building by eco-provinces that also includes road densities and impacts of roads and fragmentation on species of conservation concern. That analysis would show how certain provinces like those on Prince of Wales Island have been targeted and cumulatively impacted. Additionally, while the draft assessment refers to the Tongass wildlife conservation strategy, that strategy does not protect enough old growth habitat (Smith and Flaherty 2023). Instead, published studies request protection of Tongass old-growth and roadless areas (DellaSala et al. 2022) because of their important refugia and carbon properties (Vynne et al. 2023, Law et al. 2023) and they should be fully protected as carbon reserves in forest-climate policy (Law et al. 2022). A Tongass conservation strategy is needed in TLMP revision that protects ALL old growth and roadless areas (preferred alternative) and further enables the transition out of old growth through prior analysis (DellaSala and Furnish 2020 – below) and the agency's own young growth analysis that shows the transition is feasible, while also allowing some young growth not needed in transition volume (DellaSala and Furnish 2020) to mature and further accrue carbon stocks degraded by past logging via proforestation (Moomaw et al. 2019).

Conservation Biology

Contributed Paper

Use of Historical Logging Patterns to Identify Disproportionately Logged Ecosystems within Temperate Rainforests of Southeastern Alaska

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Abstract: *The forests of southeastern Alaska remain largely intact and contain a substantial proportion of Earth's remaining old-growth temperate rainforest. Nonetheless, industrial-scale logging has occurred since the 1950s within a relatively narrow range of forest types that has never been quantified at a regional scale. We analyzed historical patterns of logging from 1954 through 2004 and compared the relative rates of change among forest types, landform associations, and biogeographic provinces. We found a consistent pattern of disproportionate logging at multiple scales, including large-tree stands and landscapes with contiguous productive old-growth forests. The highest rates of change were among landform associations and biogeographic provinces that originally contained the largest concentrations of productive old growth (i.e., timber volume >46.6* m^3*/ha). Although only 11.9% of productive old-growth forests have been logged region wide, large-tree stands have been reduced by at least 28.1%, karst forests by 37%, and landscapes with the highest volume of contiguous old growth by 66.5%. Within some island biogeographic provinces, loss of rare forest types may place local viability of species dependent on old growth at risk of extirpation. Examination of historical patterns of change among ecological forest types can facilitate planning for conservation of biodiversity and sustainable use of forest resources.*

Keywords: forestry, fragmentation, land-cover change, old-growth forest

El Uso de Patrones Históricos de Tala para Identificar Ecosistemas Talados Desproporcionadamente en Bosques Lluviosos Templados del Sureste de Alaska Albert & Schoen 11-839

Resumen: *Los bosques del sureste de Alaska permanecen en su mayoría intactos y contienen una proporción sustancial de los bosques lluviosos templados maduros de la Tierra. Sin embargo la tala a escala industrial ha ocurrido desde los 1950s dentro de un rango relativamente estrecho de tipos de bosque que nunca se ha cuantificado en una escala regional. Analizamos los patrones históricos de tala de 1954 hasta 2004 y comparamos las tasas relativas de cambio entre tipos de bosque, asociaciones de formaciones terrestres y provincias biogeográficas. Encontramos un patrón consistente de tala desproporcionada en escalas múltiples, incluyendo grandes fragmentos y paisajes con bosques maduros productivos contiguos. Las tasas más altas de cambio estuvieron entre las asociaciones de formaciones terrestres y provincias biogeográficas que originalmente contenían la mayor concentración de bosque maduro productivo (p.ej.: volumen de madera >46.6* m^3*/ha). Aunque solo 11.9% de los bosques maduros productivos han sido talados a lo largo de la región, los fragmentos se han reducido al menos en 28.1%, bosques de karst en 37%, y paisajes con el volumen más alto de bosque maduro contiguo en 66.5%. Dentro de algunas provincias biogeográficas aisladas, la pérdida de tipos raros de bosque puede ubicar la viabilidad local de especies dependientes del bosque maduro en riesgo de extirpación. Examinar los patrones históricos de cambio entre tipos de bosque ecológicos puede facilitar la planeación para la conservación de la biodiversidad y el uso sustentable de los recursos forestales.*

Palabras Clave: bosque maduro, cambio en cobertura de suelo, fragmentación, silvicultura

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Introduction

Assessment of threats to rare ecosystems has become an increasing focus for global conservation, and factors such as geographical distribution and changes to ecosystem composition, structure, and function have been used in such assessments (Nicholson et al. 2008; Rodriguez et al. 2010). We used historical patterns of logging to assess change among forest ecosystems within the coastal temperate rainforests of southeastern Alaska and specifically to assess how current forest conditions differ from historical conditions.

Coastal temperate rainforests are globally uncommon. The largest (35% of this ecosystem worldwide) is distributed along the Pacific coast of North America from northern California through southern coastal Alaska (Kellogg 1992; DellaSala et al. 2011:16). Although the southern half of the Pacific coast rainforest is heavily developed, northern British Columbia and southeastern Alaska retain the largest amount of intact old-growth temperate rainforest on Earth and support abundant populations of species that have declined or are threatened in the southern portion of their historical ranges (e.g., Pacific salmon [*Oncorhynchus* spp.], brown bear [*Ursus arctos*], and Marbled Murrelet [*Brachyramphus marmoratus*]) (DellaSala et al. 2011:57).

In southeast Alaska, where fire is rare, natural patterns of disturbance such as wind storms, landslides, and flooding produce a fine-scale patchwork of forest types and structure that differ substantially from the more homogenous, even-aged stands that develop after clearcut logging (Kramer et al. 2001; Ott & Juday 2002; Alaback et al. 2013). Old-growth forests typically occur in a mixed-age mosaic dominated by old trees (>300 years) and have multilayered canopies, abundant understory vegetation, and high structural diversity (Harris & Farr 1974; Kramer et al. 2001). In contrast, clearcut logging is a stand-replacing event that initiates succession (0–5 years, shrubs; 5–25 years young conifers; 25–30 years, conifers that prevent light from reaching the forest floor) (Alaback 1982). Twenty to 30 years after clearcutting (stem-exclusion phase), the forest is characterized by a homogeneous structure, low understory diversity and productivity, and relatively low habitat value for native fauna. This stage typically lasts >100 years (Wallmo & Schoen 1980; DellaSala et al. 1996). Although timber volume sufficient for commercial harvest may regenerate <100 years after logging (Harris & Farr 1974), the structure and diversity of old-growth forests require several centuries to develop (Alaback 1982; DellaSala et al. 2011:49).

Large-scale timber harvesting in the region developed, following passage of the 1947 Tongass Timber Act, within a framework of subsidized, long-term timber contracts (Beier et al. 2009). Later, harvest on private lands began under the 1971 Alaska Native Claims Settlement Act (Knapp 1992). Logging in the region peaked at 2.3 million m^3/year in 1990 and declined to approximately 0.4 million m^3/year in 2004 (USFS 2008*a*) as a result of combined political, economic, and institutional factors (Beier et al. 2009). Although the location and timing of past logging is known, the pattern of logging relative to the availability of forest types has not been analyzed at a regional scale to allow for evaluation of changes in diversity and abundance of forest ecosystems and determination of the potential implications for conservation of biodiversity (Lindenmayer et al. 2000) and timber supply (Beier 2010).

Our objectives were to document current forest conditions and historic patterns of logging; estimate the original distribution of ecosystems (ecological forest types) among biogeographic provinces; and map the distribution of old-growth ecosystems that have sustained disproportionate rates of logging in the past. Uniquely, we documented in a spatially explicit manner how southeastern Alaska forests have changed as a result of logging and how the present landscape differs from historical conditions. Although researchers have evaluated change in condition of old-growth forests over time in areas farther south in the Pacific Northwest (Staus et al. 2002; Wimberly & Ohmann 2004), few have provided a sufficiently fine-grained characterization of ecological systems to identify changes in rare forest types (Strittholt et al. 2006) or specifically investigated ecological correlates of anthropogenic change (Alig et al. 2005). Recent (60 years) patterns of old-growth logging in southeastern Alaska can provide a model for understanding other temperate rainforest regions that were less well documented and now reflect a more complex mosaic of human development (Huston 2005).

Methods

Study Area

Southeastern Alaska extends approximately 800 km between Dixon Entrance (55°N, 130°W) and Yakutat Bay (59°N, 140°W) and is dominated by the Alexander Archipelago, which has >5000 islands and a total land area of 8.7 million ha (Fig. 1). Approximately 80% of the region is contained within the Tongass National Forest (6.8 million ha). Our study area was in the perhumid rainforest zone, which is characterized by a maritime climate with cool summers (<15 °C), abundant precipitation (200–600 cm), and mild winters (rarely < −10 °C) (Alaback 1996). Although the region is characterized as a rainforest, a large proportion of the landscape is wetlands, alpine tundra, and recently glaciated terrain (Nowacki et al. 2001).

Closed-canopy conifer forests are widely distributed below 600 m and are typically dominated by associations of western hemlock (*Tsuga heterophylla*), Sitka spruce

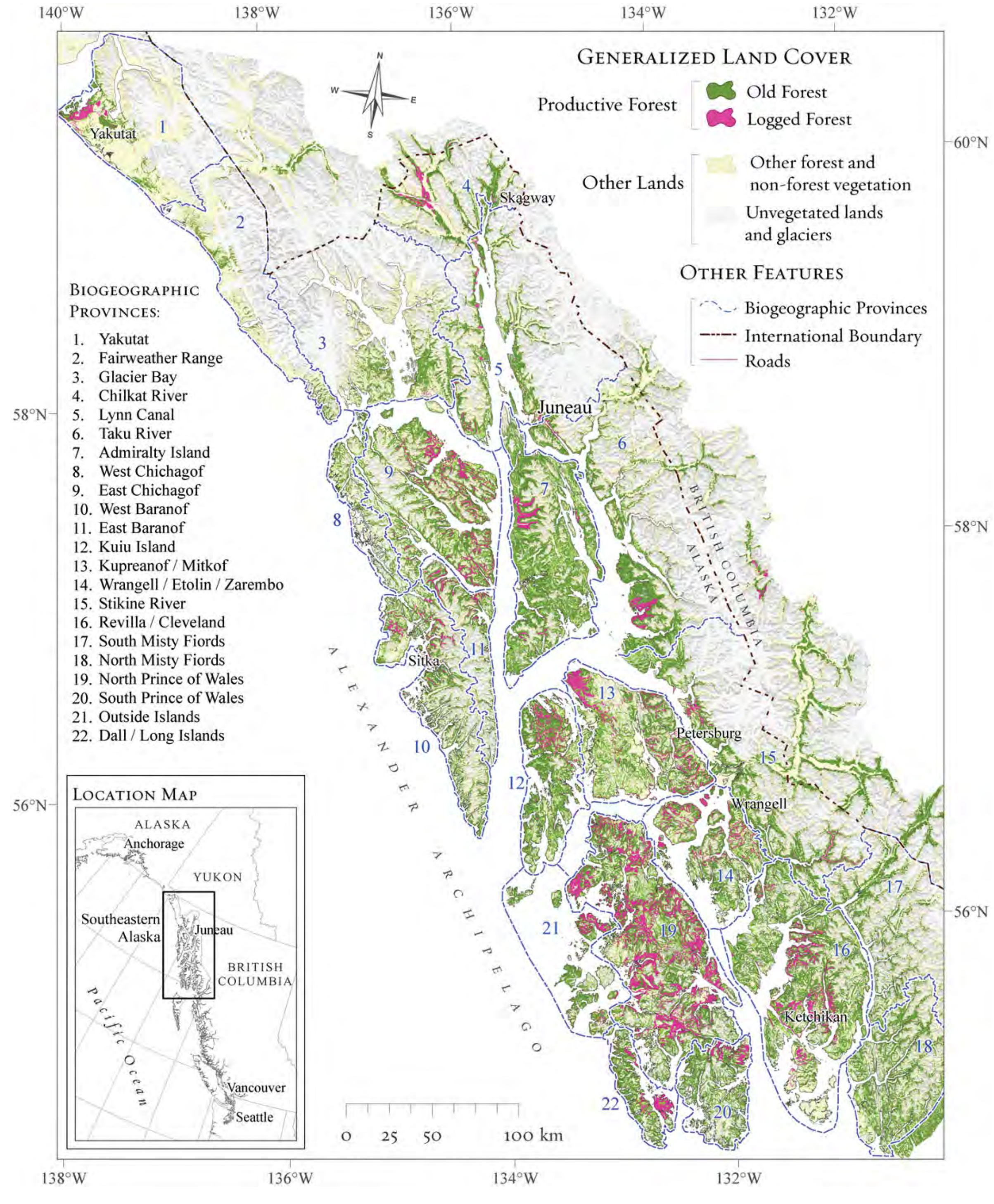


Figure 1. Generalized land cover and productive forest lands among biogeographic provinces in southeastern Alaska.

(*Picea sitchensis*), western redcedar (*Thuja plicata*), and Alaska yellow-cedar (*Chamaecyparis nootkatensis*) (Viereck et al. 1992). In general, large-tree (mean diameter >53 cm), old-growth forests are patchily distributed and tend to occur most frequently on well-drained sites, including lower elevation slopes, alluvial fans, and floodplains (Shephard et al. 1999) and on karst (i.e., porous limestone) substrates (Baichtal & Swanston 1996). We defined forest ecosystems on the basis of landforms and forest structural characteristics that correlate with important ecological processes, such as soil productivity and frequency of disturbance, species composition, and habitat value for native flora and fauna (Shephard et al. 1999; Caouette & DeGayner 2008).

Mapping of Forest Ecological Systems

To characterize forest types, we combined data on vegetation and landform associations to identify ecologically important distinctions not represented by vegetation mapping alone (Comer et al. 2003). Forest productivity is determined largely by soil characteristics and climatic gradients (Nowacki et al. 2001; USFS 2008*b*), and we followed the U.S. Forest Service (USFS 2008*a*) definition of forest productivity: a "productive forest" is land capable of producing >1.4 m^3/ha of wood fiber/year or with standing volume of timber >46.6 m^3/ha. Although not strictly a measure of net primary productivity, we assumed that given the region's low rate of forest disturbance under historical conditions (Alaback 1996; Kramer et al. 2001), characteristics of existing old-growth forest provided an index of site potential adequate for broad-scale comparison of forest productivity among landforms and biogeographic provinces (USFS 2008*b*).

Our primary source for mapping vegetation was the USFS (2008) Tongass timber inventory, which was completed in 1986. The inventory consisted of extensive ground surveys and aerial photography and periodic updates to reflect ongoing management. Productive old-growth forests are categorized by average tree size (Caouette & DeGayner 2005) and volume of standing timber. On the basis of mean diameter, productive old-growth forests are categorized as large-tree (>53 cm), medium-tree (43–53 cm), and small-tree (<43 cm) stands. Caouette and DeGayner (2008) report accuracy of 60–80% between this inventory and ground-based stand exams. Although characterization by tree size and timber volume differs from a typical forest classification that is based on species composition (e.g., Viereck et al. 1992), it is a useful indicator of structural gradients (Caouette & DeGayner 2008) that represents an important aspect of forest diversity (Noss 1990) and habitat functions for wildlife species (e.g., Schoen & Kirchhoff 1990; Iverson et al. 1996).

To map forests on lands outside the Tongass, we merged the timber inventory from the Haines State Forest (HSF) (ADNR 1985) and the Interim Land Cover Classification (ILC) (Shasby & Carneggie 1986). The HSF inventory categorizes stands on the basis of tree size, similar to the Tongass inventory. The ILC category "closed-canopy conifer" is roughly equivalent to the medium-tree old-growth category (i.e., middle 74%) of the Tongass inventory. Other ILC categories did not meet criteria for productive old growth and were excluded from further analyses. Following Caouette and DeGayner (2005), we categorized small-tree stands on hydric soils as low-volume strata, small-tree stands on nonhydric soils and medium-tree stands on hydric soils as medium volume, and all large-tree and medium-tree stands on nonhydric soils as high-volume strata (USFS 2008*a*). We used the National Wetlands Inventory (Cowardin et al. 1979) to identify hydric soils and calculated estimates of gross timber volume as a function of volume strata and geographic area (USFS 2008*a*). We digitized more recent road construction and logging activity outside the Tongass through visual interpretation of aerial photography (current in 1997) and Landsat Enhanced Thematic Mapper (ETM) imagery (current in 2000–2002).

To characterize forest conditions over a landscape matrix rather than as individual stands (Wiens 1995), we developed an index of old-growth forest density. We based the index on a moving-window analysis of gross volume within a 0.9-km radius (1.56 km^2). This index integrated information on forest structure and the degree to which productive old-growth forests are contiguous across this landscape.

Our sources for mapping landform associations were the Tongass Soils Inventory, derived from aerial photography and ground surveys (USFS 1996), and Karst Inventory, derived from field surveys and U.S. Geological Survey data on bedrock geology (Baichtal & Swanston 1996). We categorized landform associations as coastal (marine deposits and wave-cut terraces uplifted by tectonic or isostatic forces), lowland (glacial till and outwash, low topographic relief, extensive wetlands), valley floor (glacially carved U-shaped valleys with alluvial and glacial deposits), hills (rolling terrain, heavily scoured by glaciers), mountain slopes (low-to-mid slopes of mountain features, angular terrain, carved by glaciers, alluvial, and colluvial deposits), mountain summits (higher elevation, angular terrain), and volcanic (postglacial, volcanic terrain). A detailed description of landforms and the interacting effects of geology, landform, and hydrology on vegetation in this area is available in Nowacki et al. (2001). For areas lacking data on landform association, we used a supervised classification of topographic features (elevation, slope, and topographic position index) and the Tongass Soils Inventory as the training set (Hengl & Rossiter 2003). Overall agreement of this model with the soils inventory was 68%. Because karst was relatively rare, we merged all landform associations in areas of karst to preserve sufficient sample size for analyses.

To analyze the geographic distribution of forests and logging activity, we used biogeographic provinces (USFS 2008*a*) that represent ecologically important patterns of climate, glacial history, and island biogeography (Nowacki et al. 2001; Cook et al. 2006). The resulting maps of forest condition and landform associations were evaluated and considered robust by biologists and foresters with knowledge of local areas. All mapping was conducted with ArcInfo (version 9.2, Environmental Systems Research Institute, Redlands California).

Assessment of Forest Change

Data on the original composition of logged stands were available for 98,023 ha within the Tongass that were logged after 1986. We assumed the proportional rates of logging within this sample among large- (29.3%), medium- (64.6%), and small- (6.1%) tree stands were representative of all logging that occurred from 1954 to 2004. To estimate historical timber volume, we assumed the distribution of hydric soils was a suitable variable to discriminate between medium-volume (i.e., hydric soils) and high-volume stands (i.e., nonhydric) (USFS 2008*a*). These assumptions are conservative and supported by anecdotal evidence that earlier logging (before 1979) was skewed more toward large-tree and high-volume stands than logging that occurred after 1986 (Rakestraw 1981; USFS 2008*a*). We used this information to compare average density of landscape forest and patch characteristics among the forest landscapes with the highest volume of forest (>18,762 m^3/km^2) between 1954 and 2004.

We determined patterns of selectivity in logging by comparing forest types selected for logging with their original availability (Alldredge et al. 1998). We evaluated selectivity among stand characteristics (tree size and timber volume), landscape-scale forest (timber volume per square kilometer), elevation (m), categories of landform associations and biogeographic provinces (percent productive forest). We used chi-square tests for categorical variables and Kruskal–Wallis for continuous variables (Conover 1980) to test for significance. We examined the correlation between rate of logging and forest productivity (as indexed by the percentage of land in productive forest) among biogeographic provinces and landform associations with Spearman's rank correlation (Conover 1980) and logistic regression (Hosmer & Lemeshow 1989).

Logistic-Regression Model of Forest Change

We developed a multiple logistic-regression model to identify the suite of forest variables most strongly predictive of whether forests had been logged or not logged and to map this relation within remaining old growth. To control for spatial autocorrelation at a regional scale, we explicitly included differences among biogeographic provinces as a potential explanatory variable in the logistic model. At the local scale, we spaced sample locations on a systematic grid at 1-km intervals and eliminated duplicate points that fell within any single forest stand. Each observation was coded as logged (1) or not logged (0) for the logistic model. We excluded federally protected lands from the logistic analyses.

Comparing all combinations of independent variables, we identified the best model with the Akaike information criterion (Hosmer & Lemeshow 1989) in STATISTICA software (StatSoft, Tulsa, Oklahoma). To account for an inadequate sample of logging within some biogeographic provinces, we grouped provinces of Admiralty Island with Chichagof Island; Glacier Bay and Fairweather provinces with Lynn Canal; and Misty Fiords with the Stikine River mainland (Fig. 1). We used the area under receiver operating characteristics (ROC) curve and percentage of observations correctly classified to evaluate the model (Guénette & Villard 2005). We interpreted the model by evaluating the significance of independent variables and the odds ratios (Hosmer & Lemeshow 1989).

We mapped the output of the logistic model as an index of selectivity that reflects the degree to which any combination of geographic, forest, and environmental variables were either preferentially selected or avoided for logging. For the purpose of calibrating the model to observed forest conditions, we determined the cut point that provided maximum accuracy in differentiating logged and old-growth stands (Guénette & Villard 2005). We used this criterion to estimate the remaining distribution of old-growth forest types that had sustained disproportionate rates of logging.

Results

Mapping of Forest Ecological Systems

Forested lands covered 4,488,848 ha in southeastern Alaska, approximately 50% of the total land base. Productive forests (including old-growth and younger stands) covered 2,657,154 ha, approximately 30% of the region's land base. Among landform associations, the proportion of land in productive forest was highest on karst (67%), followed by coastal areas (53%), hills (53%), mountain slopes (50%), valley floors (43%), volcanoes (31%), lowlands (31%), and mountain summits (2%).

Within productive old growth in 2004 (2,320,088 ha), large-tree stands represented 10.2%, whereas medium-tree stands represented 74.7% and small-tree stands represented 15.1% of the total (Table 1). Average timber volume among old-growth stands was 194.9 m^3/ ha (SD 46.4, range = 37–263), and at a landscape scale average volume was 4,330 m^3/km^2 (SD 5,029, range = 0–25,770). As a measure of availability, productive old-growth forests were most abundant on mountain slopes (58.7%), followed by lowlands (12.5%), valley floors (10.4%), hills (10.1%), and karst (4.1%). Among biogeographic provinces, North Prince of Wales had the largest proportion of all productive old growth (10.9%), followed by Admiralty Island (10.5%), Revillagigedo Island and Cleveland Peninsula (10.0%), and East Chichagof Island (7.6%). The remaining 16 provinces contained $\leq$6.2% of productive old growth each (Table 1).

Assessment of Forest Change

Although a large majority of productive forests in 2004 were old-growth forests (88.1%), the relative rate of logging differed among forest types and biogeographic provinces (Table 1). Large-tree stands were logged

Table 1. Distribution and condition of productive forest lands and the relative rate of logging among categories of tree size, landform association, and biogeographic province in southeastern Alaska.

	Productive forest lands					
	old forest		*logged forest*			
Variable	*(ha)*	*(%)*	*(ha)*	*(%)*	*Logged (%)*[a]	*Relative proportion logged*[b]
Tree size						
large	237,591	10.2	92,900[c]	29.3	28.1	2.36
medium	1,748,187	74.7	204,825[c]	64.6	10.5	0.88
small	354,310	15.1	19,341[c]	6.1	5.2	0.43
Landform						
Karst	95,596	4.1	56,217	17.7	37.0	3.11
valley floor	242,429	10.4	45,521	14.4	15.8	1.33
Coastal	36,576	1.6	5138	1.6	12.3	1.04
Hills	235,914	10.1	28,391	9	10.7	0.90
mountain slopes	1,373,992	58.7	149,879	47.3	9.8	0.83
Lowlands	293,484	12.5	30,681	9.7	9.5	0.80
Volcanic	6,571	0.3	521	0.2	7.3	0.62
mountain summits	55,526	2.4	718	0.2	1.3	0.11
Biogeographic province						
North Prince of Wales	255,884	10.9	119,699	37.8	31.9	2.68
Dall and Long Islands	44,056	1.9	10,880	3.4	19.8	1.66
Yakutat Forelands	33,525	1.4	7402	2.3	18.1	1.52
Kupreanof and Mitkof	144,764	6.2	27,364	8.6	15.9	1.34
Wrangell, Etolin, and Zarembo	93,341	4	16,713	5.3	15.2	1.28
East Chichagof	177,353	7.6	28,928	9.1	14.0	1.18
Outside Islands	47,951	2	7448	2.3	13.4	1.13
East Baranof	36,952	1.6	5,583	1.8	13.1	1.10
Chilkat River Complex	56,064	2.4	8,069	2.5	12.6	1.06
Revilla Island and Cleveland Peninsula	234,832	10	29,476	9.3	11.2	0.94
South Prince of Wales	68,218	2.9	7,236	2.3	9.6	0.81
Kuiu Island	117,705	5	12,007	3.8	9.3	0.78
West Baranof	95,561	4.1	7,869	2.5	7.6	0.64
Taku River	139,349	6	8,717	2.7	5.9	0.49
Stikine River	135,547	5.8	6,083	1.9	4.3	0.36
Admiralty Island	245,417	10.5	10,968	3.5	4.3	0.36
Lynn Canal	85,929	3.7	2,542	0.8	2.9	0.24
Glacier Bay	61,880	2.6	81	0	0.1	0.01
South Misty Fiords	128,030	5.5	0	0	0	0
North Misty Fiords	87,883	3.8	0	0	0	0
West Chichagof	30,107	1.3	0	0	0	0
Fairweather Icefields	19,741	0.8	0	0	0	0
All productive forest	2,340,088	100	317,066	100	11.9	1.0

[a] *Percent original availability.*

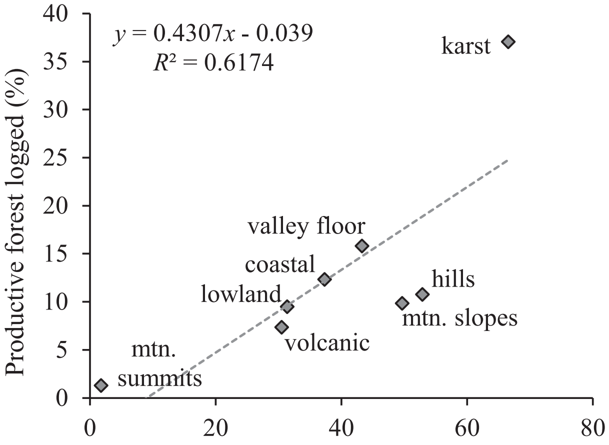
[b] *Ratio of percentage change within each category to the average change for all forest types (11.9%).*

[c] *Estimated by extrapolating the observed rates of logging from 1986 to 2004 (n = 98,023 ha) of large (29.3%), medium (64.6%), and small trees (6.1%) in all forest lands logged (n = 317,066 ha).*

2.4 times more than their relative availability, whereas medium-tree and small-tree stands were logged less than their availability (Table 1). Logging also occurred disproportionately at broader spatial scales. Logging was significantly higher in productive forests that were contiguous at a landscape scale (Wald $\chi^2 = 2910$, 1 df, $p < 0.0001$) and in the most productive landforms (Spearman's $R = 0.48$, $p = 0.02$) and biogeographic provinces, such as North Prince of Wales ($R = 0.802, p = 0.01$) (Fig. 2), than in noncontiguous forests and provinces and landforms with less productive forest lands.

As a result of selective patterns of logging, characteristics of remaining old-growth forests differed from forest types that occurred historically. Average landscape volume of old-growth forest declined region-wide by 16.8% from 1954 ($\bar{X} = 11{,}958$ [SD 5,009]) to 2004 ($\bar{X} = 9{,}941$ [SD 4,666]; $Z = 81.65$, $n = 26{,}538$, $p < 0.01$). This trend reflects a process by which large, contiguous old-growth landscapes were fragmented and interspersed with young growth and the remaining old-growth stands contain a smaller proportion of large trees than historically. The highest volume landscape forests in 1954 ($>18{,}762$ m^3/km^2) were reduced by 66.5% region-wide from 243,373 ha in 1954 to 81,611 ha in 2004. This reduction was accompanied by similar declines in the number of patches (1954 $n = 2{,}464$; 2004 $n = 1{,}660$), average

(a) Landform associations



(b) Biogeographic provinces

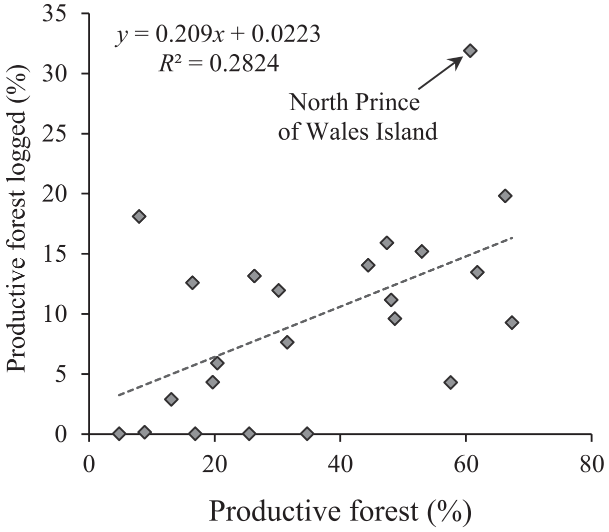


Figure 2. Percentage of lands in productive forest relative to percentage of those forests logged among (a) landform associations and (b) biogeographic provinces.

patch size (1954 $\bar{X} = 169$ ha [SD 848.4]; 2004 $\bar{X} = 105$ ha [SD 403]), and largest patch size (1954 max = 19,434; 2004 max = 9,433 ha). Due to natural fragmentation, high-volume forests contiguous at a landscape scale were always rare. The largest proportion (31%) of contiguous high-volume forest occurred on northern Prince of Wales Island, where such forests have been reduced by 93.8% (77,536 ha in 1954 to 4,801 ha in 2004) (Fig. 3) and average patch size declined from 264 ha in 1954 (SD 1,186.5) ($n = 435$, max = 11,692) to 73 ha in 2004 (SD 176.6) ($n = 164$, max = 1,321).

Logistic-Regression Model of Forest Change

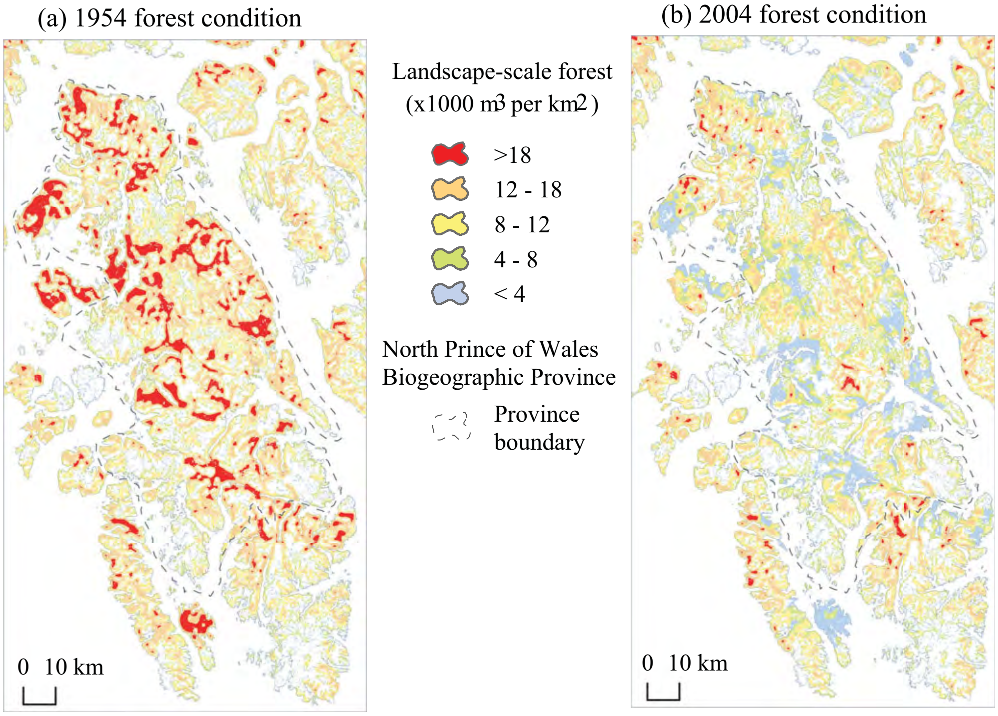
With the exclusion of federally protected lands, the logistic-regression analyses included 1,727,483 ha, or 73.8%, of all productive forest lands in the region. The logistic model identified 4 variables that provided the best discrimination between logged and unlogged sites ($G = 4{,}438.58$, 18 df, $p < 0.0001$) (Table 2). The most significant predictor variable was landscape forest (Wald $\chi^2 = 1175.5$, 1 df, $p < 0.0001$), followed by biogeographic province ($\chi^2 = 614$, 15 df, $p < 0.0001$), stand volume ($\chi^2 = 499.5$, 1 df, $p < 0.0001$), and elevation ($\chi^2 = 479.2$, 1 df, $p < 0.0001$). Due to inadequate sample size, landform was not included in the final model. The goodness-of-fit chi-square test indicated the logistic model was apt ($p = 0.95$). The ROC indicated a good fit to the observed data (AUC = 0.859) and an optimal cut point of $p = 0.18$ to differentiate between logged and unlogged stands in the logistic model.

Regression coefficients showed that with other factors held constant, landscapes with higher forest density, stands with higher volumes of timber, and those located at lower elevations had higher rates of logging, whereas more sparsely distributed forests, lower volume stands, and those at higher elevations were logged at lower rates (Table 2). Although the highest proportion of all productive forests logged during this period was on North Prince of Wales (Table 1), the logistic model indicated that with other factors held constant, the relative rate of logging on East Baranof Island was similar to that on North Prince of Wales, both of which were 2.34 times greater than the regional average (Table 2).

With a cut point of 0.18 the logistic model correctly classified 75.8% of productive forest as either logged or unlogged. Forest types most commonly selected for logging, such as high-volume contiguous forests at lower elevations ($p \geq 0.18$), accounted for 34.6% (597,052 ha) of all productive forest, had sustained rates of logging 3.43 times greater than average, and consequently had a relatively high proportion of area in second growth (40.8%). In contrast, forest types not typically selected for logging such as lower volume fragmented forests and those at higher elevations ($p < 0.18$) represented 65.4% (1,130,386 ha) of all productive forest lands, sustained less than the average rate of logging (0.48-times), and remained largely in old-growth condition (94.3%).

Discussion

Although only a small fraction of all old-growth forests in southeastern Alaska have been logged (11.9%), the systematic way the most productive stands and landscapes have been targeted indicates that the likelihood of maintaining the natural abundance of forest types, including important fish and wildlife habitat, may be lower than this percentage suggests. Landscape-scale blocks of productive forest, stands of larger trees, and forests at lower elevations were disproportionately targeted for logging, and rate of logging was positively correlated with broad-scale forest productivity among landforms and biogeographic



(a) 1954 forest condition

(b) 2004 forest condition

(c) forest change in northern Prince of Wales Island, 1954-2004

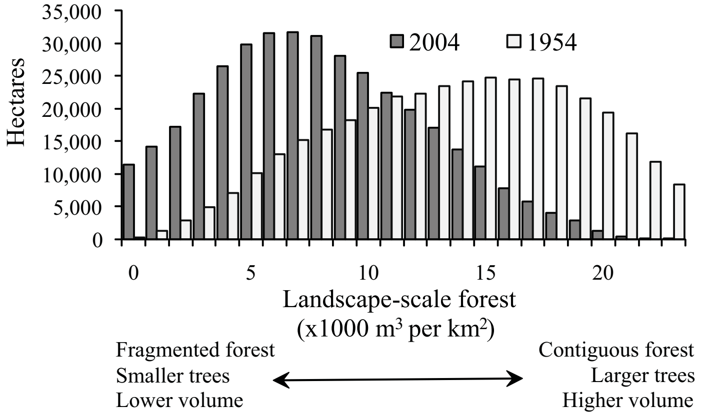


Figure 3. Change in the landscape-scale distribution of productive (i.e., timber volume >46.6 m^3/ha) old-growth forest in southeastern Alaska from (a) 1954 to (b) 2004 and (c) change in availability of remaining old-growth forests in the North Prince of Wales biogeographic province.

provinces. This spatial correlation of logging to forest productivity was consistent with patterns of change observed in coastal forests of western Oregon (Alig et al. 2005), and the more general relationship of resource development to ecosystem productivity as a common aspect of human development (DeFries et al. 2004; Huston 2005).

A consequence of depletion of rare forest types, such as large tree stands, karst forests, and high-volume forests that are contiguous at a landscape scale, is that habitat quality may also decline and adversely affect populations of fish and wildlife. For example, results of studies show a range of functions associated with large-tree forests, including provision of black bear (*Ursus americanus*) dens (Erikson et al. 1982), winter habitat for Sitka black-tailed deer (*Ococoileus hemionus sitkensis*) (Schoen & Kirchhoff 1990), nesting habitat for Northern Goshawk (*Accipiter gentilis*) (Iverson et al. 1996), and woody debris in streams that serves as structural habitat for salmon and other species (Heifetz et al. 1986; Willson & Halupka 1995). Similarly, karst exhibits attributes that make it highly productive for salmon (Bryant et al. 1998), yet

Table 2. Results of logistic regression model of forest types in southeastern Alaska that were either logged (1) or not logged (0) during 1954–2004.

Variable	*Odds ratio*[a]	*Coefficient*[b]	*SE*	*Wald* χ^2	*p*
Intercept	0.00	−7.35	0.17	1910.01	<0.0001
Landscape forest ($m^3 \times 1000/km^2$)	1.22	0.20	0.01	1175.52	<0.0001
Timber volume (m^3/ha)	1.02	0.02	0.00	499.51	<0.0001
Elevation (m × 100)	0.66	-0.42	0.02	479.22	<0.0001
Biogeographic province					
North Prince of Wales	2.34	0.85	0.05	277.46	<0.0001
East Baranof Island	2.34	0.85	0.15	30.92	<0.0001
Chichagof and Admiralty Island	2.16	0.77	0.07	119.22	<0.0001
Wrangell, Etolin, and Zarembo	2.14	0.76	0.10	62.78	<0.0001
Kupreanof and Mitkof	1.89	0.64	0.08	68.14	<0.0001
West Baranof Island	1.77	0.57	0.13	19.01	<0.0001
Revilla Island and Cleveland Peninsula	1.36	0.31	0.07	18.35	<0.0001
Dall Island Complex	1.25	0.22	0.12	3.53	0.0603
Outside Islands	1.00	0.00	0.15	0.00	0.9962
Chilkat River	0.90	−0.11	0.12	0.76	0.3836
Kuiu Island	0.56	−0.57	0.10	30.01	<0.0001
Taku River	0.44	−0.82	0.12	47.72	<0.0001
Yakutat Forelands	0.43	−0.84	0.16	25.84	<0.0001
Stikine River and Misty Fiords	0.39	−0.94	0.13	49.62	<0.0001
Lynn Canal and Glacier Bay	0.20	−1.61	0.21	56.56	<0.0001

[a] *Odds ratio represents the change in likelihood that a site was logged with a 1-unit change in a continuous predictor variable or the relative likelihood of logging among biogeographic provinces.*

[b] *Multiple logistic-regression coefficients indicate the overall preference for (coefficient > 0) or avoidance of (coefficient < 0) specific forest types or locations on the basis of historical patterns of logging with other factors held constant.*

karst is sensitive to increased soil erosion from road construction and logging (Baichtal & Swanston 1996). Landscape-scale blocks of old-growth forest are habitat for northern flying squirrels (*Glaucomys sabrinus*) on Prince of Wales Island and a key indicator of population persistence over time (Smith & Person 2007). Although both brown bears and wolves (*Canis lupus*) use a variety of areas, including old growth, they are particularly sensitive to fragmentation of landscapes by logging roads because roads increase risks of human-induced mortality (Schoen et al. 1994; Person & Russell 2008).

The sensitivity of species to changes in forested areas is recognized in the 1997 Tongass Land Management Plan that designated the Northern Goshawk as a “sensitive species,” the northern flying squirrel and Marbled Murrelet as “species of concern,” and the brown bear, wolf, and Sitka deer as “management indicator species” (USFS 2008*a*). Concerns regarding population viability of some species led the USFS to establish an Interagency Viable Population Committee that designed a landscape conservation strategy to address viability of species associated with old growth (USFS 2008*b*).

Nowhere are these factors more evident than on northern Prince of Wales Island. This province has extensive low-elevation karst, landscape-scale tracts of productive forests, high-quality habitat for a range of species (Albert & Schoen 2007), and is an important center of endemism (Cook & MacDonald 2001; Cook et al. 2006). The island has also sustained the highest rates of logging in the region (Albert & Schoen 2007; DellaSala et al. 2011:58). Although northern Prince of Wales contained only 10.9% of all productive forests in the region in 1954 it received 37.8% of all the logging. Consequently, 93.5% of its highest volume landscape-scale blocks of old growth had been logged.

The specific threshold at which habitat alteration affects population viability is difficult to determine (Fahrig 2001). However, results of a review of habitat thresholds literature (to inform forest planning in coastal British Columbia) indicated that maintaining loss of habitat below 40% of historical abundance poses a low risk to most species, whereas declines above that level result in less confidence that risks of extirpation will remain low (Price et al. 2009). On the basis of this criterion, rare forest types that have been reduced by >40% of historical abundance such as landscape-scale blocks of high-volume old growth, and particularly those on Prince of Wales Island, may warrant special consideration (Cook et al. 2006). Such a proactive approach to maintain forest diversity is particularly important because declines in the abundance and distribution of local populations of plants and animals may not be quantitatively measured for decades or centuries after habitat modification has occurred (Tilman 1994).

From a global perspective, southeastern Alaska supports a relatively low human population density, has developed industrially later than regions to the south, and continues to support populations of species such as salmon, brown bears, wolves, and Marbled Murrelets that have become rare or have been extirpated from more developed regions (DellaSala et al. 2011). Locally, the focus of logging within areas of higher productivity is typical of agrarian expansion into previously undeveloped lands (Huston 2005) and likely reflects processes that contributed to the decline of these species elsewhere. Our model provides a spatial framework within which to identify remaining old-growth forests that have been disproportionately logged and provides a historical reference for planning restoration of functional attributes such as landscape-scale connectivity among forests blocks. Such tools may be particularly relevant in the context of recent petitions to list endemic subspecies associated with productive old-growth forest such as Queen Charlotte Goshawk (*A. g. laingi*), Prince of Wales flying squirrel (*G. s. griseifrons*), and Alexander Archipelago wolf (*C. l. ligoni*) for protective status under the U.S. Endangered Species Act. These results provide a baseline for assessing the distribution and abundance of rare ecosystems (e.g., large-tree old growth) on the basis of historical patterns of change and have implications for planning for ecological sustainability (Lindenmayer et al. 2000) and future management of forest resources in southeastern Alaska and elsewhere (DeFries et al. 2004; Turner et al. 2007).

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REVIEW

Phylogeography of mammals in Southeast Alaska and implications for management of the Tongass National Forest

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Abstract

Insular evolution on archipelagos generates a significant proportion of global biodiversity, yet islands are among the ecosystems most sensitive to accelerating anthropogenic disturbance, introductions of non-native species, and emerging pathogens, among other conservation challenges. The Alexander and Haida Gwaii archipelagos along North America's North Pacific Coast support a disproportionate number of endemic taxa compared to other high-latitude terrestrial ecosystems. In this region, endemics in Canada are explicitly protected, but in the United States, endemics have been operationally ignored. We reviewed regional research on terrestrial mammals and endemics from 2000–2022 to guide wildlife management. Elevated regional endemism is due to a combination of deep and shallow temporal processes (i.e., long-term refugial isolation vs. recent colonization). With adequate sampling, genomic analyses are well-suited to identifying nuanced patterns of divergence and endemism, thereby facilitating a deeper understanding of regional diversity. We identified 18 mammalian endemics in Southeast Alaska, USA, at varying taxonomic scales, but research effort has significant taxonomic biases and sampling infrastructure remains inadequate. Of the 66 terrestrial and aquatic mammal species in Southeast Alaska, only 55% are represented by ≥10 archived samples over the last 2 decades. Across taxa, major spatial and temporal sampling gaps limit interpretations of wildlife responses to changing environmental conditions. The Tongass National Forest is spread across an island archipelago, and climate change is projected to have disproportionate impacts on island endemics worldwide. In this case, the United States Forest Service is not closely monitoring endemic taxa, as was required by the Tongass Land Management Plan in 1997. Our review underscores a need for increased consideration of how endemism can be incorporated into land and wildlife management across the Alexander Archipelago. Moving forward, we encourage state and federal agencies, Indigenous communities, and international collaborators to continue to partner with natural history biorepositories to ensure strategic wildlife sampling infrastructure is built and made accessible to the broader scientific community as part of the land management process.

KEYWORDS

biorepository, conservation, endemics, insular, islands, Tongass Land Management Plan, United States Forest Service, wildlife monitoring

The largest remaining temperate rainforest in the world is situated along a narrow stretch of coastline and 2 near-shore archipelagos: the Alexander Archipelago in Southeast Alaska, USA, and the Haida Gwaii Archipelago, 80 km to the south, off the western coast of British Columbia, Canada (DellaSala et al. 2011, Orians and Schoen 2013). For its latitude, North America's North Pacific Coast boasts disproportionately high endemism (Cook and MacDonald 2001, Cook et al. 2006). Two hypotheses have been proposed to explain regional endemism: either endemics persisted *in situ* through the Last Glacial Maximum (LGM) 20 thousand years ago (kya; paleoendemics) or they colonized post-glacially and have since diverged (neoendemics; Klein 1965, Cook and MacDonald 2001). Molecular data from a wide range of animal and plant taxa has accumulated mixed support for both hypotheses (Cook and MacDonald 2001, Greiman et al. 2013, Roberts and Hamaan 2015, Sikes and Allen 2016, Gamlen-Greene 2022), with the degree of genetic differentiation between insular and continental taxa used as a measure of the age of divergence. Neoendemics are distinctive from their continental relatives, but minimal divergence suggests that their isolation began following colonization of the region after the retreat of the Cordilleran Ice Sheet (<10 kya; Klein 1965). In contrast, paleoendemics are more deeply diverged from their sister lineages, hypothetically the result of long-term persistence in ice-free glacial refugia in or near the region during the LGM (Cook et al. 2001, Dawson et al. 2007). Together, both deep- and shallow-time evolutionary processes have shaped the complex mosaic of species now present along the North Pacific Coast, with major implications for regional endemism, conservation, and natural resource management.

Although the Alexander Archipelago is a continental or near-shore archipelago, numerous geophysical attributes have converged to produce a distinct and biodiverse fauna. The extreme prominence (~2,500 m) of the Coast Mountain Range to the east isolates the North Pacific Coast from the rest of the North American continent. River corridors, including the Unuk, Stikine, Whiting, Taku, Chilkat, and Alsek rivers in Southeast Alaska, are the primary colonization routes into and out of the region, but their broad coastal deltas form barriers to dispersal along the coast (Dawson et al. 2007). Also, along the coastline, glacier-scoured fjords, up to 900 m deep, create heterogeneous tidal patterns (Weingartner et al. 2009) that may impede inter-island movement and, farther west, the fragmented island landscape fuels the generation and maintenance of regional endemics through the process of vicariance. Geographic isolation and small population sizes increase the strength of genetic drift in island populations, which can lead to relatively rapid evolution of novel diversity (Kirchman 2012, Wiens et al. 2022). Today, islands are separated by a complex network of bays, fjords, and inlets (Smith 2016); during the LGM, however, glaciation complicated local biogeographic patterns by exposing now-submerged areas of continental shelf, temporarily connecting islands, and pushing terrestrial organisms into ice-free areas, or refugia. There was at least one large refugium (Beringian) to the northwest of the major North American ice sheets and another to the south, in the continental United States (Southern; Hultén 1937, Pielou 1992). The area between those refugia was assumed to have been covered by ice, with glacial cycles leading to repeated episodes of extirpation and recolonization by terrestrial species (Pielou 1992). Counter to this clean slate (*tabula rasa*) model, other lines of evidence suggest that some taxa persisted through the LGM in smaller, *in situ* refugia, either in Southeast Alaska (Klein 1965; Cook et al. 2001; Carrara et al. 2003, 2007) or Haida Gwaii (Foster 1963, Calder and Taylor 1968, Mathewes and Clague 2017, Mathewes et al. 2019). Molecular investigations, for example, have uncovered deep phylogenetic breaks along the North Pacific Coast that are shared by disparate organisms from across taxa (e.g., plants, mammals, birds, insects, amphibians) and suggestive of long-term allopatric isolation and divergence, characteristic of paleoendemics (Soltis et al. 1997, Pruett et al. 2013, Roberts and Hamaan 2015, Sawyer et al. 2019, Colella et al. 2021*b*). Although human occupation is not documented in Southeast Alaska until after 14 kya (McLaren et al. 2020), oceanic currents, seasonal sea ice, and exposed coastline may have facilitated temporary colonization and, ultimately, the peopling of the Americas (Royer and Finney 2020, Hebda et al. 2022, Praetorius et al. 2023).

Understanding of the paleogeological history of the North Pacific Coast is mixed and incomplete. Topographic and bathymetric reconstructions of the western edge of the Cordilleran Ice Sheet, for example, have identified numerous potential refugia along the outer islands of Southeast Alaska (Carrara et al. 2003, 2007). Palynology and radiocarbon dates from sediment cores from Baranof, Mitkof, and Pleasant islands suggest that there was suitable terrestrial habitat for forests and, perhaps, associated biotas that persisted in these areas during the LGM. Spruce trees (*Picea* spp.), for example, seem to have persisted in the region and rapidly expanded after the LGM (Hansen and Engstrom 1996; Ager 2007, 2019). In contrast, dating of other sites shows instead that parts of outer islands were covered by ice or snow until approximately 17–15 kya (Lesnek et al. 2018). To date, geologic dating within the North Pacific Coast has focused primarily on exposed surfaces (Lesnek et al. 2018, 2020). Thus, additional exploration of offshore areas, particularly now-submerged sites that may have been above sea level during the LGM, is needed to fully reconstruct local glacial extent, coastlines, and regional geologic dynamics (Mathewes and Clague 2017, Mathewes et al. 2020). Reconstructions of submerged LGM refugia, however, are further complicated by regional volcanism (Praetorius et al. 2016) and complex patterns of isostatic (i.e., rise and fall of land in response to the weight of glaciers) and eustatic (i.e., changes in sea level caused by variation in water volume) flux that occurred as ice sheets expanded and contracted (Baichtal and Carlson 2010, Shugar et al. 2014, Lesnek et al. 2020, Baichtal et al. 2021). While geological research has narrowed the potential locations of ice-free refugia, incomplete and conflicting results make the study of biological communities an important and complementary line of evidence for understanding and interpreting regional history.

The fossil record similarly shows mixed support for the presence of North Pacific Coast refugia. Fossils of ice-associated mammals, including arctic foxes (*Vulpes lagopus*), dated to the LGM, suggest that larger mammals may have been able to disperse among and between islands when sea levels were lower, but fossils of smaller organisms are scant (Heaton and Grady 2003, Cooper et al. 2006). Pre-LGM fossils are documented from Prince of Wales Island (Heaton and Grady 2003, Lesnek et al. 2018) and Haida Gwaii (Mathewes and Clague 2017, Mathewes et al. 2019). Revisiting fossils using carbon-14 analysis (Lesnek et al. 2018) uncovered nearly continuous deposition in Shu'ká Káa cave on Prince of Wales Island starting around 40 kya, with a gap between 17–20 kya (Lesnek et al. 2018). Combined with evidence of substantial species turnover before and after the LGM, their results suggest that the Shu'ká Káa cave site was covered by ice or snow during this period (Heaton and Grady 2003, Lesnek et al. 2018). Until recently, no pre-LGM fossils had been documented on the other outer islands of the Alexander Archipelago (da Silva Coelho et al. 2023), although the presence of karst (landscapes where dissolving limestone bedrock forms an intricate network of caves, springs, and sinkholes) along the western edge suggests there may be other, unexplored caves in the area (Baichtal and Swanston 1996, Heaton 2002).

Although the 2 North Pacific Coast archipelagos—Alexander and Haida Gwaii—have shared biogeographic histories (Demboski et al. 1999, Cook and MacDonald 2001), they are managed by separate international governments. In 2018, the Haida Gwaii Management Council, composed of representatives from the Indigenous Haida Nation and British Columbia, Canada, established land use objectives designed to balance biodiversity protections with socio-economic interests. Their plan uses ecosystem-level monitoring to update management practices over time with the goal of maintaining endemism and wildlife abundance (Council of the Haida Nation 1993, 2010, 2019). With that model in mind, we focused on Southeast Alaska, where wildlife and their habitats are largely regulated by the United States Forest Service (USFS) Tongass National Forest Land and Resource Management Plan (TLMP; USFS 1997), the Alaska Department of Fish and Game (ADFG), and other state and federal laws (e.g., the Endangered Species Act; 16 U.S. Code Chapter 35). The TLMP is revised approximately every 15 years and is currently (2024) undergoing formal revision.

Unlike the Haida Gwaii Management Council's holistic approach, the current TLMP focuses primarily on timber resource management (Orians and Schoen 2013) in response to the history of industrial-scale logging in Southeast Alaska, which removed 31.8% of large-tree (high volume), old-growth stands in the Tongass National Forest (Albert and Schoen 2013). Although an external scientific review of the TLMP in 1997 (Shaw et al. 2000, Boyce and Szaro 2005, Smith 2005) prompted the inclusion of monitoring of endemics, subsequent revisions of the plan (USFS 2008, 2016) continued to focus on old-growth-dependent species and failed to maintain meaningful monitoring of endemics. While old-growth forests are an undeniably valuable natural resource, isolated patches of old-growth forest are insufficient to sustain many sensitive island populations, especially endemics (Smith and Flaherty 2023), and second-growth forests in Southeast Alaska will not provide habitat for most wildlife for many decades (Parker et al. 1996). Recognizing that old-growth dependent species are part of a larger, equally important community of organisms, the 2012 planning rule (USFS 2012:21190) aimed to guide "science-based development, amendment, and revision" of the TLMP, among other management plans, to promote social and economic sustainability, ecosystem services, and the ecological integrity and diversity of natural communities. This rule, and litigation by the Natural Resources Defense Council (Natural Resources Defense Council v. United States Forest Service 2005), prompted the last revision of the TLMP in 2016, but as of mid-2024, there are no formally recognized focal wildlife species.

Further, although the TLMP has called for "surveys for endemic mammals prior to any project that proposes to substantially alter vegetative cover" since 1997 (USFS 1997:4–117), more than 2 decades later, no protocols or funding have been defined for long-term monitoring of endemics. Island endemics are especially sensitive to anthropogenic disturbance, as evidenced by the overrepresentation of insular endemics among recently extinct (>60%) and critically endangered (>35%) vertebrate species globally (Tershy et al. 2015). The idiosyncratic nature of extinction and colonization on islands, combined with recent translocations or invasions (Doherty et al. 2016), complicate regional management and highlight the need to identify appropriate units of conservation for endemics (e.g., distinct population segments [DPSs]) and goals for these units before making decisions that affect endemics (Shafer et al. 2011, Larson et al. 2012, Pauli et al. 2015). As defined by the United States Fish and Wildlife Service (USFWS; Fay and Nammack 1996), a DPS represents a discrete population or group of populations that are significant ecologically, genetically, morphologically, or otherwise relative to the entire species and which may be granted protected status under the United States Endangered Species Act (16 U.S. Code Chapter 35). The DPSs are not limited to species but extend to subspecies and lineages; that is, discrete populations with a distinct evolutionary history.

We summarized published research from 2000–2022 on the evolution and biogeography of Southeast Alaska mammals to update perspectives on endemics that can be integrated into adaptive resource management planning. We also reviewed the availability of voucher specimens to identify sampling gaps within the Tongass National Forest that continue to limit the application of cutting-edge molecular methods and other new technologies.

Literature published before the year 2000 was summarized by Shafer et al. (2010) and earlier work by Soltis et al. (1997), Brunsfeld et al. (2001), and Cook et al. (2006). Because there is still no monitoring plan in place for Southeast Alaska endemics, we predicted that available sampling would be insufficient for population-level analyses of endemism in most species and that research effort would be uneven with respect to taxonomy and geography. Based on the preliminary biogeographic patterns identified for Southeast Alaskan mammals (Cook et al. 2001, Sawyer et al. 2019) and hypothesized refugia along the western edge of the Alexander Archipelago (Carrara 2003, 2007), we further predicted that endemics would be geographically clustered on more isolated, peripheral islands.

STUDY AREA

We define Southeast Alaska as the terrestrial area of the Alaska panhandle, south and east of Yakutat Bay and bordered by Canada. The period of our study is 2000–2022. The region is approximately 90,000 km^2 and fractured into >1,000 named islands that comprise the Alexander Archipelago, plus a narrow strip of coastline (Dawson et al. 2007). The Coast Mountain Range, which bounds Southeast Alaska to the east, is among the highest coastal mountain ranges in the world, rising from sea-level to over 4,000 m (Smith 2016). This coastal temperate rainforest (DellaSala et al. 2011) is characterized by variable rainfall (70–1,158 cm annually), persistent cloud cover, and minimal annual temperature variation (generally, 0–20°C). Late spring and early summer is the driest period, with the rainy season beginning in July and peaking in October, and snowfall occurring in November and peaking in January (Smith 2016). Complex regional topography generates heterogeneous biotic assemblages, with western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), and lodgepole pine (*Pinus contorta*) as the dominant trees (Smith 2016). As a high latitude continental archipelago, the area hosts no reptiles and few amphibians (MacDonald and Cook 2007).

Over 80% of the study region is managed by the USFS as part of the Tongass National Forest (65,000 km^2). Glacier Bay National Park and Preserve (13,287 km^2), located in the northwestern corner of the region, is managed by the National Park Service. Haines State Forest (1,157 km^2), in the northeast, is managed by the Alaska Department of Natural Resources Division of Forestry, and other lands are managed by the United States Bureau of Land Management, municipalities, or Indigenous Peoples. The ADFG regulates harvest of game animals across 5 game management units (GMUs) in Southeast Alaska: GMU1 (coastal mainland and south central islands), GMU2 (Prince of Wales Island complex), GMU3 (central islands), GMU4 (Admiralty, Baranof, and Chichagof [ABC] islands), and GMU5A (Yakutat; ADFG 2022). Five major biogeographic regions have also been empirically defined within Southeast Alaska based on shared organismal communities and evolutionary histories (MacDonald and Cook 1996, Cook et al. 2006, Albert and Schoen 2007, Sawyer et al. 2019). Those regions include the northern inner islands (e.g., Admiralty), the northern outer islands (e.g., Baranof, Chichagof), the southern outer islands (e.g., Prince of Wales Island, Dall), the middle and southern inner islands (e.g., Etolin, Kuiu, Kupreanof, Mitkof, Wrangell, Revillagigedo), and the coastal mainland, including the Cleveland Peninsula (Figure 1).

METHODS

Literature review

To assess regional research effort, we performed a literature review through Web of Science on 17 January 2024 through the University of New Mexico Libraries' web portal. We queried publications released between 1 January 2000 and 31 December 2022 that contained the search terms Alaska and mammal. We restricted results to journal articles or review articles and manually removed publications not relevant to the study area and those pertaining to cetaceans (whales, dolphins, and porpoises). We reviewed the remaining publications in detail and recorded the

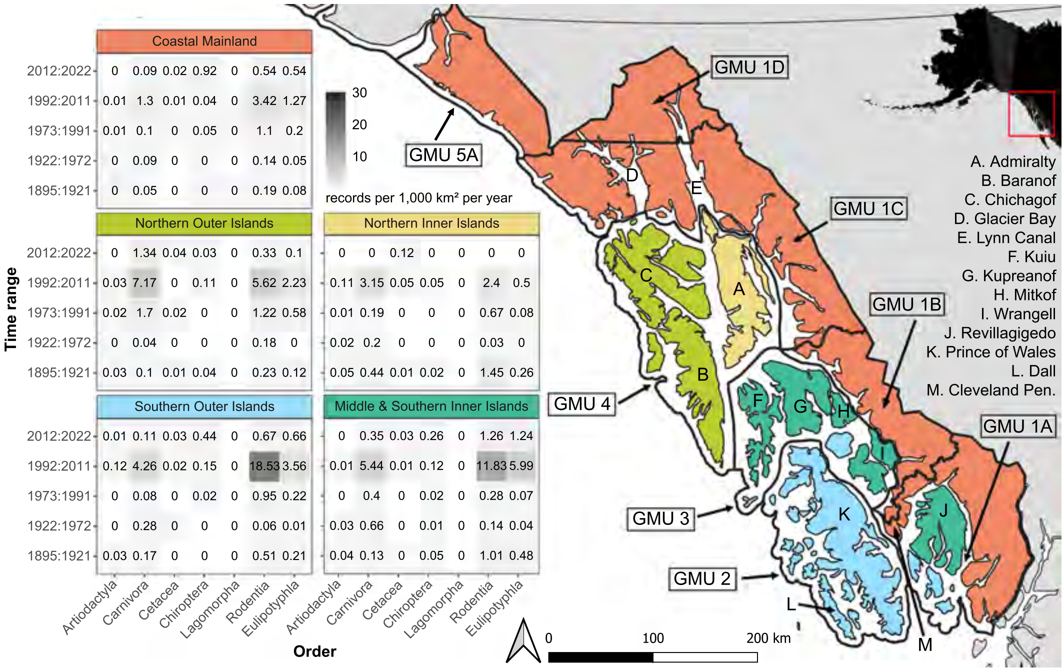


FIGURE 1 Biogeographic regions in Southeast Alaska, USA, as defined in Cook et al. (2006). Heat maps (left) report the number of mammal specimens per 1,000 km^2 in each biogeographic region per year that were sampled and preserved from each mammalian Order. Time periods on the y-axis reflect the history of regional faunal surveys from 1895–2022. Major islands, peninsulas (pen.), geographic features, and game management units (GMUs) are labeled A–M.

authors, publication year, title, digital object identifier (DOI), focal taxon or taxa, island(s) addressed, data type(s) used (e.g., molecular, isotopic, occurrence, telemetry), general results, and a link to the primary literature (Table S1, available in Supporting Information). For molecular investigations, we also recorded the number and type (e.g., mitochondrial, nuclear, multilocus, mitogenome, genomic) of marker(s) used. We also recorded description(s) of endemic taxa at any level of divergence (i.e., lineage, subspecies, species), and where they are known to occur in the region. Because many nominal endemics have not been reevaluated in decades and recent molecular investigations have identified cryptic endemics that still require formal taxonomic review, our revised list of regional endemics provides a critical foundation for management action. To determine whether research effort varied significantly across time, we performed a chi-squared test on the number of publications per year (H_0: equal number of publications each year) and a regression (H_0: no significant relationship between number of publications and year). We used the same framework to test for a taxonomic research bias, but calculated the number of publications per genus because not all studies identified taxa to species.

Assessing specimen availability

To gauge whether existing sample infrastructure is sufficient to establish molecular baselines necessary to assess endemism, we evaluated the availability of physical specimens across geography, taxonomy, and time. We queried the Global Biodiversity Information Facility (GBIF) on 8 February 2023 for preserved specimens collected in Southeast Alaska since the first documented expedition to the region in 1895 (MacDonald and Cook 2007). Preserved specimens are those with ≥1 part (e.g., skin, skeleton, tissue) archived in a publicly accessible biorepository (i.e., natural history museum) that, with increasingly powerful molecular methods, could be sequenced. We curated search results by removing fossil specimens, domestics, duplicates, and records georeferenced outside of the study area. We evaluated records of species not known to occur in the region (MacDonald and Cook 2007) on a case-by-case basis, with consideration of the specific locality, collector, and available molecular resources. We updated GBIF taxonomy to correspond to the American Society of Mammalogists' Mammal Diversity Database (Burgin et al. 2018). We calculated terrestrial area (km^2) of each GMU and biogeographic region (Cook et al. 2006) in ArcMap (calculate geometry tool; Esri, Redlands, CA, USA) from OpenStreetMap (www.openstreetmap.org) shapefiles. For temporal comparisons, we defined time windows that correspond to the history of regional collecting, as opposed to using arbitrarily fixed time units (e.g., decades), which would divide a single survey project across multiple time bins (MacDonald and Cook 2007). Early scientific collection occurred between 1895–1921, led by scientists from the Smithsonian National Museum of Natural History (Washington, DC, USA) and Museum of Vertebrate Zoology (Berkeley, CA, USA). There were few specimens preserved from 1921–1972, after which scientific collecting resumed, led by the University of Alaska Museum of the North, from 1973–1985. The most active collecting period occurred from 1991–2011, with support from a series of federally funded (National Science Foundation, USFWS, and USFS) natural history surveys awarded to Dr. Joseph A. Cook and collaborators at University of Alaska Museum of the North, Idaho State University, and the Museum of Southwestern Biology, University of New Mexico. Three projects specifically, ISLES (Island Surveys to Learn about Endemic Species project, 1991–2011; Conroy et al. 1999; Cook and MacDonald 2001, 2013), the Beringian Co-Evolution Project (1999–2012), and the Collaborative Integrative Investigations of Biomes of the Arctic Project (2013–2016; Cook et al. 2017) supported voucher-based fieldwork in Southeast Alaska. Together, these projects sampled and preserved tens of thousands of mammal specimens and their parasites from across Alaska and Canada for use and reuse in diverse scientific research (McLean et al. 2016). As these projects concluded or shifted focus, collection activity declined from 2012–2022.

We tabulated raw counts of specimens for each mammalian Order for all biogeographic regions across 5 time windows. We divided specimen totals by the size of that biogeographic region (km^2) and number of years in that time window to facilitate comparison (Figure 2). To assess sampling completeness, we compared the number of species in each Order known to occur in Southeast Alaska to the number of species represented by ≥ 1 or ≥ 10 voucher specimens (Figure 2). Collection methods and regulating agencies differ for taxa in the Order Artiodactyla; therefore, counts are reported separately for ungulates and cetaceans within that Order.

The GBIF has limited ability to search for specimens with high-quality preserved tissues; therefore, we queried the Arctos database (arctos.database.museum) on 8 February 2023 for specimens from Southeast Alaska with tissue available. Arctos includes data from >40 biocollections and is regularly published to aggregators, including GBIF. Arctos hosts data for the 3 biorepositories that house most Southeast Alaska specimens collected since 1895: University of Alaska Museum of the North (n = 19,004), the Museum of Southwestern Biology (n = 6,752), and the Museum of Vertebrate Zoology (n = 1,336). We applied the same filtering and taxonomic updates as for the GBIF data set. For records missing a collection year, we inferred the year from the verbatim collection date where possible or excluded ambiguous records.

RESULTS

Literature review

Our Web of Science search returned 2,622 journal articles published between 1 January 2000 and 31 December 2022 that included the words Alaska and mammal. Two hundred and ninety-nine of those manuscripts pertained, to some degree, to mammals in Southeast Alaska. Among those, 82 focused on cetaceans. Rather than restrict results to publications with an explicit focus on biogeography, we chose search terms that would recover publications from a variety of subdisciplines. Some relevant publications were not recovered by our search because they did not contain both prescribed search terms (Bidlack and Cook 2002, Harlin-Cognato et al. 2006, Lausen et al. 2019) in fields searched

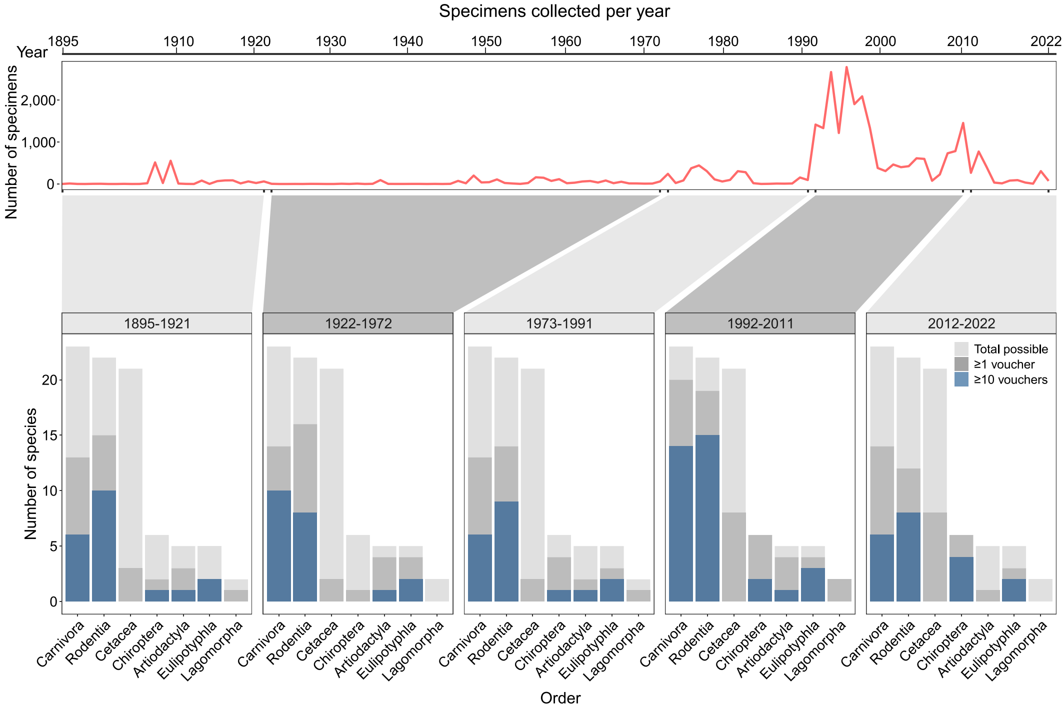


FIGURE 2 Timeline of the history of scientific collecting of mammals in Southeast Alaska, USA (top), from 1895 (left) through the end of 2022 (right). The 5 temporal windows correspond to pulses of historical sampling in the region. We also present stacked bar charts for each temporal window (bottom) to illustrate the total species diversity of Southeast Alaska per mammalian Order (light gray) compared to the subset of species with 1 (dark grey) or 10 (blue) samples available through biorepositories.

by Web of Science. Nevertheless, our literature review provides a general measure of regional research effort and a cross-section of the types of methods used over the last few decades. The remaining 217 relevant papers (Table S1) address 45 of 66 (68%) of mammal species in Southeast Alaska. Research effort, as measured by publications per year, did not differ across years ($\chi^2 = 14.639$, $P = 0.877$), and there was no relationship between year and the number of publications (adjusted $R^2 = -0.030$, df = 21, $P = 0.559$). Research effort was biased toward aquatic mammals ($n = 115$; e.g., sea otters, pinnipeds) compared to terrestrial mammals ($n = 102$), and 17 papers addressed both. If research effort was even across taxonomy, we expected 3.3 publications per species. Yet, some taxa are overrepresented and others understudied. For example, more than a quarter of relevant papers ($n = 68$) focused on Steller's sea lions (*Eumetopias jubatus*). Bears were the most studied terrestrial group, with 18 relevant papers: 12 on brown bears (*Ursus arctos*), 6 on black bears (*Ursus americanus*), and 4 on polar bears (*Ursus maritimus*), with some papers addressing >1 species. Most species, including hoary marmots (*Marmota caligata*), Keen's myotis (*Myotis keenii*), and bushy-tailed woodrats (*Neotoma cinerea*), were represented by a single publication, and 16 species were not represented in the literature search. Seventy-seven relevant papers (35%) used some type of genetic data: 27 of those used ≥1 mitochondrial genes, 4 used complete mitogenomes, 15 used microsatellites, 22 used multilocus data (i.e., ≥1 unlinked loci), and 8 used genomic-scale data (i.e., whole-genome sequencing, metagenomics, or >1k single nucleotide polymorphisms [SNPs]). We record a clear trend of increasing multilocus and, more recently, genomic-scale investigations through time (Figure S1, available in Supporting Information).

To compile an updated list of regional endemics, we started with the list published by Cook et al. (2001). We harmonized taxonomy to the American Society of Mammalogists Mammal Diversity Database and then updated the list based on our literature review and additional targeted literature searches. We classified neoendemic and paleoendemic lineages based on available data (e.g., genomic, morphological) and estimated dates of divergence. We limited endemic taxa to those occurring only in Southeast Alaska or in both Southeast Alaska and Haida Gwaii, and excluded taxa with a range beyond this area, including Haida Gwaii-only endemics. We identified 18 regional endemics (Table S2, available in Supporting Information).

Availability of specimen resources

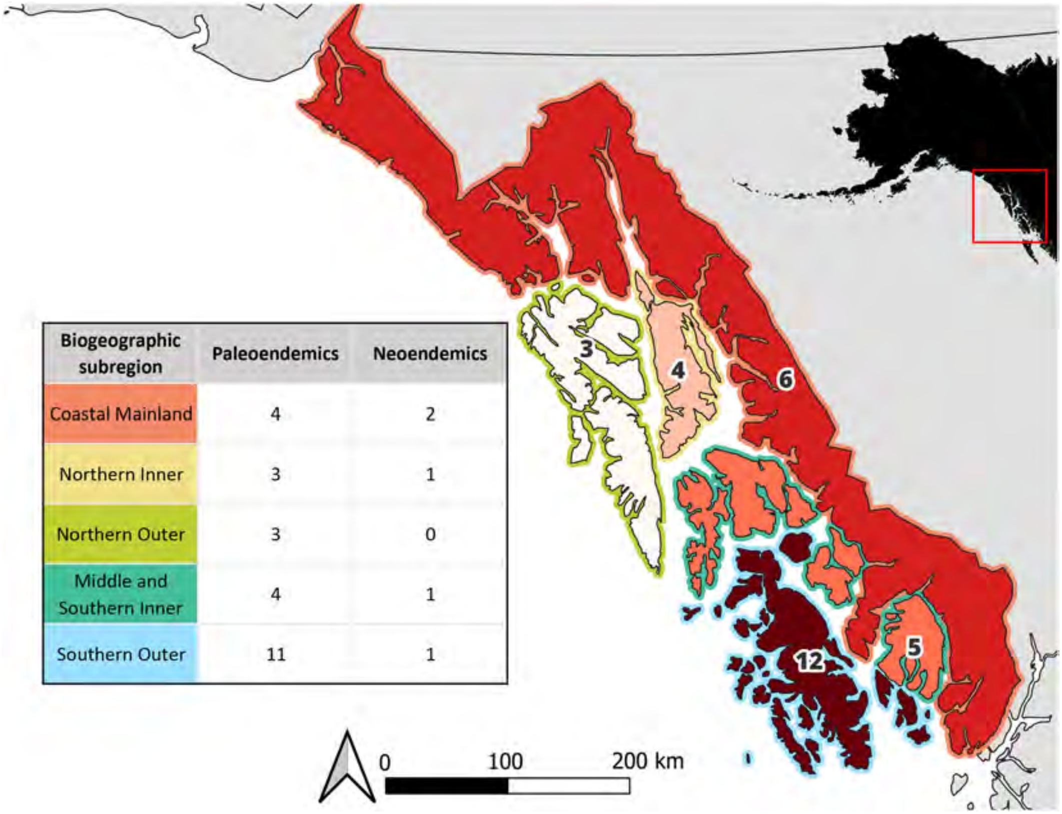
Our GBIF query returned 29,247 preserved specimens collected in Southeast Alaska. Of these records, 27,293 (93%) are permanently archived at biorepositories that use the Arctos database (Table S3, available in Supporting Information). Of the 23,591 GBIF records collected after 1990, when tissue samples began to be consistently collected, only 14 GBIF specimens are not held at institutions with specimens and data hosted on Arctos. Therefore, our Arctos query for specimens with frozen tissues is a nearly complete representation of available tissue resources. Permanently archived tissues were available for 20,293 mammals collected in Southeast Alaska. Of those, 7,418 were collected between 2000 and 2022 (Table S4, available in Supporting Information). Fifty-one of 66 Southeast Alaska species (77%) had ≥1 tissue sample recorded from the region from 2000–2022. Only 36 species (55%) had ≥10 samples available from that period. Most endemic taxa are defined below the species level (e.g., subspecies, lineage, DPS; Table S2), such that their sample availability is even lower. Four species not included in MacDonald and Cook's (2007) documentation of Southeast Alaska fauna had archived tissues available. Two were newly documented to the region: Yuma myotis (*Myotis yumanensis*; collected between 1990–2014 from Revillagigedo Island and the southern mainland, archived at University of Alaska's Museum of the North) and black rat (*Rattus rattus*; an invasive species collected from a residence in Sitka on Baranof Island, archived at the Museum of Southwestern Biology). The 2 other recent detections are the result of taxonomic revision: American ermine (*Mustela richardsonii*) and Haida ermine (*Mustela haidarum*). The Haida ermine was originally described from Graham Island (Preble 1898) and was later reported on Moresby Island (Hall 1951) and reduced to a subspecies (*M. erminea haidarum*). Later, the subspecies' range was extended to include Prince of Wales and Suemez islands in southern Southeast Alaska (Eger 1990) and re-elevated to species status (Fleming and Cook 2002; Colella et al. 2018, 2021*a*).

The most complete documentation of Southeast Alaska mammals occurred from 1992–2011, although even during that period, 11 of Southeast Alaska's 66 non-human mammal species were not documented by a single specimen, and 31 species (47%) have <10 vouchers available. Since 2012, 28 species have no vouchers available and 46 (70%) have <10. Some biogeographic regions are better sampled than others. For example, the northern inner biogeographic region is severely under-sampled, with zero terrestrial mammals archived since 2012. Samples are also not evenly distributed taxonomically. There are nearly 5 times more vouchers archived for each of Southeast Alaska's 22 rodent species (mean = 696.7) than for each of the region's 6 bat species (mean = 130.2).

Regional endemics

An endemic is a DPS (i.e., distinct lineage) or formally named taxon (i.e., subspecies, species) that shares common ancestry and an entire distribution that is restricted to a particular geographic area. We sorted extant terrestrial and aquatic mammals into 4 groups: paleoendemics, neoendemics, recent colonists that have not yet diverged, and taxa with insufficient data to make a determination (Table S2). Six subspecies (Admiralty Island beaver [*Castor canadensis phaeus*], island mink [*Neogale vison neolestes*], Prince of Wales Island river otter [*Lontra canadensis mira*], glacier marmot [*Marmota caligata vigilis*], Alaska jumping mouse [*Zapus hudsonius alascensis*], and Yakutat root vole [*Alexandromys oeconomus littoralis*]) and one species (Glacier Bay water shrew [*Sorex alaskanus*]) were not reevaluated over the last 2 decades, so there is no new information with which to validate these earlier descriptions. Overall, we identified 15 paleoendemics, 3 neoendemics, 10 recent colonists, and 7 taxa that have not been reevaluated. We suspect that this conservative inventory excludes unexamined or morphologically cryptic endemics because of poor sample availability.

We identified 15 paleoendemic mammals in Southeast Alaska (Table S2), including the only endemic species to the region, Haida ermine. This species has been documented from 7 islands and is represented by 2 subspecies. Suemez Island ermine (*Mustela haidarum seclusa*) is endemic to Suemez Island, while Prince of Wales Island ermine (*M. h. celenda*) is endemic to Prince of Wales Island and 4 islands in the Haida Gwaii Archipelago (Hall 1944). Still, not all island populations have been characterized genetically. Two paleoendemics have mixed support: the Dall Island black bear (*Ursus americanus pugnax*) and Sitka brown bear (*Ursus arctos sitkensis*; da Silva Coelho et al. 2023). These subspecies are listed in both the paleoendemic and neoendemic categories but were only counted towards paleoendemic totals to avoid inflation of the total number of endemics. Paleoendemics are found in every biogeographic region but are most common in the southern outer islands (*n* = 11). Divergence date estimates for paleoendemics cluster around 65–300 kya, although Dall Island black bear is estimated to have diverged 360 kya–1.0 Mya (Byun et al. 1997), and Haida ermine and the Sitka brown bear coastal lineage are estimated to have diverged 0.9 and 1.5 Mya, respectively (Lindqvist et al. 2010, Dawson et al. 2014, Colella et al. 2018). Most paleoendemics were described using a single mitochondrial marker but multilocus datasets and, most recently, whole-genome resequencing data have also been used. As noted in previous studies (Cook et al. 2006, Smith 2016), endemic species richness is inversely related to total species richness in Southeast Alaska, with the greatest number of endemics occurring on the relatively species-poor southern outer islands (Figure 3).



Biogeographic subregion	Paleoendemics	Neoendemics
Coastal Mainland	4	2
Northern Inner	3	1
Northern Outer	3	0
Middle and Southern Inner	4	1
Southern Outer	11	1

FIGURE 3 Biogeographic regions of Southeast Alaska, USA (outline colors), shaded based on the number of endemic mammal taxa identified from 1895–2022, with darker red indicating higher endemic richness. Each region on the map is labeled with the total number of endemic mammals. The numbers of paleoendemics and neoendemics in each biogeographic region are reported in the inset table.

Given the relatively short time since the LGM, neoendemics at the species level are not expected. Three distinctive lineages are recognized as neoendemics restricted to Southeast Alaska: 2 subspecies (the Alexander Archipelago wolf [*Canis lupus ligoni*]; Weckworth et al. 2015; and the Admiralty Island meadow vole [*Microtus pennsylvanicus admiraltiae*]; Jackson and Cook 2020) and some wolverines (*Gulo gulo*) in Southeast Alaska exhibit unique haplotypes within a coastal lineage, but limited gene flow from adjacent British Columbia may counterbalance insular divergence (Krejsa et al. 2021). Neoendemics are in every biogeographic region except the northern outer, and are most common on the coastal mainland (*n* = 2) region. Divergence dates were not explicitly estimated for neoendemics in the literature, but shallow divergence is interpreted to post-date the LGM. Molecular studies identify neoendemic colonization of Southeast Alaska from both Beringian and Southern refugia. Molecular methods used to describe neoendemics included multilocus datasets, microsatellites, and, in one case, reduced representation sequencing.

Ten purportedly endemic taxa in Southeast Alaska (Table S2) showed no evidence of divergence from their continental relatives. Although interpretation is complicated by historical wildlife translocations, several recently colonizing species occur on the coastal mainland (*n* = 4) and middle and southern inner islands (*n* = 5), while the biogeographic region with the fewest recent colonizations is the southern outer islands (*n* = 1). Routes of colonization were inferred for 7 of these taxa, with 4 expanding from a southern refugium and 3 from Beringia. Species that expanded from Beringia occurred only in the coastal mainland, northern outer, and northern inner biogeographic regions, while species that expanded from southern refugia occurred in every biogeographic region. Over the last 2 decades, single locus mitochondrial DNA, nuclear and mitochondrial multilocus, microsatellites, mitochondrial DNA, and, recently, whole genomes were employed to investigate the extent of endemism and timing of recently colonizing species.

DISCUSSION

The regional mammalian fauna of Southeast Alaska encompasses a mosaic of species that are paleoendemic, neoendemic, or recent arrivals. Molecular methods applied to Southeast Alaska wildlife over the past 3 decades have completely altered our understanding of regional endemicity and the biogeographic processes shaping this biome. Our curated list of regional and Southeast Alaska endemic mammals (Table S2) includes 15 paleoendemics and 3 neoendemics. In some cases, purported endemics were taxonomically invalid (e.g., Revillagigedo Island red-backed vole [*Clethrionomys gapperi solus*] and Wrangell Island red-backed vole [*C. g. wrangeli*]; Runck et al. 2009), whereas in other cases, deeply divergent cryptic taxa with complex histories of gene flow were uncovered (meadow vole [*Microtus pennsylvanicus*], Jackson and Cook 2020; Haida ermine, Colella et al. 2021*a*,*b*; martens [*Martes* spp.], Colella et al. 2018, 2021*b*). Availability of biological specimens has substantially improved our understanding of regional fauna through morphological, isotopic, and molecular investigations; however, substantial knowledge and sampling gaps remain. The intentional, collaborative development of temporally deep and geographically broad sample archives is a necessary investment to understand the distribution and status of endemic taxa and to monitor overall ecosystem health through time. Such a foundation is critical to adaptive management of wildlife, as it can provide insights into community assembly, shifting environmental baselines, invasive species (i.e., predators, competitors, pathogens), genetic variability, and, more generally, an understanding of change during a period of substantial environmental perturbation (Table 1).

Biogeography of Southeast Alaska

Biogeographic patterns shared across ecologically diverse species may reflect similar responses to deep-time environmental and geological processes, which can help guide conservation and management strategies. Because of their limited dispersal abilities, the phylogeographic patterns of non-volant terrestrial mammals are influenced by landscape-level changes in connectivity and isolation in ways that can provide insight into broader biogeographic processes and the long-term trajectory of populations (da Silva and Patton 1998, Avise 2000). The complex regional

TABLE 1 Proposed actions to document and monitor endemics in Southeast Alaska, the research need or knowledge gaps that may impede these actions, threats to insular species and systems addressed by each action, and desired outcomes for wildlife management on the Tongass National Forest.

Action	Research need or knowledge gaps	Threats addressed	Outcomes
Inventory endemic taxa	Population distribution, size, history or levels of connectivity to other populations or islands are unknown for most Southeast Alaska mammals, especially non-game taxa. Consensus is needed for the endemic unit that should be managed (lineages, distinct population segments, evolutionarily significant units, subspecies). For most endemics, level of divergence (and status as paleoendemic or neoendemic) remains untested. Although there are extensive opportunities for collaboration to obtain baseline information from specimens, funding and staffing shortages necessitate careful prioritization of this action to meet United States Forest Service mandates.	Habitat loss and fragmentation, introduced species, pathogens, overexploitation, and climate change	Specimen-based field inventories should be used to empirically estimate, then develop predictive models for occupancy, density, and extinction probability. Inventories and rigorous genomic investigations will help to resolve endemic taxa that have been described within different frameworks.
Identify species of conservation concern	Because sampling effort was low before 1990 and declined sharply post-2010, the trajectory of Southeast Alaska mammals and current population health are unknown.	Habitat loss and fragmentation, overexploitation	With broad population trends and population health and resiliency quantified objectively through genomic methods, management can be adapted to preserve declining endemic populations and their associated communities on a per-island scale.
Monitor endemics	Population trends for endemics are unknown on a forest-wide scale. Abundance estimates for even large game species have proven to be inaccurate (e.g., Alexander Archipelago wolf), and population trends for nongame species are not monitored on a forest-wide scale.	Habitat loss and fragmentation, introduced invasive species and pathogens, increasing accessibility, climate change, and overexploitation	The spread of introduced or invasive species can be detected quickly, and risk factors for invasion can be predicted for non-native species that are cosmopolitan (e.g., rats) or known to occur near the region. Distinctive island lineages and endemic taxa are protected from genetic swamping, outbreeding depression, and pathogenic

TABLE 1 (Continued)

Action	Research need or knowledge gaps	Threats addressed	Outcomes
			organisms to which they are naïve. Short-term population changes can be used to adaptively inform management actions.
Predict and document responses to climate change	Local ecological and behavioral adaptation of taxa within Southeast Alaska remains largely unexamined, and responses to short-term extreme weather and long-term climatic change have been speculated but only modeled or documented for a handful of species.	Climate change	Island populations are especially vulnerable to changing environments as they often cannot move off the island. Naturally low population size and limited connectivity among islands should be accounted for when modelling responses to climate change. Data input for climate response models should be informed by the distribution of lineage(s) found in Southeast Alaska with evidence for local adaptation. Monitoring data should be used to understand short-term responses to extreme weather events.

topography of Southeast Alaska has produced a mosaic of neoendemics and paleoendemics, many of which are now in contact with recent colonists into the region.

Although controversial, paleoendemic distributions are well explained by longer-term persistence in coastal refugia. Those taxa are also most common in the southern outer biogeographic region, which may have been west of the maximum extent of the Cordilleran Ice Sheet or proximal to now submerged refugial areas located even farther west (Carrara et al. 2007, 2009; Matthews and Clague 2017; Ager 2019; Sawyer et al. 2019). Populations in these glacially persistent refugia would have been isolated from continental populations, leading to divergence over time. Except for black bears, the only paleoendemics on the Southeast Alaska coastal mainland identified to date are small mammals. Medium- and large-bodied paleoendemics (e.g., Haida ermine, Sitka brown bear) are restricted to outer islands, and are also often found on Haida Gwaii. Small mammals may have more easily dispersed eastward from coastal refugia to interior islands and eventually reached the mainland, as their larger population sizes and shorter generation times can buffer against stochastic processes (e.g., genetic drift) that may lead to extirpation in larger bodied organisms (Burger et al. 2019). Explicit tests to identify colonization routes into Southeast Alaska are needed to understand the degree of isolation, connectivity, and resiliency of metapopulations to disturbance. Such tests are tractable only with expanded geographic sampling and genomic analyses.

On outer islands, extra vigilance for human-mediated invasions is needed to maintain the integrity of unique communities. Potential source populations for introductions or genetic rescue should be chosen to preserve the deeper history and potential adaptive divergence of island lineages. Further, many of the outer islands identified as centers of endemism experienced heavy logging under prior USFS timber management regimes. The Prince of Wales Island complex, for example, has a high concentration of endemic mammals (Cook et al. 2006, Dawson et al. 2007) but has had over a third of its productive old-growth forest stands harvested, with up to 77.5% of contiguous old-growth forest lost in the northern part of the island (Albert 2019). The substantial infrastructure associated with this history of deforestation (6,760 km of roads) leaves little unaffected habitat for endemics (Smith 2016).

Neoendemics are found across biogeographic regions. River corridors, which provide the primary terrestrial colonization routes through the Coast Mountains into Southeast Alaska, were glaciated until ≥11 kya (Lesnek et al. 2020). As glaciers melted, sea levels rose, resulting in a narrow window of time for leading-edge, continental colonists to reach the Southeast Alaska coastline and disperse westward before the landscape became fragmented into islands. The northern inner islands host 3 neoendemics, highlighting an emerging biogeographic theme in Southeast Alaska: there is a phylogenetic break between the northern outer (i.e., Baranof, Chichagof) and northern inner islands (i.e., Admiralty). Based on the distribution of endemics, we can further infer that colonization routes from the coastal mainland to nearby island groups (northern inner, middle and southern inner biogeographic regions) remained open for longer than routes connecting to the outer islands (Bidlack and Cook 2001, Runck and Cook 2005, Weckworth et al. 2011, Jackson and Cook 2020). While recently colonized mammals are rare on outer islands, there are examples (e.g., American ermine, Sitka deer [*Odocoileus hemionus sitkensis*], root vole [*Alexandromys oeconomus*]) that show limited to no evidence of differentiation from coastal mainland congeners.

Exceptions to general biogeographic trends may reflect differences in distribution, persistence, and colonization ability. Exceptions may also be due to a lack of comprehensive geographic sampling or use of a small set of genetic markers (Brito and Edwards 2009). An updated management framework should reflect current understanding of regional biogeography because the 5 biogeographic regions have distinctive histories of community assembly that will require specialized, mindful management. One size does not fit all regions or islands.

Genomic perspectives in Southeast Alaska

Molecular methods offer an affordable, expedient, and objective means of identifying and monitoring endemics, regardless of taxonomic level. Until recently, Sanger DNA sequencing or microsatellites were the only tractable molecular methods for most wildlife (i.e., non-model systems). These techniques were applied to at least 26 Southeast Alaska mammals between 2000 and 2022. Recently, a few taxa have been assessed using more detailed genomic data (e.g., bears, Liu et al. 2014, Cahill et al. 2015; wolves, Zarn 2019; weasels, Colella et al. 2021*a*,*b*). In cases where genomic data are available, a more nuanced biogeographic history has been revealed. In the case of brown bears, for example, whole genomes show evidence of a deep phylogenetic split between bears on Admiralty Island and bears on Baranof or Chichagof islands (Liu et al. 2014, Lan et al. 2022). Admiralty Island brown bears are more closely related to brown bears from Yukon Territory, Canada, and Montana, USA, than they are to bears on neighboring Chichagof and Baranof islands. That geographic disjunction is explained by a mitochondrial capture event that was not observable when only mitochondrial DNA was examined (Lindqvist et al. 2010, Liu et al. 2014, Lan et al. 2022, de Jong et al. 2023). Notably, 2 bear taxa originally described as paleoendemics in numerous early molecular studies were recently flagged as neoendemics. Mitogenomes from pre- and post-LGM fossil black bears and brown bears from Dall and Coronation islands suggest replacement of Southeast Alaska bears by new arrivals occurred during the LGM but does not rule out post-LGM genetic swamping of a refugial population or population contraction and genetic drift in endemic Southeast Alaska bears (da Silva Coelho et al. 2023). Paleogenomics using ancient DNA, environmental DNA, or sedimentary DNA is an exciting new avenue for interpreting complex phylogeographic patterns in Southeast Alaska mammals (Bohmann et al. 2014). Multiple lines of evidence (e.g., historical, contemporary, biological, geologic) can then more holistically inform interpretation of the complex history of this region; however, those approaches also require well-distributed sampling.

Among the Southeast Alaska taxa examined with multilocus or genomic data, geographic sampling has been limited to only a handful of major islands (Latch et al. 2009). Whole-genome resequencing of Pacific martens, for example, hints at the presence of a coastal endemic, currently recognized at the subspecies level (Pacific coast marten [*Martes caurina nesophila*]), but only 2 genomes have been sequenced from this island clade, each from a different island population (Colella et al. 2021*b*). Similarly, initial descriptions of several endemics include records from only one or a few islands. Thus, it remains unclear whether these are truly single-island endemics or part of a more widely distributed lineage. Dall Island black bear, for example, is a Southeast Alaska subspecies described within the context of a wide-ranging western lineage (Byun et al. 1997, Stone and Cook 2000) but which may be distinctive within that lineage (Puckett et al. 2015). One paleoendemic lineage corresponds to no nominal subspecies of mountain goat (*Oreamnos americanus* coastal lineage; Shafer et al. 2011), which underscores the urgent need to unite or validate taxonomy with phylogeographic studies based on spatially broad sampling (Table 1).

While the majority of infraspecific endemic diversity in the region was originally described in terms of subspecies, recent molecular studies have shifted toward delimiting lineages. Although the definition of an endemic species is relatively straightforward, the geographic and phylogenetic level at which an infraspecific endemic taxon (i.e., subspecies or lineage) becomes a focal conservation unit is not (Crother and Murray 2011). The inclusion of endemic lineages in conservation plans is supported by the legal framework for species conservation in the United States through the concepts of evolutionarily significant units (ESUs) and DPSs (USFWS 1996). Genetic evidence provides critical insight into whether populations in Southeast Alaska are distinctive from conspecifics outside of the region.

Sampling, or lack thereof?

Mammals are among the best-studied organisms in Southeast Alaska. As a result of multiple federally funded surveys in the region, Southeast Alaska is better sampled than much of the world (Hughes et al. 2021), but given the landscape complexity of the region, we still have an incomplete picture of endemism. Of the 66 terrestrial and aquatic species in Southeast Alaska, only 55% are represented by ≥10 archived samples since the year 2000, the minimum required for many population-level analyses (Gautier et al. 2013, Lou et al. 2021), depending on the type and depth of coverage of genomic data (Pruett and Winker 2008, Fumagalli 2013). The quality of these samples aside, 10 tissue samples is likely insufficient for characterizing population-level variation in a highly heterogeneous landscape when diagnosing endemics or other taxonomic units or assessing spatial or temporal variation.

Despite regular permitted harvests, carnivores, game species, and marine mammals represent major sampling gaps in Southeast Alaska, which limits the power of genetic studies and prevents assessments of risk or change through time for these taxa. Wolves, for example, are among the mammals least represented in biorepositories, with just 28 tissue samples archived since 2000. Wolves were identified as a management indicator species in early versions of the TLMP (USFS 2008, 2016) and remain a controversial insular endemic subspecies (Cronin et al. 2015, Weckworth et al. 2015) that exhibits both novel phenotypes and feeding strategies (Roffler et al. 2021). Annual wolf harvests (Bogle 2019, ADFG 2020) offer an easy avenue for regulation-based sampling that, if proactively connected to a wildlife biorepository, would significantly increase permanent sample availability for this species. In Alaska, thousands of draw, subsistence, and general season harvest permits and trapping licenses are issued annually (Alaska National Interest Lands Conservation Act 1980, Dombrowski 2007) and further sampling is regularly conducted by agency biologists and other researchers. Regardless of their original collection purpose, archiving salvage samples in established biobanks is ethical, critical for scientific replication and extension, and useful for monitoring organismal and ecosystem change across space and time (Colella et al. 2020). A renewed investment in coordinating efforts among state and federal agencies and local communities to contribute to specimen-based biorepositories would provide powerful infrastructure for future management initiatives. There is also a curious disconnect between sample availability and research output for aquatic species. Steller's sea lions have 327 samples publicly available (1.6% of all queried tissue samples) in biorepositories, yet this species was the subject of >30% of all publications related to Southeast Alaska mammals published since 2000. Marine and aquatic mammal species are generally more poorly known and more threatened than terrestrial species (Schipper 2008); therefore, emphasizing the need for improved public sample availability, or at least improved archival practices from stranding networks and other sources that contact marine mammals, could significantly benefit management.

Building biorepositories to monitor change in endemic wildlife

Resource management plans guide the implementation of science into decision-making on public lands. Because 80% of the Alexander Archipelago falls within the jurisdiction of the USFS, the current revision of the TLMP is an opportunity to incorporate research on endemic mammals into contemporary land management planning in a way that reflects the archipelagic complexity of this national forest. The USFS Pacific Northwest Research Station played a central role in addressing knowledge gaps identified during the drafting of the 1997 TLMP (Boyce and Szaro 2005), but resulting inventories of endemics were limited (Hanley et al. 2005). Future planning efforts should prioritize island endemics as indicators of overall landscape health and predictors of environmental change and long-term sample archival with biorepositories.

Landscape- and population-level sampling that build holistic biorepositories establish baselines that are critical for monitoring changing conditions. Voucher specimens are essential for extensible and replicable science (Nachman et al. 2023) and capture patterns of biodiversity better than unvouchered observation records (Daru and Rodriguez 2023). Motion-sensitive cameras and other passive monitoring techniques cannot provide the depth or integration of information on organismal and population health and ecology that voucher-based population genomics, viromics, and isotopic chemistry can (Cook et al. 2016). Many species, especially small mammals, are difficult or impossible to identify to species from photographs (Kays et al. 2022). Further, as there are no baseline data on the abundance of most Southeast Alaska taxa, genomic data are uniquely able to provide rigorous estimates of effective population sizes and historical demographic trajectories. Still, specimen availability is uneven across species, time, and geography, and many taxa remain understudied or unsampled. The Alexander Archipelago presents an extremely complex landscape that will require a substantial commitment to sustained sampling to effectively manage.

Recognition of biogeographic regions enables coherent management action

Game management units, which establish state management regulations in the region, are not well aligned with biogeographic regions in Southeast Alaska. This complicates application of a single comprehensive management strategy to the entire region or even per-GMU. A single GMU may encompass vastly different species assemblages with distinctive evolutionary histories. For example, GMU4 lumps the ABC islands together, despite recent evidence that Admiralty is distinct from Baranof and Chichagof islands (Liu et al. 2014, Jackson and Cook 2020, Colella et al. 2021*b*, Lan et al. 2022). Similarly, Revillagigedo and surrounding smaller islands are biogeographically distinct from the rest of the coastal mainland included in GMU1 (Hope et al. 2016, Sawyer and Cook 2016). Biogeographic regions, delimited almost 20 years ago (MacDonald and Cook 1996, Cook et al. 2006), have been empirically validated with a variety of data types, including morphology (Merriam 1897, Eger 1990, Colella et al. 2018), molecules (Lucid and Cook 2004, Dawson et al. 2007, Sawyer et al. 2019, Colella et al. 2021*a*, Lan et al. 2022), and ecology (Smith and Nichols 2004, O'Brien et al. 2018, Roffler et al. 2021).

Correcting the mismatch between GMUs and biogeographic regions would provide a powerful scaffold for regional management priorities across this complex landscape. Evolutionary and biogeographic patterns are, on some level, being incorporated into management efforts through specialized restrictions within GMUs, at least for game species (ADFG 2024). For example, specific management prescriptions to limit marten trapping on Kuiu Island resulted from research conducted on endemic island marten populations (ADFG 2023). Documenting the effects of island endemism, in this case insularity and associated hybridization leading to potential population declines, can result in management decisions that reflect biogeographic realities.

Interagency cooperation is needed for effective wildlife management

The USFS has an obligation to sustainably manage and conserve wildlife on federal lands (National Forest Management Act [16 U.S. Code Chapter 1600]; Zellmer et al. 2017). This is often done through federal programs that fund states' implementation of wildlife conservation. For example, the state of Alaska has received federal funding from the State Wildlife Grant program to proactively work towards the recovery of imperiled species before they meet the criteria for federal listing. Twenty-eight Southeast Alaska mammals are included in ADFG's Species of Greatest Conservation Need, but few are highly ranked, despite endemism being factored into the rankings (ADFG 2015). Alaska's Wildlife Action Plan will be updated in 2025, but little new information has been generated for these poorly studied species since the 2015 revision, a challenge that ADFG has recognized. Most of its high-ranking Species of Greatest Conservation Need are those that have already been intensively studied (e.g., Alexander Archipelago wolf; ADFG 2015). Given USFS management of the majority of land that supports island endemics in Southeast Alaska, meeting the mandates of TLMP and ADFG to prevent further loss of endemic biodiversity will require greater coordination and cooperation between state and federal agencies.

Climate change and anthropogenic activity threaten insular endemics

Human activities, from industrial- to subsistence-scale, have transformed the landscape and wildlife of Southeast Alaska. Wolves on Prince of Wales Island, for example, exhibit levels of inbreeding depression similar to that of wolves in Isle Royale National Park, where inbreeding has led to severe population crashes (Zarn 2019). The purported pressures of hunting, trapping, and habitat loss led to a positive 90-day finding for listing this subspecies under the United States Endangered Species Act (16 U.S. Code Chapter 35; USFWS 2020), but, after 2 deferrals, a not warranted 12-month finding was issued in August 2023, in spite of severe inbreeding and the fact that gene flow between Southeast Alaska wolves and wolves in British Columbia has yet to be examined (USFWS 2023). Identification and proactive monitoring of other endemics may help avoid the costly and risky endeavor of recovering already-endangered populations. Conversely, some mammals appear to be thriving, including introduced species (e.g., elk [*Cervus canadensis*]) and natural expansions (e.g., moose [*Alces alces*]). The effects of these new colonizers have also been inconsistently monitored (but see Harper 2014).

Numerous translocations and invasions have reshuffled species among islands, with some better documented than others (Paul 2009), and these manipulations now serve as natural experiments. American martens, for example, were introduced from multiple mainland sites onto Prince of Wales and Baranof islands, among others (MacDonald and Cook 2007, Pauli et al. 2015). Such manipulations can lead to unintentional introductions of parasites or pathogens with potentially devastating consequences for naïve island species and ecosystems (Table 1; Wikelski et al. 2004, Durden et al. 2016). Notably, the only mammalian species endemic to the region, Haida ermine, is not listed for protection at the state or federal level in the United States (Colella et al. 2019). Previously considered a subspecies of the Beringian ermine (*Mustela erminea*), Haida ermine have been protected by trapping restrictions in British Columbia since 1985 and are listed as Threatened under Canada's Species at Risk Act (Edie 2001). The 2 subspecies of Haida ermine in Southeast Alaska occupy ranges of 6,670 km^2 and 152 km^2 on Prince of Wales and Suemez islands, respectively. Considering these extremely limited ranges, the susceptibility of insular mustelids to pathogens of humans or their pets (i.e., distemper, SARS-CoV-2) is cause for concern and should be monitored.

Management recommendations

We propose 4 recommendations for the TLMP revision. The first is to establish and implement a plan for systematic identification, characterization, and monitoring of endemics based on holistic biorepositories. This is the first step toward designating focal taxa and measuring change through time, including gauging the results of management initiatives. A working list of endemic taxa (extending beyond mammals) would provide the initial framework for a holistic specimen-based monitoring program. Many taxa remain data deficient or unexamined, and limited sampling hinders understanding of regional biogeography and prevents the application of data-driven predictive models for guiding regional management. Improved salvage networks, along with holistic, spatially representative, and temporally regular sampling, will provide essential information on the status of endemics and overall community responses to management actions and global change. Given the expense and logistic difficulties of field work in remote Alaska, we propose to expand existing collaborative specimen networks between agencies and community members that have, over the years, resulted in a substantial series of high-latitude mammal samples (Cook et al. 2017). The challenges of maintaining long-term archives and associated databases are being met by biorepositories (Hedrick et al. 2020, Miller et al. 2020).

Second, we recommend leveraging new technologies to better characterize and monitor insular communities. Genetic studies beginning 30 years ago have provided key insights into endemicity and complexity in Southeast Alaska, but our understanding remains superficial. New high-throughput sequencing methods (e.g., genomic, proteomic, transcriptomic) provide an objective means of monitoring biological units relevant to conservation and management (Hogg et al. 2022). Such protocols could be formally considered through the land management planning process and included in plan requirements. The revelations provided thus far from genomic data hint at our incomplete understanding of endemism in the region and underscore the need to identify and monitor endemics using increasingly affordable molecular techniques. Most endemics from Southeast Alaska were originally identified morphologically at the subspecific level. Given the variable definitions of subspecies across taxonomic groups (Zink and Klicka 2022), genomics will be key to providing phylogenetic and temporal context for divergence in these taxa, a critical component of conservation status (Faith 2002, 2008; Moritz 2002) High-quality tissues collected and preserved long-term, with genomic applications in mind, can also be analyzed with other emerging technologies to tackle a range of questions relevant to management, including ecological and physiological analyses of stable isotopes (O'Brien et al. 2018, Manlick et al. 2024) and contaminants (Witt et al. 2024). Integrating sustainable collection, archival, and digitization of specimens with biorepositories will give researchers the raw material needed to deploy these new technologies to inform management of organismal responses to local and global changes, obtain critical historical context for these changes, and prioritize conservation actions.

Third, we need to prioritize climate change in an island-based management plan. Island archipelagos provide special challenges for managers under a regime of accelerating climate change. Many island species cannot move or migrate as environments change in response to climate disruption. Potential impacts from indirect threats, such as invasive species, increase on islands (Table 1; Whittaker et al. 2017, Macinnis-Ng et al. 2021). For example, warmer winters and a pattern of more rain on snow events are causing declines in Alaska yellow cedar, one of the few tree species found in both Haida Gwaii and the Alexander Archipelago (Mercer et al. 2022). Scientific reviews and assessments, prior to initiating formal forest planning, should include robust modeling of climate change impacts on isolated island populations and identification of potential vulnerabilities of island endemics (Leclerc et al. 2020). An effective monitoring program will also include studies of ecological requirements for each endemic taxon to ensure that landscape-level requirements are met within the context of projected climate and anthropogenic changes to the region. Given the high proportion of taxa and islands that have never been examined and the interdependence of species in insular communities (Simberloff 2019, Smith and Flaherty 2023), faunal and floristic surveys and rigorous monitoring protocols are needed before new extractive activities. Recognizing its importance in global natural climate solutions (Leighty et al. 2006, DellaSala et al. 2022), management of the Tongass National Forest should prioritize both climate change mitigation and biodiversity conservation.

Last, we emphasize the need for both greater international cooperation (U.S.-Canada) and formalized Tribal co-management of North Pacific Coast archipelagos to achieve conservation goals at a meaningful scale and scope, as our literature review confirms that many North Pacific Coast endemics are shared between the southern Alexander and Haida Gwaii archipelagos (Cook and MacDonald 2001). There is already a framework for Indigenous co-management of Haida Gwaii wildlife that could be emulated on USFS-managed land. Small steps have already been made in this direction: a handful of culturally significant sites in the Tongass National Forest are being co-managed in various ways by 3 Tribal organizations (The Hoonah Indian Association, The Organized Village of Kake, and The Organized Village of Kasaan), in accordance with Joint Secretarial Order 3403 (United States Departement of Agriculture and Department of the Interior 2021). Authorities exist to both create and financially support co-management agreements to steward biological diversity across the Tongass National Forest (Mills and Nie 2022). Especially given the cultural and economic interests of self-governing Alaska Native Tribes in both private lands adjacent to the Tongass National Forest and public lands managed by the USFS, a shared or co-produced management framework should be expanded to better incorporate Traditional (Timeless) Ecological Knowledge into wildlife management by including Tribal governments in landscape-level planning efforts.

MANAGEMENT IMPLICATIONS

Though changes can be made to monitoring programs outside of formal planning processes, the Tongass National Forest is now undergoing new management planning that should highlight the importance of island endemism and biodiversity conservation in the face of climate and ecosystem change. Despite past collecting efforts across the complex landscape of Southeast Alaska, we still find a concerning lack of specimen-based resources from which the current status of and future outlook for endemic mammals can be evaluated. We outlined a list of priority endemics for which distribution and ecological relationships can be defined and monitoring programs established to meet forest planning legal requirements. To this end, we recommend that the USFS and other cooperating management agencies, Tribal governments, and diverse stakeholders in the region prioritize biodiversity infrastructure through partnerships that will obtain, preserve, and openly share natural history specimens. The knowledge generated from these actions will equip agencies to work towards sustaining viable wildlife populations in a complex, incomparable, and rapidly changing region.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study did not involve sampling or handling of wild mammals. Specimens examined were collected according to the American Society of Mammalogists' guidelines for handling of wild mammals (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016) and Institutional Animal Care and Use Committees, following updated American Veterinary Medical Association Guidelines, with appropriate state and federal permits.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information.

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TEMPERATE AND BOREAL RAINFORESTS OF THE WORLD: ECOLOGY AND CONSERVATION

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CHAPTER 1

Just What Are Temperate and Boreal Rainforests?

Dominick A. DellaSala, Paul Alaback, Toby Spribille, Henrik von Wehrden, and Richard S. Nauman

When most people think of rainforests, they think of lush, tropical "jungles" teeming with poison arrow frogs (*Dendrobates* spp.), toucans (e.g., *Ramphastos sulfuratus*), mountain gorillas (*Gorilla gorilla beringei*), and jaguars (*Panthera* spp.). Tropical rainforests are indeed special places, as they account for over half the terrestrial species on Earth (Meyers et al. 2000) while representing just 12 percent of the world's forest cover (Ritter 2008). Their temperate and boreal counterparts are another story, though, one yet to receive the kind of global recognition rightfully merited by tropical rainforests. Their story is told here, beginning with historical and recent accounts to define and map the temperate and boreal rainforests of the world.

Any discussion of rainforests must begin with what we mean by this term and how we map rainforests. Definitions and mapping standards are the mortar with which scientists visually construct biome delineations such as temperate and boreal rainforests. Consequently, the modeling techniques used in this chapter frame the entire book, as each of the regional chapters is built from the approaches set herein. In cases where it is necessary to deviate from globally based models and maps, explanations are given by regional authors of the book. Nevertheless, we now build on earlier approaches and definitions of temperate and boreal rainforests by providing a standardized modeling approach and a consistent methodology for mapping these rainforests. While it was our original intent that readers of this book would use our approach as the up-to-date standard for defining and delineating temperate and boreal rainforests, we note that this is a work-in-progress requiring further refinement and real-world verification as new data sets become available. Similarly, in Chapter 10, we present standardized mapping techniques aimed at determining just how much of this rainforest biome is in strict protection, a necessary step for developing a unifying vision for rainforests globally and for calling on decision makers to protect these rainforests as we do in Chapter 11. Because the process used in this opening chapter is central to the entire book, we put more emphasis here compared to the regional chapters that follow.

SCIENTIFIC HISTORY OF TEMPERATE AND BOREAL RAINFORESTS

Throughout this book we refer to either temperate or boreal rainforests that differ mainly with respect to latitude, climate, and plant associations. For descriptive purposes we separate these rainforest types in this chapter but refer to them jointly throughout much of the book.

Temperate Rainforests

Temperate rainforests have been recognized in some fashion by ecologists for nearly a century (Köppen 1918; Holderidge et al. 1971; Whittaker 1975; Jarmon and Brown 1983; Veblen 1985; Read and Hill 1985; Omernick 1987; Moore 1990; Hickey 1990; Alaback 1991; Kirk and Franklin 1992; Kellogg 1992, 1995; Gallant 1996; Lawford et al. 1996; Schoonmaker et al. 1997; Moen 1999). Most researchers classify them as distinct biomes based on broad differences in dominant vegetation and/or climate, or as inclusions within larger ecoregions (large areas distinguished by their dominant vegetation, climate, and land form). Yet a simple internet search for "temperate rainforest" yields inconsistencies in mapping locations due to gross differences in definitions and mapping techniques.

An earlier term, "high-latitude rainforest," was proposed by researchers to describe the pan-American portion of the biome (Lawford et al. 1996), since this is the most simple and unambiguous way to define *temperate* as contrasted with *tropical* (low-latitude) rainforests, but "high-latitude rainforests" has increasingly been replaced by "temperate rainforests," which generally have milder climates than boreal rainforests, due primarily to comparatively low latitudes. A number of temperate rainforest subtypes are described later in this chapter in order to distinguish rainforests from one another, and this terminology is used throughout this book.

Boreal Rainforests

The border between boreal and temperate has traditionally been defined as the zone where conifer forests give way to deciduous forests, or, in drier regions, grasslands, roughly equated by Köppen (1918) with the –3°C January isotherm in the south (Tuhkanen 1984). The delineation of boreal versus temperate is blurred in montane regions, where temperate coniferous forest transitions seamlessly to boreal conifer forest. The important thing to note here is that *boreal* is a latitudinal zone and should not be conflated with terms such as *continental*; biogeographers are unanimous in recognizing some high-precipitation oceanic regions as part of the boreal zone. Tuhkanen (1984) compared a wide variety of different approaches to delineating the northern and southern limits of the boreal zone, and in the integrated classification he proposed that several of the rainforest regions treated here as "temperate" would be considered part of the boreal zone. Nonetheless, throughout this book, we use the term *boreal* to describe the cold northern rainforests of what in other studies have been more generally termed *subpolar*. As we will see later, these include the Pacific Coast of North America north of ~55°N latitude (chapter 2), the northern half of the inland rainforest of Northwestern North America (chapter 3), much of the wet forests of Eastern Canada (chapter 4), portions of Norway (chapter 6), and Inland Southern Siberia (chapter 9). Because there is no boreal zone in the Southern Hemisphere, relatively colder areas in this hemisphere are considered subpolar.

In reality, many temperate rainforests straddle the abiotic (nonliving chemical and physical factors) boundaries between temperate and boreal, both latitudinally and altitudinally, and more so for oceanic boreal systems. Thus, these rainforests serve as a phytogeographical bridge, facilitating the exchange of mesic (moist) floral elements among neighboring systems and as corridors of latitude- and slope- related south-to-north, north-to-south and slope-up, slope-down migrations of wildlife during periods of climate change. How much of the forests included in this book is boreal versus temperate depends on which classification system chosen. The fact that highly similar forest-species assemblages can be found on both sides of artificially drawn lines is a topic best reconciled to biogeography debates.

RAINFOREST DEFINITIONS

Where and how to draw the line between temperate and boreal rainforests has changed over time as more and better data have become available regarding these unique rainforests and the conditions that have created them. Several geographers who developed classifications for the world's climate included a category for temperate rainforest based, for instance, on some combination of cool temperatures and high rainfall, or cool temperatures and a small annual range of temperatures (see below). Whittaker (1975) in his classic ecology text *Communities and Ecosystems* also identified a temperate rainforest type. Most of these early efforts separated the Southern Hemisphere forests into a broadleaf evergreen forest type, further complicating a comprehensive global definition. These classifications vary widely in how they portray the distribution of temperate rainforests, and especially what types of temperate rainforests occur on Earth.

The prevailing definition of temperate rainforest began with work in the 1980s, when the environmental group Ecotrust and its collaborators proposed a more precise definition so that more accurate global maps and conservation strategies could be developed (Alaback 1991, 1996; Kellogg 1992, 1995). The first iteration of this work included a definition for these rainforests consisting of: (1) annual precipitation exceeding 1,200 millimeters with 10 percent or more occurring during summer months; (2) mean July temperature of 16°C or less; (3) cool dormant seasons; and (4) infrequent fire that is an unimportant evolutionary factor (Alaback 1991). Soon it became apparent that this definition was too restrictive, and more important, it did not accurately characterize availability of moisture, since there was no direct link between evaporation and the required minimum amount of rainfall. The most biophysically precise method of doing this would be to calculate potential evapotranspiration, which corrects for latitude—with increasing latitude, less precipitation is required to maintain the same humidity levels (Stephenson 1990). Potential evapotranspiration was also later shown to precisely predict the distribution of at least one common rainforest tree in northwestern North America, western hemlock (*Tsuga heterophylla*), even including its distribution in interior rainforests of northwestern North America (Gavin and Hu 2006). In the absence of detailed models and global spatial coverages, a more inclusive definition was proffered by Alaback (1996). In this case, temperate rainforests meeting the original criteria for annual rainfall were divided into four subtypes (or zones, including boreal), analogous to subtypes of tropical forests, based on seasonality of precipitation and annual temperatures:

- *Subpolar*—summer rainfall is above 20 percent of the annual total, summers are cool, and snow is persistent in winter, with mean annual temperature below 4°C.
- *Perhumid*—summer rainfall is above 10 percent of the annual total, summers are cool, and typically transient snow is present in winter, with

mean annual temperature of 7°C. "Cool-temperate" also has been used in this context.

- *Seasonal*—summer droughts and fires can periodically occur, summer rainfall is less than 10 percent of the annual total, with mean annual temperature of 10°C.
- *Warm-temperate*—summer precipitation is less than 5 percent of the annual total, winter snow is rare, drought can occur during any season, and mean annual temperature is 12°C or above (Alaback 1996; Veblen and Alaback 1996; Alaback and Pojar 1997).

The threshold values of temperature and precipitation for each of the forest subtypes was determined by examining climatic conditions in areas along the west coast of North and South America that possessed key ecological characteristics associated with rainforests. This has been the prevailing set of definitional parameters for describing rainforest regions used throughout the chapters of this book.

A NEW GLOBAL RAINFOREST MODEL

Building on concepts from Alaback (1991), we developed a strongly organism/ecosystem–driven model for temperate and boreal rainforests that has identified a very small amount of land surface of the earth within the same biome and sharing climatic characteristics and associated ecological processes that rightfully and generally can be called temperate and boreal rainforest. The processes described herein build on earlier work of rainforest ecologists by providing a broad suite of climatic criteria and a standardized approach to mapping rainforests globally.

In this chapter, we use computer modeling to develop defensible criteria for identifying temperate and boreal rainforests and to locate forests not widely recognized as rainforest but meeting our criteria. Further, we create a computer model with high-resolution climate data and compare it to maps created by regional experts.

Rainforest Distribution Model

This book's chapter authors, from a wide range of rainforest regions, provided locations of sites they considered typical of temperate or boreal rainforest in their area. Based on this input, we used climate data for 117 localities from six regions for the initial modeling step: the Pacific Coast of North America (*n* = 55, mostly coastal); Chile and Argentina (*n* = 9); New Zealand (*n* = 10); Tasmania (*n* = 6); Norway (*n* = 15); and Japan (*n* = 22). These regions were selected because we had localities from collaborators, and because there was little dispute that the locations represent rainforests (especially the Pacific Coast of North America, Chile, and New Zealand). Baseline predictors were extrapolated from a global climate data set (Hijmans et al. 2005); redundancy in the model variables was reduced based on a principal-components analysis of the complete data set. The final model was constructed using a MaxEnt modeling approach (Phillips et al. 2006), consisting only of predictors that improved the model. This yielded 11 discrete climate-related parameters. We used the MaxEnt model since it is known to be more conservative compared to other presence-only models, which tend to overestimate occurrence of a particular variable of interest (in this case, temperate and boreal rainforest).

The model was evaluated with a bootstrapping method (Burnham and Anderson 2002), resulting in strong support of the predictive ability of the model (*AUC* = 0.90; values less than 0.5 indicate no predictive capabilities; see Phillips et al. 2006). Based on 100 repeated runs, we quantified the heterogeneity of the ground-truth climate data set, thus ensuring a demarcation of core zones with a high probability of rainforest occurrence in comparison to areas with a lower probability (for mapping simplicity, only high-probability areas were depicted).

The rainforest distribution model generated four additional regions with climate suitable for temperate and boreal rainforests: the Inland Northwest of North America (figure 1-1, middle-right portion of panel a—inland British Columbia), Eastern Canada (figure 1-1, panel b), Great Britain and Ireland (figure 1-1, western corner of panel d), and portions of the Alps (figure 1-1, lower middle of panel d). Notably, two of these regions have not been widely recognized as rainforest by scientists, including the wettest parts of Eastern Canada, which appeared in some form in all map iterations, and some valleys of the eastern Alps, in particular the Salzburg Alps and mountain ranges of western Slovenia. Interestingly, these regions support rainforest lichen assemblages remarkably similar to those of the Pacific Northwest of North America or coastal Norway.

Two lower-latitude regions often considered rainforest by some (e.g., Kellogg 1992), such as the Colchic (Georgia) and Hyrcanic (Iran) forests of the Western Eurasian Caucasus, and the forests of the southern cape of South Africa, were shown to be in a class of their own compared to the more definitive rainforests of the Pacific Coast of North America and Valdivia. Including these warmer and drier outliers in the model calibration invariably resulted in overestimating the global extent of these rainforests by also including South

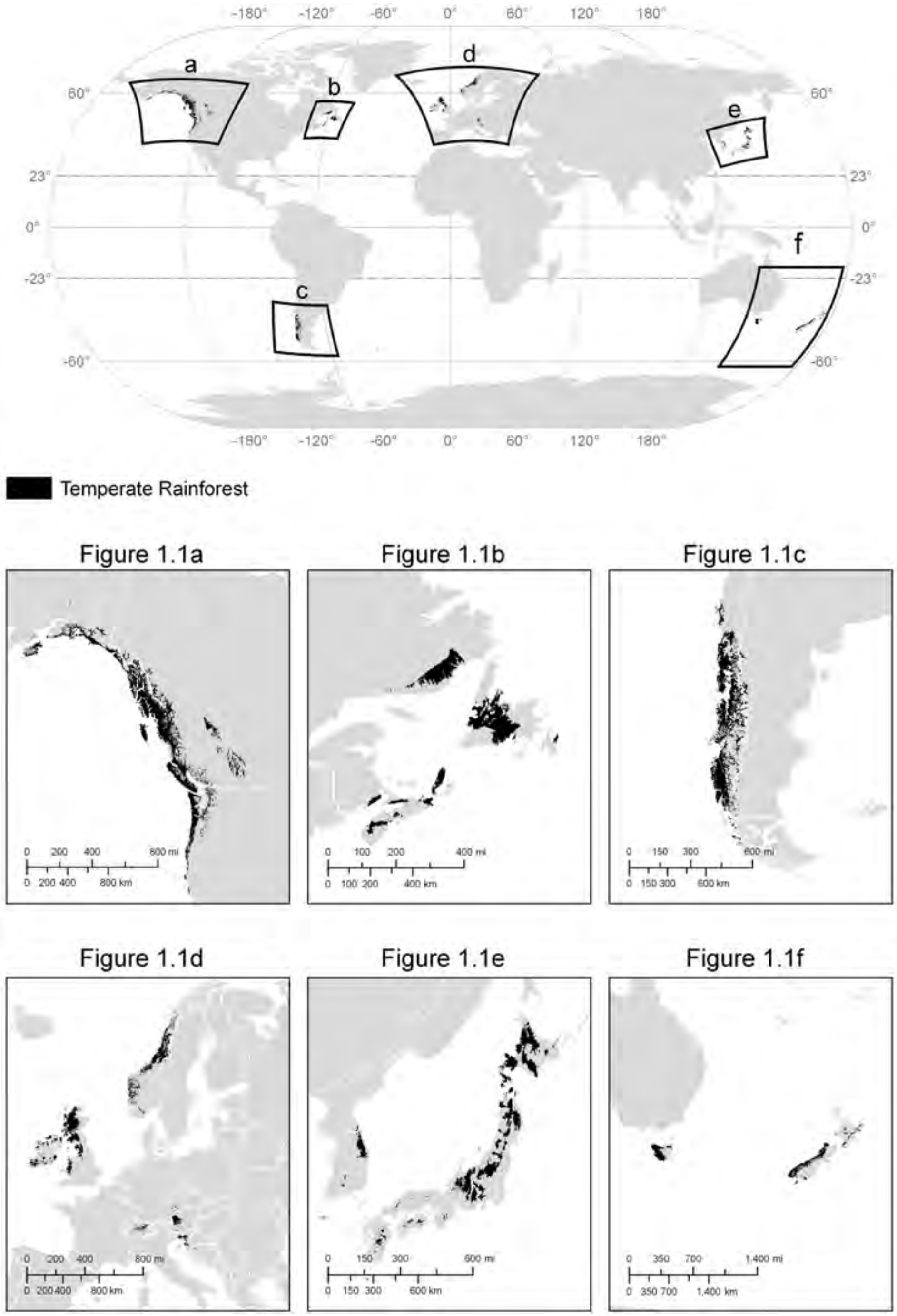

Figure 1.1a

Figure 1.1b

Figure 1.1c

Figure 1.1d

Figure 1.1e

Figure 1.1f

Figure 1-1. Temperate and boreal rainforests of the world based on the global rainforest distribution model, including: (a) Pacific Coast and Inland Northwestern North America; (b) Eastern Canada; (c) Chile and Argentina; (d) Europe; (e) Japan and Korea; and (f) Australasia.

American páramo, high-elevation African equatorial fog forests, and nearly half of the Alps. Retention of the eastern Black Sea region (Colchic), in particular, resulted in model inclusion of large areas of eastern North America, parts of which are indeed climatically similar, but did not agree with our initial criteria on several counts. We settled on a conservative definition of temperate and boreal rainforest based generally on the climate data (see table 1-1; figures 1-2, 1-3) presented for nine regions (some were combined from the set above) as follows:

- Annual (minimum, maximum) temperatures from ~4 to 12°C.
- Annual (minimum, maximum) precipitation from 846 to 5,600 millimeters.
- Snowy winters in high latitudes.
- Significant precipitation (that is, up to 25 percent of annual precipitation) during the driest quarter.
- Low annual temperature fluctuation (based on low annual temperature variability).
- Temperature of warmest quarter (summer) from 7 to 23°C.

This is the first time a spatially explicit global data set was made available for the world's temperate and boreal rainforests that was based on a suite of climate variables obtained from a global data set (available in raster—or grid—GIS format), improvements in computer processing capacity, and statistical models. The model therefore represents an initial cut at producing a global rainforest map, requiring further refinements through the use of regional climate data sets, regional rainforest classifications, and regional maps. Notably, while the minimum precipitation and maximum temperature values reported seem extreme in comparison to earlier rainforest definitions, rainforest communities persist in these regions due to compensatory factors as discussed below and in the regional chapters of this book. This is why regional ground-truth of the model and further study of rainforest classifications are essential.

CLIMATIC PATTERNS OF TEMPERATE AND BOREAL RAINFORESTS

Based on the rainforest distribution model, rainforests were clustered along precipitation and temperature gradients that distinguished them from one another and other forest types.

Table 1-1. Abiotic conditions (climate, altitude) of temperate and boreal rainforests used in the rainforest distribution model, based on a global climate data set.[a]

Model Variable[b]		**Norway**	**Great Britain**	**Inland Northwest of North America**	**Eastern Canada**	**Alps**	**Pacific Coast of North America**	**Japan and Korea**	**Chile and Argentina**	**Australasia**
Mean Diurnal Range (mean of monthly; max temp–min temp; °C)	Min	3.9	5.4	9.2	7.0	6.3	4.3	5.8	4.2	6.1
	Max	7.3	7.6	12.1	11.9	10.4	11.9	11.1	12.1	11.4
	Mean	6.1	6.6	10.8	8.9	8.9	7.6	8.6	7.2	8.9
Isothermality (diurnal temperature/annual range of temperature, °C)	Min	24.1	30.4	27.6	22.3	27.8	24.9	19.2	42.8	44.1
	Max	31.2	42.2	33.2	32.3	34.6	63.6	31.9	60.1	52.2
	Mean	27.9	36.4	30.2	25.9	31.8	33.4	25.1	48.3	47.6
Mean Temperature of Driest Quarter (°C)	Min	–0.9	5.5	–0.1	–11.1	–4.8	–7.0	–14.8	1.2	–1.0
	Max	9.3	13.6	15.2	15.0	15.1	17.9	10.5	16.2	15.2
	Mean	5.4	9.3	3.2	1.7	0.4	9.9	–2.6	9.9	10.0
Mean Temperature of Warmest Quarter (°C)	Min	10.3	10.3	10.8	10.4	10.9	9.9	10.6	6.8	6.8
	Max	14.8	15.2	17.9	18.7	19.5	17.9	22.8	16.3	17.8
	Mean	11.5	12.9	13.5	13.6	15.4	12.5	17.9	11.9	13.2
Precipitation of Driest Quarter (mm)	Min	124	169	106	162	188	6	97	74	143
	Max	447	352	198	399	317	619	487	1378	1169
	Mean	262	248	152	248	245	252	233	499	458

Table 1-1. Continued

Model Variable[b]		**Norway**	**Great Britain**	**Inland Northwest of North America**	**Eastern Canada**	**Alps**	**Pacific Coast of North America**	**Japan and Korea**	**Chile and Argentina**	**Australasia**
Precipitation of Coldest Quarter (mm)	Min	210	244	187	209	209	125	97	230	241
	Max	859	697	458	439	388	1473	506	1403	1803
	Mean	428	431	267	309	269	642	263	801	613
Altitude (m)	Min	25	74	356	86	284	0	69	0	4
	Max	754	842	1487	1319	1548	1263	2612	1066	2334
	Mean	327	314	973	267	826	364	811	278	580

[a] See Hijmans et al. 2005.

[b] Annual mean temperature, temperature annual range, annual precipitation, and precipitation seasonality (coefficient of variation) were included in the model but not in this table as the data are summarized in figures 1-2 and 1-3.

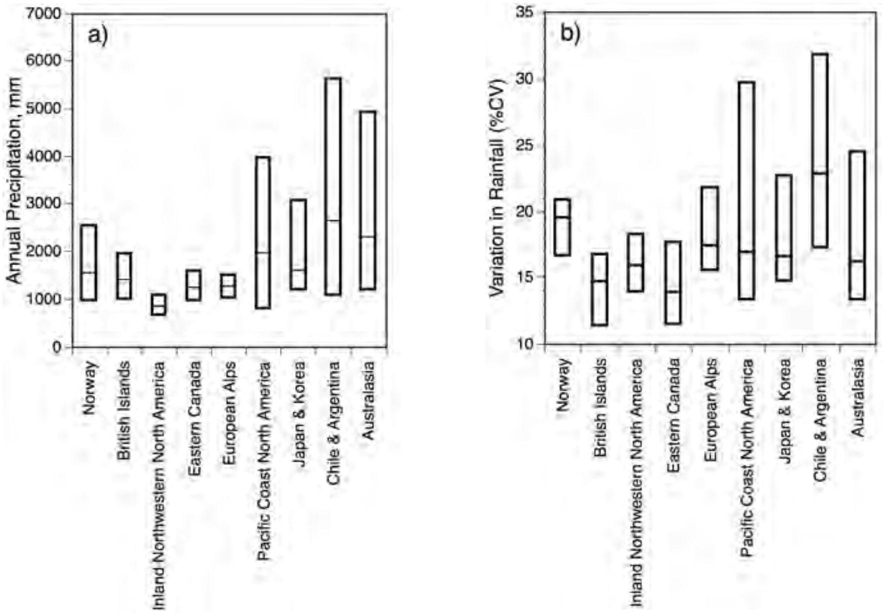

Figure 1-2. Annual precipitation (a) and variation in rainfall (b) of definitive temperate and boreal rainforests, based on a global climate data set (Hijmans et al. 2005) and the rainforest distribution model.

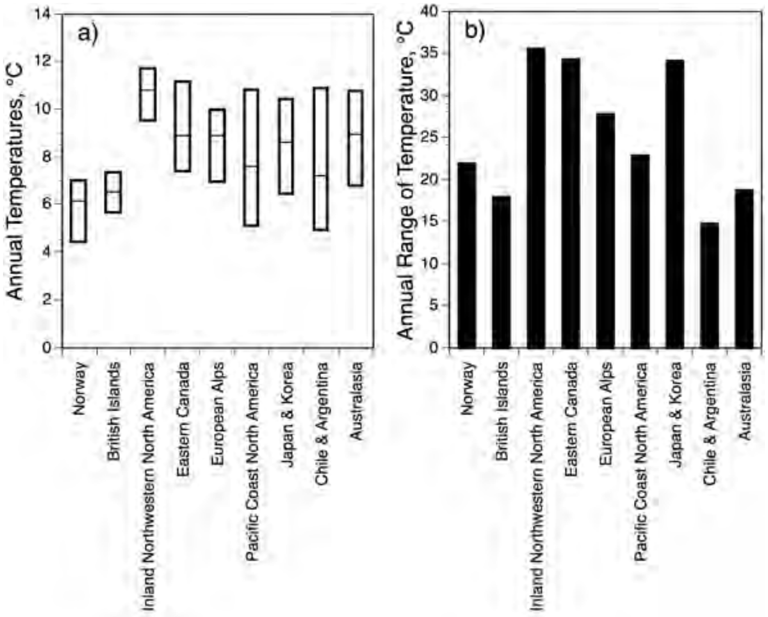

Figure 1-3. Annual temperature (a) and annual range of temperature (b) of definitive temperate and boreal rainforests, based on a global climate data set (Hijmans et al. 2005) and the rainforest distribution model.

Precipitation Gradient

A broad range of annual rainfall amounts occurs in the "classic" temperate rainforests of the Pacific Coast of North America, Chile and Argentina, and Australasia (see figure 1-2a). As in tropical rainforests, seasonality of precipitation is a key element of rainforest climate that can influence rates of decomposition, the roles of fire, drought, epiphytes, and species composition (Alaback 1996; Losos and Leigh 2004). Just looking at the coefficient of variation of monthly precipitation shows the greatest range in the rainforest regions with the greatest latitudinal ranges (e.g., the Pacific Coast of North America, Chile and Argentina) and also the greatest seasonality, but a less clear pattern in the seasonality of precipitation in smaller regions (see figure 1-2b). More work is needed to clarify how seasonality of precipitation helps effect such differences among rainforest regions.

Temperature Gradient

Based on the global climate data set, Norway had the coolest annual temperature and Inland Northwestern North America (based on southern locales) the warmest (see figure 1-3a). Notably, climate data sets derived from a global reference (Hijmans et al. 2005) may differ from data sets presented in the regional chapters due, for instance, to topographical influences on local climate and the location and density of weather stations.

The comparatively wide range of annual temperatures on the Pacific Coast of North America and in the Valdivian temperate rainforest reflects both its broad latitudinal distribution and a large range in climates from boreal and subpolar to nearly subtropical. Similarly, the Japanese archipelago spans many climate types (alpine to subtropical, and continental to oceanic), with rainforests distributed zonally.

The annual range of temperature provides a good measure of seasonality of a given region (see figure 1-3b). The regions with the greatest influence from interior climates, such as Inland Northwestern North America, Eastern Canada, Japan, and Korea, all clearly show this influence. The more oceanic climates, such as Norway, the British Islands, and the Southern Hemisphere rainforests, by contrast show a much smaller range of monthly temperatures. This also helps explain why some of the forests in these regions can develop rainforest characteristics with less rainfall than in comparable continental regions.

In sum, rainforests can be grouped both by differences in annual temperature and annual precipitation, with the Inland Northwest of North America the warmest, driest rainforest globally, Norway the coolest (with moderate precipitation), and Chile, Argentina, and Australasia the wettest, with relatively cool-to-moderate temperatures.

OUTLIERS AND OTHER CONSIDERATIONS

The rainforest distribution model did not predict some areas as rainforest which, upon further inspection, showed signs of rainforest conditions or communities. We chose to include some of these as "rainforests at the margins" (or outliers), based on input from regional scientists specializing in the specific regions (see chapter 9). For instance, in some places rainforest communities can persist at precipitation levels lower than the range used in the model as long as there is enough moisture at critical times of the year (e.g., warm summer months) to support moisture-loving species such as lichens and mosses, either directly through some rainfall or indirectly through compensatory mechanisms (e.g., low evapotranspiration rates, high humidity, cool summer nighttime temperatures, and fog). Evidence for this exists for the Knysna-Tsitsikamma forests of South Africa and the Colchic and Hyrcanic forests of the Western Eurasian Caucasus, where persistent fog and high humidity compensate for low summer precipitation and/or hot summers (chapter 9). Such conditions prove suitable for oceanic lichens and humidity-dependent vegetation. The Ussuri taiga of the Russian Far East and the Sayani Mountains of Inland Southern Siberia were too dry for inclusion in the model but have relatively low temperatures and high humidity (chapter 9). Low evaporative losses apparently compensate for drier conditions, allowing humidity-dependent forests to flourish.

The rainforest distribution model also did not identify rainforest in some areas previously suspected to be rainforest. For instance, while Taiwanese montane forests receive sufficient rainfall and cool-enough temperatures zonally (at high elevations) to be considered "temperate rainforest" by some (see Wikipedia[1]; also see Farjon 2005), the lack of a well-defined cool dormant season makes them more ecologically equivalent to cloud or subtropical forests (Alaback 1991), and thus we did not give further consideration to these forests. Iceland's scant boreal forests, though recognized as rainforest by Kellogg (1992), were not included in our rainforest model because the mean annual temperature is below even the minimum used to define rainforests. Icelandic forests also lack the structural complexity associated with temperate and boreal rainforests,

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[1] www.en.wikipedia.org/wiki/Temperate_rain_forest

such as well-defined canopy layers and gap-phase disturbance dynamics, as trees usually are not long-lived or productive due to severe weather. There are no naturally occurring boreonemoral tree species (see chapter 6) such as elms (*Ulmus* sp.) and oaks (*Quercus* sp.), and there are few of the rainforest lichens common to Norway's rainforests (e.g., *Biatora toensbergii*, *Fuscopannaria ahlneri*, and *Lobaria hallii*).

Although the Appalachian mixed-mesophytic forest of the southeastern United States has been recognized as temperate rainforests by some (see Netencyclo.com[2]; Shanks 1954; see chapter 4), it was not predicted by the rainforest distribution model, presumably because the region has relatively high year-round temperatures and dry summers. However, because there was evidence of rainforest conditions at high elevations (moist pockets of spruce-fir within the larger ecoregion), we briefly mentioned them as a southerly extension of Appalachian boreal rainforests from Eastern Canada that require further study (see chapter 4). In sum, we hope the techniques used here will inspire additional research into these areas in order to further refine our approach.

INTRODUCING TEMPERATE AND BOREAL RAINFORESTS

In the following sections of this book, we discuss seven definitive regions (some regions from above were combined) identified by the model and three outlier regions that collectively make up the global network of temperate and boreal rainforests.[3] We generally organized regions north to south (Western Hemisphere) and west to east (Eastern Hemisphere), as presented sequentially as the book's regional chapters.

Definitive Regions

- Pacific Coast of North America (chapter 2)
- Inland Northwestern North America (chapter 3)
- Eastern Canada (chapter 4)
- Chile and Argentina (chapter 5)
- Europe: Norway, Ireland, Great Britain, portions of the Alps, the Bohemian region, and the Balkans (chapter 6)
- Japan (chapter 7—note that Korea was included in the Russian Far East and Inland Southern Siberia profile, based on author expertise)
- Australasia: Australia, Tasmania, and New Zealand (chapter 8)

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[2] www.netencyclo.com/en/Temperate_rain_forest

[3] Maps available at www.databasin.org

Outliers (chapter 9)

- Western Eurasia Caucasus (Colchic and Hyrcanic forests)
- Russian Far East and Inland Southern Siberia
- South Africa (Knysna-Tsitsikamma forests)

REGIONAL VS. RAINFOREST DISTRIBUTION MAPS

While the global model was useful in predicting general locations of temperate and boreal rainforests, we often found differences in global projections versus regional delineations made by local experts (see table 1-2). Thus, comparing predicted distributions with regional maps was necessary to ensure that an agreed-upon set of maps was used in the regional chapters. Digital maps for this step were obtained for the Pacific Coast of North America (Kellogg 1995; see figure 4), Inland Northwestern North America (Craighead and Cross 2007), Eastern Canada (described below), Chile and Argentina (provided by Patricio Pliscoff—see below), Australasia (Kirkpatrick and Dickerson 1984), Japan (Miyawaki et al. 1980–89), and Norway (described below). Here, we describe the differences in mapping delineations and reasons for including regional maps, where we had them, in the chapters of the book that follow.

Pacific Coast of North America

Differences in mapping estimates between the global model and regional mapping (Kellogg 1995) were fairly minor (see table 1-2; figure 1-4). The rainforest distribution model yielded a rainforest estimate that was ~9 percent higher than regional mapping (see table 1-2). We present the map by Kellogg (1995) in Chapter 2 because it allowed us to base conservation priorities on regionally specific zones (finer scale) that were not apparent from the coarser rainforest distribution model.

Inland Northwestern North America

The model predicted rainforest to occur on nearly 2.2 million hectares, but only for eastern British Columbia (see figure 1-5; table 1-2). In comparison, using the distribution of western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) (i.e., Interior Cedar Hemlock forests) yielded over 3 times the amount of rainforest at 7.3 million hectares (Craighead and Cross 2007; see chapter 3), with nearly equal amounts in British Columbia and the United States. While the rainforest distribution model and the vegetation-based map showed strong agreement in British Columbia, the Interior Cedar Hemlock

Table 1-2. Global (rainforest distribution model, Kellogg 1992) and regional (based on digital maps from published sources) estimates for temperate and boreal rainforests.

	Rainforest distribution model		Regionally based estimates[a]	Kellogg (1992)	
Region	**(ha)**	**(%)**	**(ha)**	**(ha)**	**(%)**
Pacific Coast of North America[b]	27,274,225	35.0	25,097,930	20,726,700	50.3
Inland Northwestern North America					
British Columbia	2,179,733	2.8	3,879,730		
United States	0	0.0	3,366,874		
Total Inland Northwestern North America	2,179,733	2.8	7,246,604		
Eastern Canada	5,969,641	7.7	6,085,063		
Valdivia					
Chile	12,211,573	15.7	9,752,451	11,675,100	28.4
Argentina	348,371	0.4	2,211,888	323,300	0.79
Total Valdivia	12,559,944	16.1	11,964,339	11,998,400	29.1
European Relicts					
Iceland				195,200	0.47
Norway	4,887,739	6.3	3,747,090	1,459,000	3.5
Great Britain	5,064,759	6.5		1,149,300	2.8
Ireland/Republic of Ireland	1,578,545	2.0		157,300	0.38
Northeast Alps and Swiss Prealps	745,915	1.0			
Bohemia	220,199	0.3			
Southeastern Alps and Northwest Balkans	577,425	0.7			
Total European relicts	13,074,582	16.8		2,960,800	7.2
Japan and Korea	8,295,241	10.6	2,404,404		
Australasia					
Australia	55,989	0.07	1,652,933		
New Zealand	5,458,170	7.0	4,969,590	4,040,400	9.8
Tasmania	3,132,684	4.0	692,300	551,700	1.3
Total Australasia	8,646,843	11.1	7,314,823	4,592,100	11.2
Total Rainforest	78,000,209	1.95[c]		41,177,500	1.1
Outliers[d]					
South Africa (Knysna-Tsitsikamma)	235,483	1.2			

Table 1-2. Continued

Region	Rainforest distribution model (ha)	(%)	Regionally based estimates[a] (ha)	Kellogg (1992) (ha)	Kellogg (1992) (%)
Western Eurasia					
Hyrcanic	1,960,000	10.3			
Colchic[e]	3,000,000	15.8		899,500	2.2
Total Western Eurasia	4,960,000	26.1			
Russia/Siberia					
Russian Far East	6,800,000	35.8			
Inland Southern Siberia	7,000,000	36.9			
Total Russia/Siberia	13,800,000	72.6			
Total Outliers	18,995,483	0.47[c]			
Combined temperate and boreal rainforest total	96,995,692	2.42[c]			

[a] Regional estimates were provided for comparisons to the rainforest distribution model but, due to differences in mapping methodologies, did not include percentages except in the case of Kellogg (1992), which was based on more consistent mapping methodologies.

[b] Differences in rainforest estimates between the two Kellogg references (1992, 1995) are presumed due to refinements in mapping techniques, mainly the addition of the western Cascades in Washington and Oregon, which were not included in the original maps.

[c] Percentages were derived from global forest cover (all forest types) estimated at 4 billion hectares based on FAO (2005) estimates that define forests as >10% tree cover. Plantations are included in estimates.

[d] Outlier estimates, provided by regional authors, were derived from different mapping methodologies not directly comparable to rainforest distribution estimates or other regional estimates.

[e] Kellogg (1992) lists this region as Eastern Black Sea (Turkey, Georgia).

map extends this rainforest type southward for roughly 430 kilometers into northeastern Washington, northern Idaho, and northwestern Montana (see figure 1-5a). Based on local knowledge, we choose the map of Interior Cedar Hemlock forests for Chapter 3.

Eastern Canada

For this region, we overlaid the Thornthwaite (1948) index for perhumid regions (100+ moisture index) onto digital layers of vegetation obtained from coniferous and mixed forest types (source: Canadian Vegetation and Land Cover data set, www.nrcan.gc.ca). This shapefile is based on satellite data obtained in 1995 by the Advance Very High Resolution Radiometer

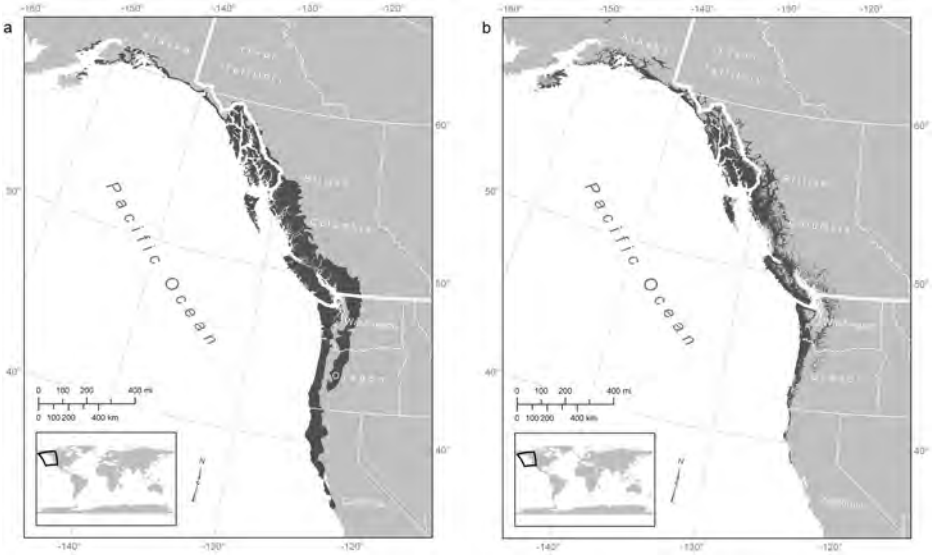

Figure 1-4. Temperate and boreal rainforests of the Pacific Coast of North America based on (a) regional mapping (Ecotrust 1995) and (b) the rainforest distribution model.

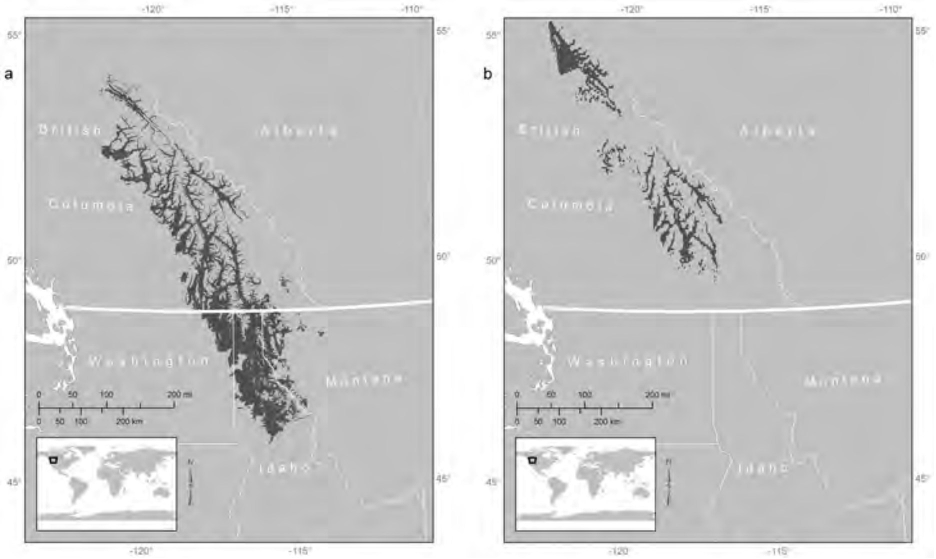

Figure 1-5. Temperate and boreal rainforests of Inland Northwestern North America based on (a) regional mapping (Craighead and Cross 2007) and (b) the rainforest distribution model.

(AVHRR) on board the NOAA-14 (National Oceanic and Atmospheric Administration) satellite. We assumed these forest types were most likely to include important lichen assemblages and rainforest structure that matched perhumid climatic conditions in the region.

Both the rainforest distribution model and regional map (Thornthwaite 1948) yielded nearly identical area estimates (see table 1-2). However, predicted locations of rainforests from the rainforest distribution model vs. regional mapping differed appreciably (see figure 1-6). Thus, we used the regional map in

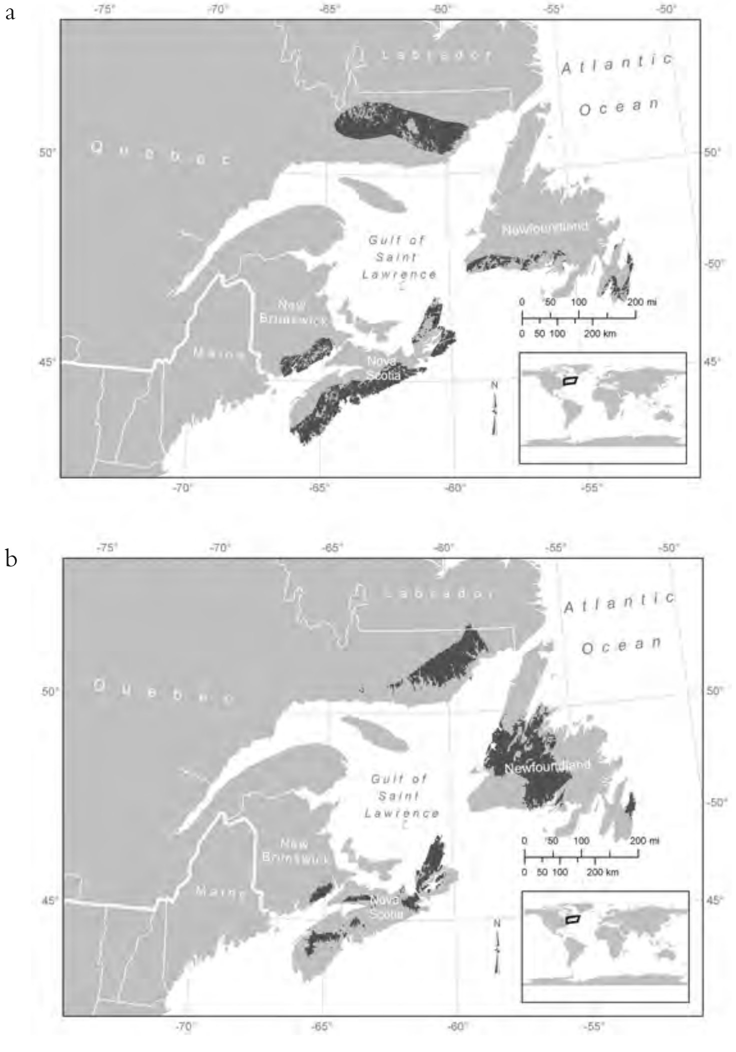

Figure 1-6. Perhumid boreal and hemiboreal rainforests of Eastern Canada based (a) on regional mapping (modified from Thornthwaite 1948) and (b) the rainforest distribution model.

Chapter 4 because it was thought to have higher predictability and greater concordance with forests supporting rainforest lichen assemblages based on local knowledge.

Chile and Argentina

The primary map source for Chile was the national vegetation survey. This was originally produced using aerial photography at a scale of 1:50,000 and with varied level of verification on the ground. Later updates to this information were produced using Landsat imagery and essentially serve to track loss of forest cover. As a representation of forest cover, the national vegetation survey is widely used in Chile, is embraced the official source by Chile's Native Forest Law of 2008, and is fairly reliable. For Argentina no such forest survey exists; thus we used the same criteria and methods from Chile's national survey and a series of aerial photos to produce a forest-cover map at 1:500,000 scale without ground verification.

The rainforest distribution model and regional map yielded similar area estimates for Valdivia (see table 1-2; figure 1-7). However, there were significant differences in rainforest locations, with the rainforest distribution model extending farther south into the Magellanic (subpolar) rainforests, considered a separate ecoregion by Chilean scientists (see chapter 5), but missing important

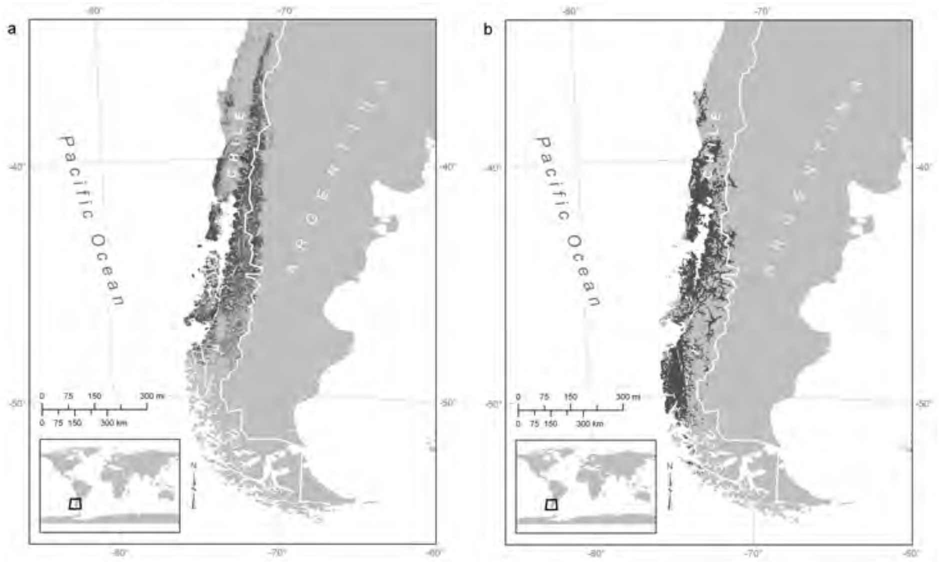

Figure 1-7. Valdivian temperate rainforests of Chile and Argentina based on (a) regional mapping (digitized from national vegetation surveys) and (b) the rainforest distribution model.

rainforest locations in the north and in Argentina. Notably, because the Magellanic forests can be considered rainforest by the standards set forth herein, regional authors included some mention of them in Chapter 5. We used the regional map in Chapter 5 because it is widely accepted in regional conservation planning.

Europe

Norway was the only regional map available for comparisons to the rainforest distribution model in Europe. The regional map in this case was based solely on floristic data, namely distribution of epiphytic lichens housed at the Norwegian Lichen Database.[4] Notably, the core area of boreal rainforest in Norway (and Europe) is rather well outlined by the distribution of just two lichens—*Rinodina disjuncta* and *Pyrrhospora (Lecidea) subcinnabarina*—also known from the Pacific Coast of North America (see Tønsberg 1992, 1993; Sheard 1995). The distribution of three other lichens demark the northern and southern limits, with *Lobaria hallii* delimiting boreal forests with occurrences in ravines and by waterfalls, and *Leptogium burgessii* and *Pyrenula occidentalis* the southern boreonemoral (temperate) rainforests.

The rainforest distribution map of Norway estimated about 1.1 million hectares (~30 percent) more rainforest than the estimate generated by regional authors (see table 1-2; figure 1-8). In this case, the rainforest distribution model may have correctly predicted conditions suitable for rainforests but local differences in soils, wind exposure, or human disturbance may preclude rainforest development. Therefore, the Norway regional map was used because it was prepared with regional forest inventories based on known rainforest lichen assemblages (see chapter 6).

Japan

About 5.9 million hectares (over 3 times) more rainforest was estimated by the rainforest distribution model compared to a digitized map of Japan's rainforest zones (see table 1-2); figure 1-9), which were based on finer-scale mapping and therefore used in Chapter 7.

Australasia

About 1.3 million hectares (18 percent, table 1-2) more rainforest was predicted by the rainforest distribution model compared to regional mapping (see figure 1-10). Differences were greatest for Tasmania, where the rainforest

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[4] www.nhm.uio.no/botanisk/lav/index.html

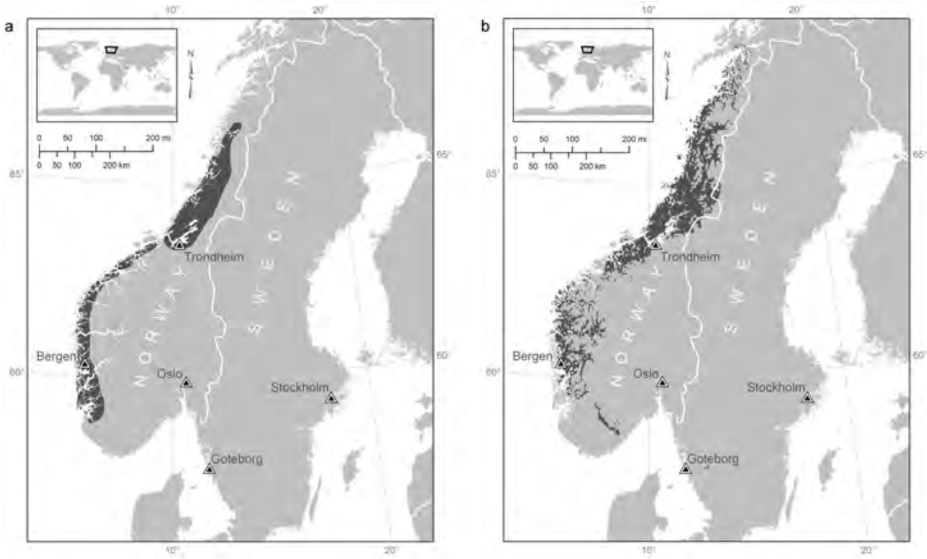

Figure 1-8. Boreal and boreonemoral rainforests of Norway based on (a) regional mapping (derived from lichen distribution maps) and (b) the rainforest distribution model.

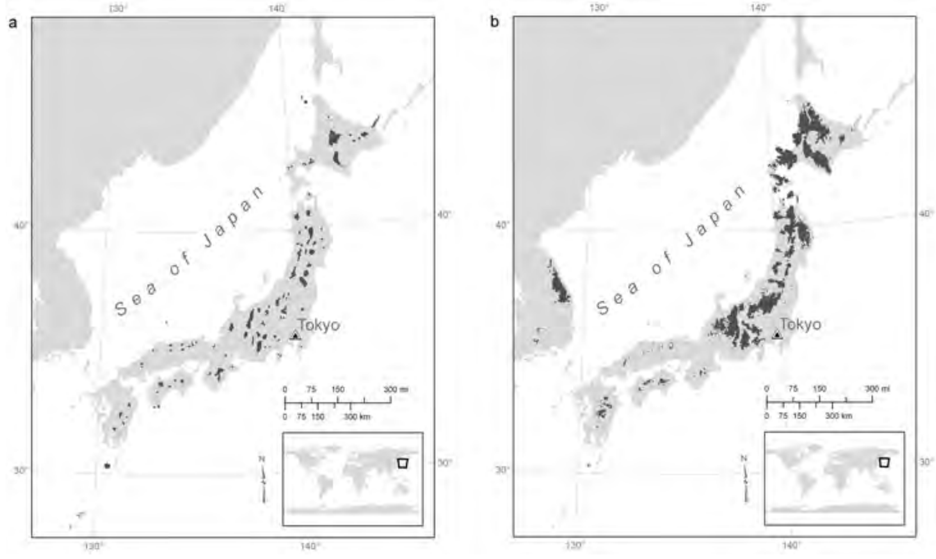

Figure 1-9. Temperate rainforests of Japan based on (a) regional mapping (Miyawaki et al. 1980–1989) and (b) the rainforest distribution model.

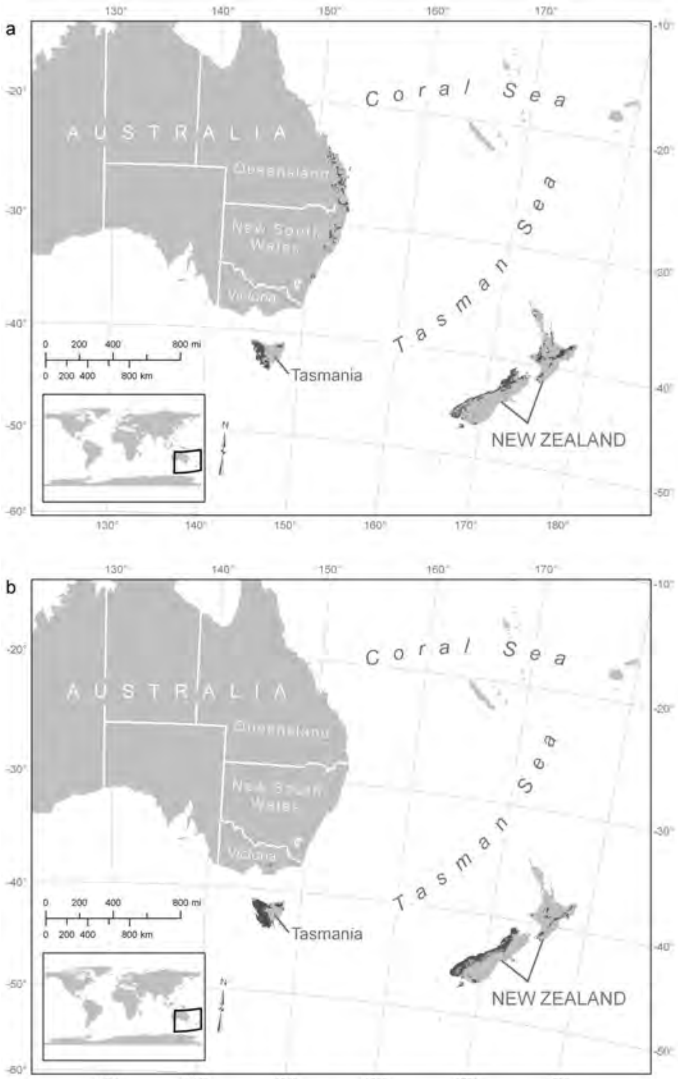

Figure 1-10. Temperate rainforests of Australasia based on (a) regional mapping (Kirkpatrick and Dickerson 1984) and (b) the rainforest distribution model.

distribution model estimated about 2.4 million hectares (over 4 times) more rainforest than the regional map. Conversely, the rainforest distribution map estimated about 1.6 million hectares less rainforest along the Australian coastline (New South Wales). Notably, about 151,173 hectares and 830,769 hectares of the regionally based totals (Kirkpatrick and Dickerson 1984) were classified as clear felled or forests patchily distributed, respectively, at the time. So the overestimate of rainforest by the model may have been partially compensated by the mapping of cleared forests by regional experts. Because the regional maps included more of the Australian coastline where rainforests are known to occur, they were used in Chapter 8.

In sum, the rainforest distribution model was useful in establishing an objective upper range of potential rainforest, was the only standardized data set available for comparisons among regions, and provided a reliable global rainforest total. However, the model had a tendency to overestimate rainforest extent in most, but not all, regions when compared to site-specific mapping and regional expertise. The rainforest distribution model was potentially confounded by human disturbance and local site conditions. Rainforest estimates derived from regional maps, however, also have limitations, as they cannot be compared among regions due to differences in mapping techniques, data sources, and mapping scales. Thus, in making relative comparisons among regions and predicting new localities, the global rainforest distribution model performs quite well; however, for regional specificity we relied on regional maps, as they had a higher degree of reliability at that scale. Follow-up mapping assessments and modeling is recommended in both cases—regionally and globally—to improve rainforest estimates and mapping techniques.

TEMPERATE AND BOREAL RAINFOREST TOTALS

Based on the rainforest distribution model, the Pacific Coast of North America (British Columbia and the United States combined) by far contains the most expansive temperate and boreal rainforests globally, representing over one-third of the world's totals (see table 1-2). Our estimate for this region is notably less than prior estimates (50 percent). Differences are due largely to rainforest areas added in the rainforest distribution model and different mapping techniques, which obviously affected regional totals. Nonetheless, in decreasing order, rainforest extent was then highest for European rainforest relicts (disjunctly distributed); Chile and Argentina; Australasia; Japan; Eastern Canada; and Inland Northwestern North America. However, these percentages do not indicate intactness of rainforests within a given region. For instance, some of the last remaining large blocks of temperate rainforests in the world occur in Valdivia, Tasmania, and New Zealand (see chapters 5 and 8), in comparison to highly fragmented European relicts (see chapter 6); and some of the most intact old-growth rainforests occur in the British Columbia and Alaska (see chapter 2). However, regional totals are not affected by conservation status.

In addition to definitive regions, outliers added nearly 19 million hectares to the global temperate and boreal rainforest total (roughly 0.5 percent), with the Russian Far East and Inland Southern Siberia by far containing the largest (73 percent) expanse and South Africa the smallest (~1 percent, table 1-2).

In sum, our estimate for global temperate and boreal rainforest extent (2.42 percent) was more than twice that of previous estimates (1.1 percent; Kellogg 1992), due largely to additional regions estimated by the rainforest distribution model and differences in mapping techniques. However, some regions (Iceland) previously considered rainforest (Kellogg 1992) were not included here as they do not appear to support rainforest communities. Nonetheless, despite these differences there was considerable overlap in regional estimates, with the net result that temperate and boreal rainforests still represent just a fraction of the global forest cover.

RAINFOREST DIFFERENCES IN THE NORTHERN AND SOUTHERN HEMISPHERES

In this section, we examine major differences in gross rainforest characteristics that can be readily grouped by differences in biogeography between hemispheres where these rainforests are found.

Northern Hemisphere

Temperate and boreal rainforests in the Northern Hemisphere are remarkably similar in species composition, at least at the genus level. The largest of these rainforests in terms of areal extent are dominated by conifers (e.g., Pacific Coastal and Inland Northwest North America, parts of Japan, Norway), usually broadly distributed but closely related species of the pine family, including hemlock, true firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menzeisii*), spruce (*Picea* spp.) or pine (*Pinus spp.*), and species of Cupressaceae, especially red cedars (*Thuja* spp.). Other, smaller regions are dominated especially by beeches (*Fagus* spp.; found in Japan and central European fragments) or beech-spruce mixtures (found, for example, in Norway). In general, temperate and boreal rainforests of the Northern Hemisphere have a dense understory of largely deciduous woody shrubs, a variety of widely distributed (often circumboreal) herbaceous plants and a thick mat of bryophytes (mosses and liverworts), lichens, and many fern species. The broad commonalities among these rainforests make sense from a biogeographical standpoint, since the floras of the Northern

Hemisphere are believed to have been derived in large part from common Tertiary ancestors 60–80 million years ago (see Axelrod 1976).

Southern Hemisphere

In Southern Hemisphere rainforests (southern Chile, Argentina, New Zealand, Tasmania and nearby areas), most trees are broad-leaved evergreens, which form a patchy canopy with many layers beneath the dominant overstory, including a broad diversity of both evergreen and deciduous trees and shrubs. The trees are tall and dense, with small tough leaves (Veblen et al. 1996).

Southern vs. Northern Hemisphere

Southern Hemisphere trees are unlike most of the familiar broad-leaved trees in the North. The "southern beech" or *Nothofagus* trees, for example, are not closely related to beeches of the Northern Hemisphere. They are in their own family (Nothofagaceae) and originated in ancient Gondwana before it split into what have become the small areas of temperate rainforest scattered across the Southern Hemisphere (Veblen et al. 1996). This explains why there are many species of trees that are shared at least at the genus level among rainforests in New Zealand, South America, and Australia (Ezcurra et al. 2008). Another big surprise is in the pine family. While pines, spruces, firs, and related species dominate high-latitude forests of the Northern Hemisphere, this entire family is absent in the Southern Hemisphere (Lusk 2008). The principal tree families shared are the most ancient ones, such as the cedars and cypress species (family Cupressaceae), that were well developed before the continents split apart.

While the Northern Hemisphere is dominated by conifers in the pine family (Pinaceae), trees in temperate rainforests of the Southern Hemisphere belong to a wide assortment of mostly small, specialized families. Among these, the myrtle family (Myrtaceae) is often the most diverse. Some other, more-modern families are also shared between the Northern and Southern Hemispheres, such as the heath and heather family (Ericaceae). In this case, these plants are particularly well adapted to cool, moist conditions, either alpine or subalpine, and have apparently been able to disperse along the Rockies and Sierra Madre in North America down the Andes all the way to Tierra del Fuego. The crowberry (*Empetrum nigra*), for example, has black berries in rainforests of the Northern Hemisphere, but red berries in the Southern Hemisphere (*E. rubrum*), and otherwise looks very similar between hemispheres. The occurrence of these two families may be, in part, attributable to dispersal of the seeds by migratory birds moving between hemispheres, a prospect that also has been proposed for some lichens. A striking exception to the pattern of divergence is the case of an increasing number of possibly relictual lichen lineages being discovered to be shared between the Pacific Coast of North America and Tasmanian and/or Valdivian rainforests (Spribille et al. 2010). However, the overwhelming pattern is one of disparity, with contrasting assemblages recurring with bryophytes, most nonmigratory birds, mammals, fishes, and insects. Why are these forests so taxonomically different between hemispheres? Let's explore some of the leading hypotheses.

Continental Drift and Isolation

This is generally considered the key factor explaining hemispheric differences. While the continents in the Northern Hemisphere were well connected many times in the past, including as recently as a few tens of thousands of years ago during glacial cycles, in the Southern Hemisphere many of the land masses that now have temperate rainforests have been isolated from each other since the late Tertiary period (over 60 million years ago—see Lawford et al. 1996; Veblen et al. 1996; Arroyo et al. 2000). This has lead to adaptive radiation events in species with ancient lineages, resulting in many unique forms (endemics).

Geography

Most of the Southern Hemisphere is dominated by ocean, and at the high latitudes land masses are highly fragmented and have been since the upper Tertiary some 2 million years ago, when the rainforest zone became progressively isolated by xeric climates to the east and north triggered by the uplift of the Andes (Arroyo et al. 1996). Thus, most temperate rainforests have milder winter climates with rainfall evenly distributed over the growing season. This unique climate leads to a more subdued role for wildfire and to a more limited adaptation to extreme cold. Even subalpine species from the Southern Hemisphere are generally not hardy enough to survive in continental rainforests of the Northern Hemisphere (Lawford et al. 1996; Veblen and Kitzberger 2002).

Endemism

The vast majority of species in temperate and subpolar rainforests of the Southern Hemisphere are unique to each continent (South America, Africa, and Australasia), and sometimes to a specific area due to their relictual taxonomic status and long periods of isolation (Lawford et al. 1996; Smith-Ramirez 2004; Hinojosa et al. 2006; also see chapters 5 and 8). By contrast, in the Northern Hemisphere fewer species are limited to specific habitats or areas, although island biogeographical effects in northern coastal latitudes have triggered speciation events at the subspecies level (see chapter 2).

Species Mutualisms

Many species in the Southern Hemisphere evolved from tropical affinities (e.g., Valdivia—see chapter 5), including complex interactions between plants, herbivores, pollinators, and seed-dispersing species. Further, most trees in Southern rainforests produce edible fruits and have co-evolved with seed-dispersing animal species (Armesto et al. 1996). In contrast, most rainforest trees of the Northern Hemisphere are conifers with less direct and specific co-evolution with pollinators and seed dispersers (e.g., Willson et al. 1990).

TEMPERATE AND BOREAL RAINFORESTS VS. TROPICAL MOIST RAINFORESTS

Tropical rainforests, as their name implies, are bracketed by the tropics of Cancer and Capricorn (see figure 1-11; table 1-3). They cover about 6 times more area than temperate and boreal rainforests (~2 percent versus 12 percent of the world's forests). Tropical rainforests are generally drenched in warm, moist climates with little seasonal temperature variation within 1 kilometer of sea level. On the other hand, temperate and boreal rainforests are generally but not

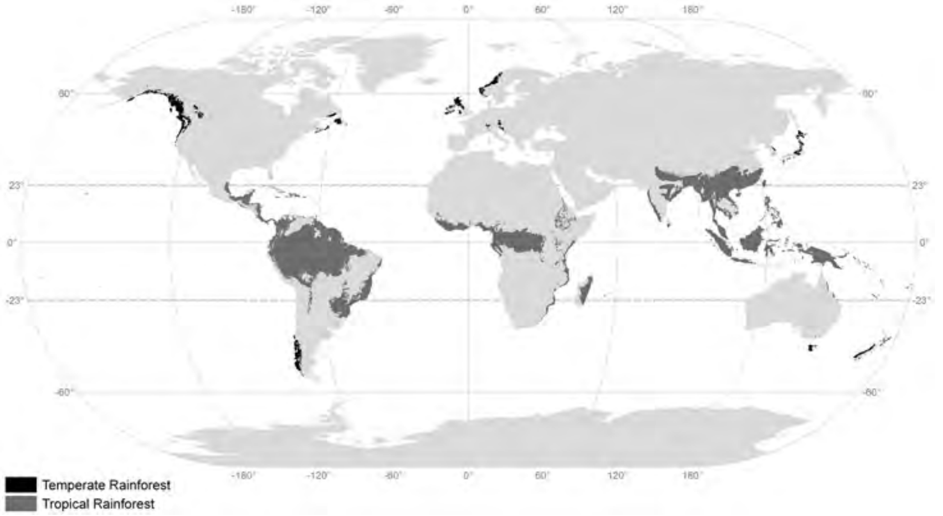

Figure 1-11. Tropical moist (Olson and Dinerstein 1998) and temperate and boreal rainforests of the world.

Table 1-3. General features distinguishing tropical moist rainforests from temperate and boreal rainforests.

Feature	Tropical Moist Rainforest[a]	Temperate and Boreal Rainforest
Distribution	up to 23° latitude from the equator: large belts across South America, Central America, Southeast Asia, and Africa	~30–69° latitude, disjunct, mainly coastal: Pacific Northwest, Alaska, British Columbia, Chile, Argentina, Tasmania, New Zealand, Australia, Japan, Europe
Extent	~12% of present global forest cover, reduced by over half of estimated historic levels	~2% of present global forest cover, reduced by ~half of estimated historic levels
Deforestation (2000–2005)	1-2% annual[b], especially high in South America and Africa, mostly converted to agriculture	forest cover generally increasing, but old growth replaced by tree plantations
Annual Mean Temperature	23–27° Celsius	~4–12° Celsius
Seasonality	uniform temperature with wide variation in rainfall patterns (up to a 3-month dry season)	varied temperatures, snow in winter, greater precipitation in fall and winter with summer rains over 14% of annual precipitation
Moisture	over 1,700 mm, high humidity, high evapotranspiration	846–2658 mm, high humidity, low evapotranspiration
Canopy diversity	multilayered, rich epiphytes (orchids, bromeliads), and abundant lianas	generally multilayered, rich epiphytes (lichens, mosses), lianas less developed
Forest height	20–50 m	10–70 m
Soils	thin litter layer, infertile and severely leached except in volcanic and riparian areas; large nutrient pools in trees	rich humus, highly productive and rich in invertebrates, large amount of coarse, woody debris
Biomass	moderate (100–250 metric tons/ha), highest in dipterocarps (Southeast Asia)	low (Europe) to exceptional (redwoods, Pacific Northwest, Tasmania, Valdivia) (100–1867 metric tons/ha)
Productivity	high-exceptional	exceptional (marine, freshwater, terrestrial)
Nutrient cycling	rapid decomposition rates	slow decomposition rates
Pollination	exceptional	low in conifers
Plant and animal richness	exceptional, over half of terrestrial species on Earth, generally 5–10 times that of temperate forests	low (Europe) to moderate (Japan, Valdivia), but high for mosses and lichens
Endemism	exceptional, many species unique	low (Europe), moderate (California), high (Chile and Argentina)
Tree richness	exceptional (50–200 species/ha)	low to moderate (1–20 species/ha)

[a] Synthesized from Terborg (1992); Richards (1996); Kricher (1997); Myers et al. (2000); and Losos and Leigh (2004).

[b] Deforestation rates based on total forest cover lost on a continental scale (FAO 2005). Individual countries with rainforest, however, may have higher or lower rates of deforestation or show afforestation due to tree planting.

exclusively found along coastlines at middle to upper latitudes, and can extend to nearly timberline (exceptions include Inland Northwest of North America, the Alps, and Inland Southern Siberia).

Climatically, temperate and boreal rainforests have a more distinctive seasonality (especially wider temperature swings), and greater range of precipitation types including snow and sleet, than tropical counterparts (see table 1-3). High temperatures in the tropics lead to high evaporation rates and the development of daily clouds above the forest, so that they can recycle 70 percent or more of their annual rainfall. Temperate rainforests, on the other hand, are cool and wet, with slower rates of decomposition and low evaporation rates. To better understand the differences between these rainforest types, we turn to some key concepts in forest ecology.

Ecologists today generally recognize that forest ecosystems are comprised of three main "ingredients": *composition*—the mix of species in a forest; *structure*—the vertical and horizontal dimensions and spatial patterns of a forest; and *function*—the workings of a forest expressed through nutrient cycling, food-web and disturbance dynamics, forest succession, pollination, and many other processes (Perry et al. 2008). The regions identified as temperate and boreal rainforest in this book have a suite of underlying characteristics along these lines that can be used to further distinguish them from each other as well as from their tropical counterparts.

Structure

Both temperate and tropical rainforests (boreal less so) have complex forest canopies composed of many canopy layers, creating dense and continuous vegetation cover that provides for rich fauna from the ground up. In both forest types, canopy gaps and emergent crowns of dominant trees create complex spatial patterns in the lower strata. A key difference in rainforest canopies is that temperate rainforests are dominated by conifers (except in the Southern Hemisphere, where they are dominated by broadleaf evergreens, and in Japan and Europe, where they can be deciduous), while tropical rainforests are dominated by broad-leaved trees enveloped by numerous lianas (Valdivia, New Zealand, Hyrcanic, and South African temperate rainforests also have lianas). Both rainforest types often have a high degree of standing dead trees (snags) and fallen logs that provide structure and habitat for scores of plant and animal species (Baker et al. 2007; Perry et al. 2008).

Function

Biomass in temperate rainforests is exceptional on a global scale, exceeding that of tropical rainforests (Smithwick et al. 2002; Losos and Leigh 2004; Keith et al.

2009; see table 1-3). For instance, one study of a young temperate rainforest in Oregon showed that it could fix as much carbon per year as some mature tropical rainforests (e.g., 36 metric tons of organic matter per hectare annually—Fujimori 1971). Another study found primary forests in Australia capable of storing up to 1,867 metric tons per hectare, the world's highest known total biomass carbon density (Keith et al. 2009). However, while tropical forests are not exceptionally carbon-dense systems, they still play the dominant role for forest contributions to global carbon cycles due to their high rates of productivity, decomposition, long growing seasons, and the large land area they still occupy.

Evergreen needles (or leaves) are a common characteristic of the vast majority of tree species that grow in temperate and boreal rainforest climates. They allow rainforest plants to photosynthesize throughout the year in most coastal temperate areas, helping to explain the high productivity of these rainforests (Waring and Franklin 1979). The mild climate of these rainforest regions may explain why most of the tallest trees in the world grow there. Examples from around the world include towering *Eucalyptus* forests in southeastern Australia, massive coastal redwoods and alerce in California and Chile, respectively, and ancient coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) of northern California and the Pacific Northwest. Finally, a continuously mild, wet climate, combined with minimal genetic losses during Pleistocene glaciations, may have played a role in maintaining the rich genetic diversity of conifer species in the Pacific Northwest but led to losses in other regions (Waring and Franklin 1979; Premoli et al. 2000).

Coastal rainforests also are productive places for marine life, with strong linkages between marine and terrestrial ecosystems (Simenstad et al. 1997). Well-known examples include the marbled murrelet (*Brachyramphus marmoratus*) of the Pacific Coast of North America, a coastal seabird that summers at sea but breeds and nests in the tops of old-growth trees; and historical links between Pacific sea-run salmon (*Oncorhynchus* sp.) and terrestrial predators such as bears (*Ursus* spp.) and wolves (*Canis lupus*), which, in the Great Bear Rainforest of British Columbia, prey upon salmon and help fertilize coastal riparian forests through their droppings (see chapter 2).

Composition

Compared to the tropics, in Northern Hemisphere rainforests plant and animal species richness is generally low, and endemism low to moderate, with some noted exceptions (see table 1-3), including island systems (e.g., Cook et al. 2001). However, lichens appear to be much more diversified at high latitudes than in the tropics (witness ~750 species for a single southeast Alaskan rainforest fjord compared to ~550 species in all of Thailand; Spribille et al. 2010). Even if many more lichens are discovered in the tropics and the relative richness gap closes, it appears that the tropics are by no means richer on the orders of magnitude that apply to some other groups of organisms. Outstandingly high levels of species richness also have been documented in basidiomycete fungi ("mushrooms") with hyper-diverse floras documented in coastal rainforests of British Columbia (Roberts et al. 2004) and over 750 macro-fungal species from a single stand of old-growth forest on a hill in rural Victoria on Vancouver Island (Češka 2009). Here, too, numbers may be far higher than in the tropics, especially of ectomycorrhizal fungal species (a type of mycorrhizae composed of a fungus sheath around the outside of root tips—Allen et al. 1995). How these numbers stack up in the long term against species numbers in the more poorly known Tropics remains to be seen, but the fact that key physiological processes for many fungal and lichen species are optimal at cool temperatures through community adaptation (Friedman and Sun 2005) suggests that, for lichens at least, the pattern may hold.

The generally low diversity of trees species in temperate rainforests, with some noted exceptions such as Valdivia and Japan (see table 1-3), should not seem too surprising, since these rainforests tend to have dense overstory canopies and occur in cloudy climates at high latitudes, leaving little light available for understory canopy layers. Many endemic plant species are associated with warm-temperate or seasonal rainforests, such as the forests in south-central Chile and northern California, as well as all rainforests that occur on islands, and other areas in the Southern Hemisphere. In addition, many moisture-adapted taxa that provide a unique physiognomy and structure closely tied to these rainforests, including epiphytic mosses, liverworts, and lichens, are associated with moist rainforest climates (Goward and Spribille 2005; see table 1-3). In these groups, endemism is locally high in Tasmania and New Zealand, Japan, Valdivia, and parts of northwest North America while it is low to nonexistent in the isolated patches of rainforest in Europe and Eastern Canada. This is likely correlated with the extent of glaciation and/or availability of extensive glacial refugia, combined with a long history of good dispersal across and between continents in these regions. Other species-rich taxa in these rainforests include insects (mostly soil and canopy species) and gastropods (mainly in the Pacific Northwest), with high levels of endemism in certain taxa. Apart from that, tropical rainforests are exceptional across taxa (see table 1-3).

Disturbance Dynamics

Stand-replacing disturbances are relatively rare in temperate and boreal rainforests, as they are in tropical moist forests. As a result, both rainforest types are dominated by ancient trees that have a complex structure and pattern, due to a long history of small patch or gap disturbances (see box 1-1). This history, along with the evolution of tree defenses against diseases, has allowed certain tree species to reach very old ages (Waring and Franklin 1979) in not only temperate rainforests (see above examples for tree species) but tropical rainforest trees as well (e.g., *Hymenolobium mesoamericanum* of Costa Rica can live for hundreds of

BOX 1-1

Gap Phase Dynamics of Temperate and Boreal Rainforests.

While most temperate and boreal rainforests are subject to various stand-replacing disturbances such as canopy fires, hurricanes, and landslides, forests in moist climates often have small-scale disturbances that serve to maintain the species composition and structure of the forest over time. Some authors have called these disturbances "maintenance dynamics" (see Veblen and Alaback 1996; Perry et al. 2008). A key ecological consequence of frequent gap disturbances is that a wide range of light environments and ecological conditions can be maintained in a forest that enriches its structural and compositional diversity. This also promotes a rich assortment of plant and animal species requiring vastly different light levels (e.g., both shade-tolerant and -intolerant species), and implies forest structure and composition can be theoretically maintained indefinitely. The extent to which a given rainforest is dominated by gap dynamics depends on many factors, including susceptibility to intense windstorms or geomorphic disturbances (landslides and flooding), as well as the susceptibility of individual trees to mortality, insects, and disease.

Key disturbance features of temperate and boreal rainforests are summarized as:

- Usually small-scale events affecting 1–4 percent of the forest area annually, although these gaps are eventually filled by light-seeking plants, creating a continuous push-pull dynamic between gap-dependent and gap-avoiding (anti-gap) species (Nowacki and Kramer 1998; Franklin et al. 2002).
- A small number of trees are killed in each disturbance event, usually fewer than 10 trees (Lertzman et al. 1996; Ott and Juday 2002).
- Gaps vary widely in size and shape, creating a rich mosaic of conditions in the forest (Ott and Juday 2002).

BOX 1-1

Continued

- When gaps are created by wind events, root-throw can create a rich diversity of soils and microhabitat conditions in the forest, including "pit and mound" micro-topography (Bormann et al. 1995) and nesting sites for birds (e.g., winter wrens *Troglodytes troglodytes* often nest in root-wads).
- Tree architecture, including rooting depth, height and exposure of canopy, and resistance to decay fungi play key roles in determining susceptibility to windthrow.
- Openings in canopy created by gaps promote regeneration of tree and understory species, leading to greater diversity in the forest (Spies et al. 1990; Franklin et al. 2002).
- While in theory gap disturbances can maintain the structure and composition of the forest indefinitely, in practice gap dynamics can lead to changes in forests due to changes in the environment at the time of gap creation, including seed availability and dispersal, microclimate, and specific characteristics of a given gap event (see Lertzman et al. 1996).

years—Fichtler et al. 2003). The infrequency of natural fires in both rainforests adds to tree longevity (e.g., see Gavin et al. 2003).

While both tropical and temperate rainforests are affected by and in turn affect regional climates, tropical rainforests, along with the world's oceans, play a major role in the planet's climate regulation. When either rainforest type is cut down, much of their stored carbon is released as carbon dioxide, thus contributing to global warming as well as regional changes in moisture (evaporative losses) and temperature (as discussed in Chapter 11). Understanding this basic fact is key to climate change negotiations for protecting the world's mature forests in both the tropics and temperate zones for their pivotal role in long-term carbon storage (see chapters 10, 11).

RAINFORESTS: GOING, GOING, GONE?

Unfortunately, both temperate-boreal and tropical rainforests have been reduced by at least half their estimated original extent (i.e., before widespread human-related destruction of rainforests—see Bryant et al. 1997; Myers et al. 2000; Ritter 2008; see table 1-3). Logging in the tropics is typically accompanied by the burning of vegetation and conversion of biologically rich forest to agriculture fields also used by livestock. A recent development is the clearing of rainforest to grow crops for biofuels (e.g., Borneo, Malaysia, and forest thinning in the temperate zone). In the tropics, this comes with severe depletion of already nutrient-deficient laterite (acidic) soils due to the leaching of nutrients otherwise held in place by rainforest trees, thus hampering afforestation efforts. Temperate and boreal forests, on the other hand, mainly have been degraded by conversion of biologically rich, older rainforest to simplistic tree plantations, or have been high-graded, where old high-value trees (or forest patches) are removed without providing for adequate rates of regeneration of older age classes or ecological types (as discussed throughout this book).

Notably, some researchers (Kauppi et al. 2006) contend that the world's forests have been increasing over a 15-year period (1990–2005) measured by accruing wood volume, biomass, and captured carbon (growing stock). While this is certainly a positive development, it misses the point about ongoing losses to intact and high-quality forests such as old-growth or primary forests. Globally, very few large, intact primary forests (e.g., "frontier forests") remain (Bryant et al. 1997). In addition, according to estimates provided by the World Wildlife Fund, approximately 13 million hectares of forests are destroyed globally each year mainly in the tropics.[5] But these losses are not just restricted to the tropics. For instance, the United States was recently ranked seventh in the world in deforestation, an annual rate of 215,000 hectares (FAO 2005). These alarming losses come at a time when deforestation (including forest conversion as used here) was second only to fossil-fuel emissions in global contributions to greenhouse-gas pollutants, although growth in emissions from forestry slowed from 1970 to 2004 (IPCC 2007). These forests are not equated by tree farms achieved through planting, as the difference in terms of quality of forest composition, genetics, function, structure, and long-term storage of carbon (and its release by forestry operations) is hard to measure at a global scale, but such comparison is certainly feasible at regional scales through measures of forest quality, remote sensing, and landscape change-detection analysis.

Ongoing consumption of wood products, particularly in the United States, Canada, Japan, and Europe (where per capita consumption levels are highest), will continue this alarming trend of forest conversion in the temperate zone and complete deforestation in the tropics. Recycling, the use of alternative

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[5] www.worldwildlife.org/climate/northsouthpartner.html

fibers, and improvements in manufacturing technologies are offsetting this trend somewhat. Greater interest in the conversion of cellulosic fiber from forests to liquid fuel (biofuels), however, will put more pressure on the world's forests, both tropical (UNEP 2009) and temperate/boreal (Searchinger et al. 2009). Afforestation cannot keep pace with ongoing demand without further degradation of rainforest biota from the loss of primary forests and the suite of ecosystem services they uniquely provide.

ABOUT THIS BOOK

This book, while focused primarily on the ecology of temperate and boreal rainforests, is intended as a rallying call for global action to conserve these rainforests, which, like so many of the world's rainforests, are at a critical juncture. Each of the regional chapters is a closer examination of the history and ecological characteristics of the largest remaining examples of temperate and boreal rainforest, and provides essential information that can be used to make clearer global priorities for the conservation of these important rainforests.

The regional chapters (chapters 2–9) largely maintain a consistent structure throughout that includes basic information on rainforest location and types, climatic conditions, significant ecological attributes of regional and global importance, ecological processes such as natural disturbances and forest succession, keystone or exemplary rainforest species, regional rainforest classifications (zones or subtypes), threats, and conservation priorities. In Chapter 10, we summarize key findings from each of the rainforest regions in order to stitch together a unifying vision, based on fundamental concepts of conservation biology, for conserving the world's temperate and boreal rainforests. We end the book in Chapter 11 with a call for an international accord to prepare these rainforests for the inevitable consequences of climate change. Most important, we hope that the principles and concepts outlined in this book provide a scientific foundation for expanding rainforest protections around the globe, so that these remarkable rainforests will continue to meet the growing demands of human communities for the life-giving services that these forests have provided to us for millennia.

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EFFECTS OF SILVICULTURAL MODIFICATIONS OF TEMPERATE RAINFOREST ON BREEDING AND WINTERING BIRD COMMUNITIES, PRINCE OF WALES ISLAND, SOUTHEAST ALASKA[1]

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Abstract. We inventoried breeding and wintering bird communities in four treatments of temperate rainforest on Prince of Wales Island, southeast Alaska during 1991–1992 and 1992–1993. The four forest treatments sampled included: (1) young growth (20 years) originating from clearcut logging with no silvicultural modification (non-modified), (2) young growth (20 years) precommercially thinned along uniformly-spaced thinning grids (thinned), (3) young growth (20 years) with gaps in the overstory canopy created by felling trees in 0.05-ha openings (gapped), and (4) virgin old growth (≥150 years). Of 16 common breeding bird species observed, six showed significant responses to young-growth modifications. One species was more abundant and two species were less abundant in thinned sites, while one species was more abundant and two species were less abundant in gapped sites than at least one of the other treatments. None of the three common wintering species of birds observed was influenced by young-growth modification. Breeding bird communities, in general, were less similar between young- and old-growth treatments than among young-growth treatments. Three of the 16 common breeding bird species were more abundant in old growth than each of the young-growth treatments and one uncommon species was detected almost exclusively in old growth during both the breeding and wintering seasons. Four other breeding bird species were more abundant in young-growth treatments than in old growth. Higher use of old growth by wintering birds was related to winter severity. To enhance habitat for wintering and breeding birds we recommend: (1) thinning young growth along variable-spaced grids to create additional canopy layers and improve snow-intercept properties of young growth for canopy-foraging birds, (2) retention of old-growth clumps in clearcuts for bird species associated with old-growth structure, and (3) long-term conservation of old-growth temperate rainforest for breeding and wintering birds positively associated with old growth.

Key words: breeding birds; canopy gaps; old growth; precommercial thinning; southeast Alaska; temperate rainforest; wintering birds; young growth.

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INTRODUCTION

The Tongass National Forest ("Forest") in southeast Alaska supports approximately ¼ of the world's remaining temperate rainforest (Alaback 1988, 1991, Samson et al. 1989, Beebe 1991). The Forest is characterized primarily by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla,* Alaback 1991) that is distributed along the Alexander Archipelago extending from the Dixon Entrance (54° N) to the Yakutat forelands (59° N). Temperate rainforests in this region occupy a distinct climatic zone, consisting of high annual precipitation (> 1,400 mm), cool (midsummer isotherm < 16°C) and frequently overcast summers, dormant seasonal periods, and relatively infrequent fires (Alaback 1988, 1991).

Approximately 90% of 4 million ha of commercially productive temperate rainforest in the Forest is old growth (USDA Forest Service 1991). In general, old-growth temperate rainforest is characterized by multi-layered tree canopies, a preponderance of large trees, snags, and downed woody material. Abundant and diverse forb and shrub layers are usually present when the dominant and codominant trees are ≥ 150 years old (Alaback and Juday 1989, Capp et al. 1992). About 7% of the commercially productive old growth in the Forest has been harvested since the 1950s, with another 23% of the old-growth area to be harvested by the year 2150 (USDA Forest Service 1991). Most commercial logging has taken place in low-elevation forests (< 245 m), because such areas are relatively accessible and contain the most productive timber (with the highest volume) in the Forest (Schoen et al. 1988, Alaback and Juday 1989). Logging in low-elevation forests has reduced habitat for breeding bird species (Kessler and Kogut 1985). Wintering birds also may have been affected because such forests accumulate less snowfall and are thermally more suitable to some bird species than high-elevation forests (Schoen et al. 1988, Suring et al. 1988).

Temperate rainforest that is managed intensively for timber production in southeast Alaska seldom develops the structural attributes important to bird species associated with old growth, such as large-diameter trees and snags within the limits of commercial forest cutting rotations (≤ 100 years; Alaback 1982b, Alaback and Tappeiner 1991). Most managed forests in this region are characterized by relatively little structural complexity in both the understory and overstory vegetation as compared to old-growth forests (Alaback 1982a, 1982b). In some young forests, large trees, logs, and snags remain after logging, thus retaining structural complexity in these otherwise homogeneous forests. Young forests also have been modified silviculturally by precommercial thinning and by creation of small (0.05-ha) openings (gapping) within the overstory canopy to enhance tree growth and/or maintain understory vegetation for Sitka black-tailed deer (*Odocoileus hemionus sitkensis,* see DellaSala et al. 1994 for discussion of silvicultural modifications). Light thinning (trees thinned to 2.4 × 2.4 m spacing) to moderate thinning (3.7 × 3.7 m spacing) has been most effective in retaining understory layers, but the peak vegetation response is reached within 3–5 years following thinning (Alaback and Tappeiner 1984, Alaback and Herman 1988). Because both thinning and gapping involve structural changes in the forest canopy, they may alter forest microclimates and snow intercept properties of young forests and render them less suitable as habitat for wintering birds.

Approximately 29,000 ha of young (15 to 20 years old) naturally regenerating, temperate rainforest in the Forest have been gapped or thinned by the USDA Forest Service. Our main objective was to evaluate the effectiveness of gapping and thinning of young-growth forest for enhancing and/or maintaining habitat for breeding and wintering bird communities in an area intensively managed for timber production. We compared species composition and abundance of breeding and wintering birds among thinned, gapped, and non-modified young-growth treatments and between young growth and old growth, and identified structural attributes of treatments that explained patterns of occurrence and abundance of bird species. Because winter conditions in southeast Alaska vary substantially among years, we also examined whether annual variation in snowfall during two winters influenced abundance and distribution of wintering birds in each of the treatments.

STUDY AREA

The study area (Fig. 1) was located on the northern portion of Prince of Wales Island ("the Island;" 5,778 km^2) approximately 35 km northwest of Ketchikan, Alaska (56° 01′ N, 132° 51′ W). The Island is separated from the Alaskan

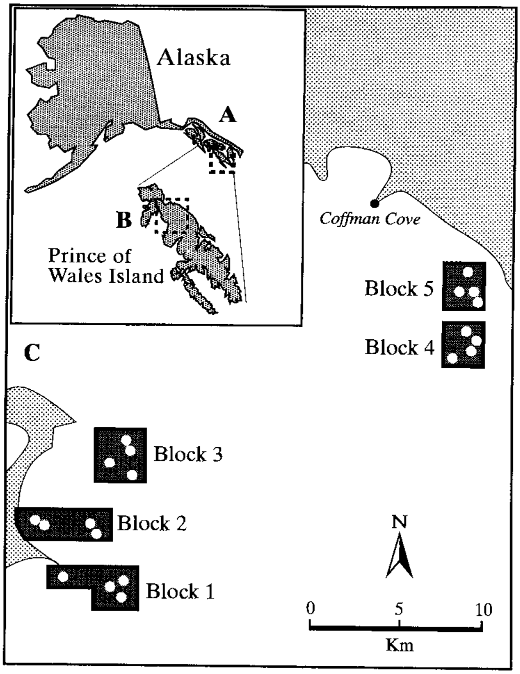

FIGURE 1. Location of study area in southeast Alaska (A), Prince of Wales Island (B), and geographic blocks (C) containing forest treatments (dots).

mainland by other mountainous islands and salt water channels at least 9 km in width. Vegetation on the Island was comprised primarily of western hemlock/blueberry (*Vaccinium* spp.) associations. Dominant tree species included western hemlock, Sitka spruce, western redcedar (*Thuja plicata*), and Alaska cedar (*Chamaecyparis nootkatensis*). Red alder (*Alnus rubra*) was associated with scarified soils and streambeds, and shore pine (*Pinus contorta*) was common in some small patches of muskeg. Dominant shrub species included devil's club (*Oplopanax horridum*), currants (*Ribes* spp.), salmonberry (*R. spectabilis*), blueberries, and rusty menziesia (*Menziesia ferruginea*). Common forbs included goldthreads (*Coptis* spp.), bunchberry (*Cornus canadensis*), deer cabbage (*Fauria cristagalli*), skunk cabbage (*Lysichitum americanum*), and five-leaf bramble (*Rubus pedatus*). Elevation on the Island ranged from 0–1,092 m above sea level.

METHODS

We divided the study area into five geographic blocks within which four sample sites were selected ($n = 20$ sample sites; Fig. 1). Geographic blocks were separated by 1–16 km and were selected because of ease of access and presence of sites meeting our sampling design criteria. All sites within a block were within 1 km of each other and were grouped according to similarities in physiographic factors (slope, elevation, aspect) reflective of the block. In general, sites within blocks 1 and 2 had the lowest elevations (0–122 m) and most gradual slopes (10–20%), those in blocks 3 and 4 had intermediate (61–229 m) elevations and moderate (15–30%) slopes, and those in block 5 had the highest (61–305 m) elevations and steepest (25–40%) slopes. Grouping sites by physiographic factors, rather than using a completely randomized approached, allowed us to partition some of the variability associated with site conditions from treatment effects and to expand the scope of inference to include a variety of forest conditions represented on the Island. Each block included the following experimental treatments: (1) young growth (20 years) originating from clearcut harvesting with no silvicultural modification (non-modified), (2) young growth (20 years) precommercially thinned along uniformly-spaced thinning grids (thinned), (3) young growth (20 years) with gaps in the overstory canopy created by felling trees in 0.05-ha openings (gapped), and (4) virgin old growth (≥ 150 years). All sites were within 1 km of logging roads and imbedded in a highly fragmented matrix consisting of recent clearcuts, regenerating- (20–40 years) and old-growth forests, salt water marshes, lakes, and streams. The Island's recent logging history and naturally low incidence of wildfires (Alaback 1988, 1991) have resulted in a lack of intermediate (50–149 years) forest age classes.

Each young-growth treatment had reseeded naturally and primarily to hemlock and spruce. Non-modified sites received no silvicultural modification post-harvest and averaged 70 ha (range = 50–95 ha). Thinned sites averaged 63 ha (range = 35–106 ha), were treated in 1987–1988 by thinning trees along uniformly-spaced (3.7 × 3.7 m or 4.3 × 4.3 m) thinning grids, and were sampled for vegetation and bird use 3–5 years post-thinning. Thinning produced piles of slash that were scattered throughout the site. Gapped sites averaged 59 ha (range = 36–83 ha), individual canopy gaps averaged 0.05 ha and gap density ranged from 0.60 to 0.86 gaps/ha. Gaps were created in 1988–1989 by felling trees along the perimeters of existing natural gaps, or creating new openings by tree removal, and were sampled 2–4 years post-gapping. Gap sizes most closely resembled natural gaps caused by blowdown of large trees, which is a common disturbance throughout the region. Slash produced by the creation of canopy gaps was left within each gap. Old-growth sites averaged 75 ha (range = 39–106 ha) and met the regional criteria for old-growth characteristics (Capp et al. 1992).

Vegetation, snow depths, and avian communities were sampled at 5 count point stations at each site. Count points were at least 50 m from the nearest edge and were spaced at random distances of 150 to 300 m along a 1,500-m transect established as part of a related study (DellaSala et al. 1994). A minimum distance between count stations of 150 m was chosen to minimize the probability of counting the same bird at multiple stations (Reynolds et al. 1980).

VEGETATION SAMPLING

One nested, circular vegetation plot was positioned in each of four cardinal directions, at random distances of 10 to 40 m from the center of each of the five count stations in each site (n = 20 plots/site). Plots in old-growth had a 10-m, 5-m, and two 2-m radius; in young growth there was a 5-m and two 1-m radius plots. Smaller plots were used in young growth because of the denser tree spacing and higher conifer stem densities relative to old growth. At each plot, we recorded 15 variables: stem densities (stems/ha) of conifers and snags (> 2 m tall) in three size classes, small (6–35 cm dbh), medium (36–55 cm dbh), and large (> 55 cm dbh); stem densities of hardwoods (small size class only); numbers of tree species; tree and shrub height (m); percent conifer cover; and percent cover of shrubs, forbs, and slash in two depth categories, < 50 cm and ≥ 50 cm. Ten-m radius plots in old growth and 5-m radius plots in young growth were used to record tree and snag densities, dbh in size classes, tree height, and percent tree-canopy cover. Tree-canopy cover was estimated by sighting through an ocular tube (James 1971) for the presence of vegetation from five sample points (plot center and four cardinal directions) located within each vegetation plot. Average tree height was estimated by measuring the heights of two dominant/codominant trees nearest plot center using a clinometer. Five-m radius plots (in both old-growth and young-growth sites) were used to estimate percent shrub cover and shrub height. Vegetation recorded in the small (1- or 2-m radius) plots included percent forb and slash cover.

We also mapped canopy gaps and patches of residual old-growth trees in young-growth sites from current (1991) aerial photos. Residual trees were identified on aerial photos as isolated clumps of unharvested trees taller (> 15 m) than the surrounding canopy of young-growth sites. Residual tree clumps were mapped as polygons; area occupied by clumps was calculated using the ARC/INFO GIS software. Canopy gaps were mapped from aerial photos at a minimum scale of 0.05 ha; no distinction was made between natural and artificial gaps. Mapped locations of gaps and residual tree clumps were verified opportunistically while walking between count stations. Once verified, the GIS was used to calculate distances from each count station to the nearest gap.

AVIAN SAMPLING

Avian communities were surveyed four times at each site during one-week intervals in the breeding (1 June to 23 June) and wintering (7 December to 29 February) seasons of 1991–1992 and 1992–1993. Surveys were conducted at sunrise during the breeding (03:30 and 04:00) and wintering (07:30–08:30) seasons and continued for 3–4 hours and 5–6 hours after sunrise in each season, respectively. No surveys were conducted during heavy precipitation or high winds. Sites within a block were surveyed on the same day and the order in which count stations were visited within sites was rotated systematically to help reduce biases associated with diurnal variations in bird activity (Robbins 1981).

We estimated bird abundance by counting all birds detected at each count point during an 8- and 10-min count period in the breeding and wintering seasons, respectively. We assumed that 8-to 10-min count periods were sufficient to detect the majority of bird species at the count stations because the number of bird species detected began to level-off within the count period (Scott and Ramsey 1981, Verner 1988). Bird detections were limited to a 100-m radius plot centered on each count station (Verner 1985, 1988) because this was the maximum range over which the majority of species in this study were detectable. In addition, we estimated the horizontal distance from observer to each individual bird detection (i.e., detection distance).

MEAN MONTHLY TEMPERATURES AND SNOW DEPTHS

We described winter weather conditions by (1) obtaining mean monthly temperatures for an 81-year period (1909–1990) from the Ketchikan, Alaska, weather station located approximately

30 km southeast of the study area at 23 m elevation and (2) measuring snow depths at count points within each site. Mean monthly temperatures for each year of the study were compared to the 81-year monthly averages. A meter stick was used to measure snow depths at three sampling points spaced at random distances along a 50 m transect bisecting each count station. A total of 15 snow-depth measurements (3 measurements per count point × 5 count stations/site) was taken in each site.

STATISTICAL ANALYSES

Individual sites served as the experimental units for statistical analyses. Vegetation variables were averaged over the 20 vegetation plots and snow depths were averaged over the 15 snow-depth plots representing each site. Vegetation and snow depths were compared among the four treatments using an Analysis of Variance (ANOVA), blocking on the five geographic areas (i.e., blocks). The Randomized Block design was used to take advantage of the increased statistical power achieved by grouping treatments within the same geographic area (Neter and Wasserman 1983). Tukey's HSD test (Wilkinson 1990) was used to locate differences between specific treatment means for significant ANOVAs.

An abundance index for each common (≥ 30 total detections/year) breeding and wintering bird species was calculated by averaging detections over the four site visits for each treatment type in each season. Common species were used in comparisons of abundance among treatments to meet assumptions of statistical models (i.e., stable variances). No abundance estimate was calculated for uncommon species (< 30 total detections/year); however, total detections of uncommon species were examined separately for general patterns across treatments. To determine whether bird species were equally detectable among treatments, we compared the mean detection distance and the effective detection distance (i.e., distance from count points at which the number of birds observed begins to decline, Reynolds et al. 1980) for each breeding bird species among treatments using ANOVA. Low numbers of winter bird detections precluded determination of their detection distances. Winter bird detections were therefore truncated at plot sizes of 40 m, 75 m, and 100 m and abundance of each species was examined for consistency in response to treatments.

Species richness (total number of species), total abundance (number of detections of all species combined), and proportional similarity (Brower et al. 1984) were used as avian community indices and were compared among treatments. The proportional similarity index reflects the proportion of species occurring within a given treatment that also occurred in another treatment. This index ranges from 0 (no overlap in species composition) to 100% (complete overlap). Only those species with ≥ 2 detections in the study area were used in comparisons of species richness and proportional similarity. Proportional similarity indices were not determined for winter birds because of low species richness. Avian community indices and abundance of each bird species were compared among treatments and between years using the Split-plot ANOVA procedure. Year served as the whole plot, treatment as the subplot, and geographic area as the blocking variable. The treatment-by-geographic block error term was used to test both the treatment effect and the treatment-by-year interaction. Because breeding bird abundance was similar across breeding seasons and there were no significant interaction terms for all but one bird species, abundance estimates were combined between years and Tukey's HSD was used to identify differences among treatment means if a treatment effect was indicated. For the one breeding bird species with a significant treatment-by-year interaction, the treatment effects were evaluated using a separate ANOVA for each year. Because abundance of winter birds varied greatly between years and among treatments, the Least Squares Means test (SAS Institute 1985) was used to identify differences among specific treatment means within a year for species with significant treatment effects.

Variables not meeting assumptions of normality (Kolmogorov-Smirnov one sample test, Wilkinson 1990) or homogeneity of group variances (Bartlett's F-test, residual scatter plots, Wilkinson 1990) were transformed using either arcsine or square-root transformations (Zar 1984). A non-parametric Friedman's test was used if transformations did not adequately improve normality or variance homogeneity based on reexamination of assumptions. The power of statistical tests (Zar 1984) was calculated using PASS software (Hintze 1991) for nonsignificant results at $\alpha > 0.05$.

To explore habitat attributes important to breeding birds, we related the abundance of each common bird species to vegetation variables using stepwise regression (forward selection). We restricted this analysis to the young-growth treatments due to the larger sample sizes (n = 15) relative to old growth (n = 5), and to breeding birds because of low abundance of wintering birds. Vegetation variables having tolerance factors > 0.70 were excluded from the model to reduce multicollinearity (Wilkinson 1990). These analyses were performed using SYSTAT (Wilkinson 1990).

RESULTS

VEGETATION CHARACTERISTICS

Young growth. Eight of the 15 site characteristics measured differed among the three young-growth treatments (Table 1); six of these were associated with thinning and two were associated with gapping. Of these characteristics, thinned sites had 4 × as many snags (P = 0.04), 2 × as much forb (P = 0.04) and slash ≥ 50 cm-deep cover (Ps < 0.02), and ⅓ as many small conifers (Ps < 0.001) as other young-growth treatments. Thinned sites also had marginally less (P = 0.07) canopy cover and marginally greater (Ps < 0.06) shrub cover than at least one of the other young-growth treatments. As expected, gapped sites had substantially (18 ×) greater gap densities (Ps < 0.001) and much lower (⅕) distance to nearest gaps (P = 0.01) than other young-growth treatments. All young-growth treatments were characterized by few residual old-growth tree clumps. Sixteen residual tree clumps ranging in size from 0.05–1.3 ha were located in two thinned, one gapped, and one non-modified site.

Young growth vs. old growth. Ten of 15 site characteristics measured differed between young- and old-growth treatments; four of these characteristics, medium (Ps < 0.001) and large conifer (none were recorded in young growth) densities, tree heights (Ps < 0.001), and snag densities (Ps < 0.004) were 4–46 × greater in old growth (Table 1). A total of 245 snags was counted in old-growth sites, approximately 43% were > 35 cm dbh and 20% were ≥15 m tall. Only 32 snags were counted in the young-growth sites, 6% of which were > 35 cm dbh and 6% of which were ≥ 15 m tall. Old growth also was characterized by lower densities of small conifers (Ps < 0.001), lower shrub (P = 0.04) and slash ≥ 50 cm-deep cover (P = 0.005), lower gap density (P < 0.001), and greater forb cover (P = 0.04) than at least one of the young-growth treatments.

BREEDING BIRD ABUNDANCE

We identified 16 relatively common (Table 2) and 12 uncommon (Appendix A) breeding forest bird species during 40 survey days (720-person hr) in both years. Eight species accounted for > 75% of the total detections (n = 6,072): Winter Wrens (18%), Orange-crowned Warblers (14%), and Swainson's Thrushes (13%) were the three most abundant species, followed by Dark-eyed Juncos (8%) and Townsend's Warblers (8%), Pacific-slope Flycatchers (5%), Varied Thrushes (5%), and Hermit Thrushes (5%). Uncommon species collectively accounted for approximately 5% of the total detections in both years (Appendix A).

Mean detection distances for each of the 16 common breeding bird species did not differ (Ps > 0.10) among treatments. In addition, the effective detection distance varied by ≤ 10 m among treatments for nine of 16 common breeding bird species (Chestnut-backed Chickadee, Dark-eyed Junco, Fox Sparrow, Golden-crowned Kinglet, Orange-crowned Warbler, Pacific-slope Flycatcher, Swainson's Thrush, Townsend's Warbler, and Winter Wren) and by 20–30 m for two species (American Robin and Wilson's Warbler). No effective detection distance was identified for the five remaining common species, whose detections varied unpredictably with distance from count points.

Young growth. Percent similarity ($\bar{x}$ ± SE) of breeding bird communities was consistent among all pairs of young-growth treatments: non-modified vs. gapped (76.3 ± 2.5%), gapped vs. thinned (75.5 ± 1.5%), and non-modified vs. thinned (74.9 ± 1.6%) sites. Total abundance and species richness did not differ (Ps > 0.10) among young-growth treatments (Table 2).

Abundance of five of the 16 common breeding bird species differed among young-growth treatments (Table 2). American Robins were 5 × more (P = 0.08) abundant in gapped than in non-modified sites, while Fox Sparrows (Ps ≤ 0.03) and Wilson's Warblers (P = 0.03) were ⅓–⅐ × as abundant in gapped than in other young-growth treatments, respectively. In addition, Dark-eyed Juncos were 3 × more (P = 0.008) abundant in thinned sites than in non-modified sites, while Hermit Thrushes were ½ as abundant (P = 0.03) in thinned than in gapped sites.

TABLE 1. Mean (± SE) site characteristics of non-modified, canopy gapped, and precommercially thinned young-growth (20 years) and old-growth (≥ 150 years) treatments (n = 5 sites/treatment) on Prince of Wales Island, southeast Alaska, 1991 and 1992.

Site characteristic	Treatment[a]			
	Non-modified	Gapped	Thinned	Old growth
Small conifers (6–35 cm dbh)/ha	1,117.9 ± 75.2A	1,117.9 ± 233.0A	435.4 ± 30.0B	411.6 ± 36.9B
Medium conifers (36–55 cm dhb)/ha	1.3 ± 1.3B	2.5 ± 2.5B	0[b]	60.2 ± 4.5A
Large conifers (> 55 cm dbh)/ha[b]	0	0	0	52.8 ± 9.4
Hardwoods (6–35 cm dbh)/ha	45.8 ± 34.5A	85.3 ± 70.5A	17.8 ± 12.0A	2.9 ± 2.9A
No. tree species	3.2 ± 0.4A	3.2 ± 0.4A	2.8 ± 0.6A	3.8 ± 0.5A
Canopy cover (%)	62.4 ± 4.9B	58.2 ± 9.0BC	38.4 ± 5.2C	86.2 ± 8.2A
Tree height (m)	7.1 ± 0.2B	7.3 ± 0.5B	8.0 ± 0.3B	29.1 ± 1.9A
Snags/ha	6.4 ± 2.8C	8.9 ± 2.5BC	25.5 ± 7.8B	78.6 ± 10.4A
Slash cover < 50-cm deep (%)	7.9 ± 1.4A	11.1 ± 2.2A	12.4 ± 1.6A	8.4 ± 3.7A
Slash cover ≥ 50-cm deep (%)	7.7 ± 1.1B	8.5 ± 1.0B	17.4 ± 3.2A	7.0 ± 1.2B
Shrub cover (%)	47.5 ± 5.3B	43.3 ± 3.0B	66.2 ± 6.1A	45.2 ± 4.7B
Shrub height (m)	1.3 ± 0.1A	1.2 ± 0.1A	1.1 ± 0.1A	1.3 ± 0.1A
Forb cover (%)	11.2 ± 2.2B	16.4 ± 2.4AB	22.9 ± 5.0A	21.9 ± 3.9A
No. canopy gaps[c]/ha	0.1 ± 0.1B	0.7 ± 0.1A	0.1 ± 0.1B	0.1 ± 0.1B
Distance to gap[c] (m)	288.4 ± 56.7A	54.6 ± 10.7B	191.0 ± 40.8AB	162.6 ± 55.8AB

[a] Means sharing the same letters do not differ (ANOVA and Tukey's HSD, $P > 0.10$).
[b] No statistical tests were run because means have no variance.
[c] Canopy gaps included in the analysis were at least 0.05 ha.

TABLE 2. Mean[a] (± SE) numbers of detections (abundance) of common (≥ 30 total detections/year) breeding birds, total abundance (all species combined), and species richness in non-modified, canopy gapped, and precommercially thinned young-growth (20 years) and old-growth (≥ 150 years) treatments ($n = 5$ sites/treatment) on Prince of Wales Island, southeast Alaska, 1991 and 1992.

	Treatment[b]			
Species	Non-modified	Gapped	Thinned	Old growth
Red-breasted Sapsucker (*Sphyrapicus ruber*)	0.1 ± 0.1B	0.4 ± 0.1B	0.1 ± 0.1B	1.3 ± 0.3A
Pacific-slope Flycatcher (*Empidonax difficilis*)	0.4 ± 0.1B	0.9 ± 0.3B	0.8 ± 0.2B	5.6 ± 0.6A
Steller's Jay (*Cyanocitta stelleri*)	0.6 ± 0.3A	0.4 ± 0.1A	0.8 ± 0.2A	0.2 ± 0.1A
Chestnut-backed Chickadee (*Parus rufescens*)	1.0 ± 0.3A	1.0 ± 0.2A	0.9 ± 0.2A	1.7 ± 0.4A
American Robin[c] (*Turdus migratorius*)	0.2 ± 0.1B	1.0 ± 0.3A	0.7 ± 0.3AB	0.1 ± 0.1B
Varied Thrush (*Ixoreus naevius*)	2.3 ± 0.5A	1.9 ± 0.6A	1.3 ± 0.3A	2.2 ± 0.5A
Hermit Thrush (*Catharus guttatus*)	1.8 ± 0.4AB	2.7 ± 0.4A	1.2 ± 0.3B	2.0 ± 0.3AB
Swainson's Thrush (*Catharus ustulatus*)	6.4 ± 0.3A	6.1 ± 0.6A	5.2 ± 0.6A	1.5 ± 0.3B
Golden-crowned Kinglet (*Regulus satrapa*)	0.5 ± 0.2B	0.5 ± 0.3B	0.4 ± 0.1B	2.3 ± 0.6A
Orange-crowned Warbler (*Vermivora celata*)	6.4 ± 0.6A	7.3 ± 0.5A	7.2 ± 0.5A	0.6 ± 0.2B
Townsend's Warbler (*Dendroica townsendi*)	3.0 ± 0.4AB	2.8 ± 0.2AB	1.8 ± 0.3B	4.2 ± 0.9A
Wilson's Warbler (*Wilsonia pusilla*)	1.5 ± 0.5A	0.2 ± 0.1B	0.7 ± 0.2AB	0.1 ± 0.1B
Dark-eyed Junco (*Junco hyemalis*)	2.0 ± 0.5BC	3.5 ± 0.7AB	5.7 ± 1.1A	1.1 ± 0.3C
Fox Sparrow (*Passerella iliaca*)	2.8 ± 0.6A	0.9 ± 0.4B	3.3 ± 0.5A	0[d]
Song Sparrow (*Melospiza melodia*)	0.2 ± 0.1A	0.8 ± 0.4A	0.5 ± 0.2A	0.1 ± 0.1A
Total abundance	39.4 ± 0.4A	39.7 ± 1.6A	40.6 ± 2.0A	31.9 ± 2.1B
Species richness	14.4 ± 0.5A	15.8 ± 0.6A	16.4 ± 1.0A	15.4 ± 0.7A

[a] No differences (*P*s > 0.10) were detected in abundance of each species between years. Thus, abundance was pooled between years by averaging total counts (including only observations within 100-m of observers) for each species at each site across four visits in each breeding season. Winter Wrens (*Troglodytes troglodytes*) were not included due to the interaction of year and treatment effects.

[b] Means sharing the same letters do not differ (ANOVA, Tukey's HSD-test, $P > 0.10$).

[c] Friedman's test, Tukey's HSD-test, $P \leq 0.10$.

[d] No statistical tests were run because means have no variance.

Abundance of Steller's Jays, Chestnut-backed Chickadees, Varied Thrushes, and Song Sparrows did not differ (*P*s > 0.10) among young-growth treatments. Statistical power may have been too low to detect differences among treatments for Song Sparrows (0.10), Varied Thrushes (0.16), Steller's Jays (0.24), and Chestnut-backed Chickadees (0.38).

Young growth vs. old growth. Percent similarity of breeding bird communities was substantially lower between old growth and each of the young-growth treatments than among young-growth treatments. Percent similarity ($\bar{x}$ ± SE) was lowest for old growth vs. thinned (45.1 ± 2.2%), followed by old growth vs. non-modified (50.4 ± 2.9%) and gapped (52.2 ± 2.2%) sites. During both years, total abundance differed (*P*s < 0.001) between young- and old-growth treatments; however, species richness did not differ (*P*s > 0.10) among treatments (Table 2). Although total abundance was lowest (*P*s < 0.01) in old growth, the difference was considered small (0.8 × fewer detections).

Six of 16 common breeding bird species differed in abundance between old growth and each of the young-growth treatments (Table 2). Abundance of Golden-crowned Kinglets (*P*s < 0.005), Pacific-slope Flycatchers (*P*s < 0.001), and Red-breasted Sapsuckers ($Ps < 0.004$) were 6–14 × greater in old growth than in each of the young-growth treatments. In contrast, abundance of Orange-crowned Warblers, Swainson's Thrushes, and Fox Sparrows was 3–4 × greater in each of the young-growth treatments than in old growth ($Ps < 0.001$). Four other common species differed between old growth and one of the young-growth treatments: Dark-eyed Juncos, American Robins, and Wilson's Warblers were 6–15 × more abundant in thinned ($P = 0.001$), gapped ($P = 0.03$), and non-modified ($P = 0.004$) sites compared to old growth, respectively, whereas Townsend's Warblers were 2 × more ($P = 0.02$) abundant in old growth than in thinned sites.

Uncommon species. Brown Creepers occurred exclusively (11 total detections each year) in old growth; however, because creeper detections were low and confined to only one treatment (old growth) no statistical comparisons were made among treatments. In addition, both Red Crossbills and Pine Siskins occurred in higher numbers in old growth; however, numbers of crossbills (68 in 1991 vs. 20 in 1992) and siskins (78 in 1991 vs. 2 in 1992) varied substantially between years also precluding statistical comparisons among treatments.

Treatment × year interactions. Differences in Winter Wren abundance among treatments differed ($P = 0.004$) between years. In 1991, Winter Wrens ($\bar{x} \pm SE$) were more ($P = 0.03$) abundant in thinned (5.4 ± 0.6) than in gapped (3.0 ± 0.6) sites; however, in 1992, wrens were more ($Ps < 0.01$) abundant in non-modified (9.4 ± 0.7), gapped (9.7 ± 0.5), and thinned (10.4 ± 0.6) sites than in old growth (6.0 ± 0.6) sites.

BREEDING BIRD ABUNDANCE AND VEGETATION CHARACTERISTICS

Only three of 15 vegetation variables measured in young-growth treatments were associated with differences in the abundance of breeding bird species: percent forb cover, total conifer densities (all size classes combined), and number of gaps. Abundance of Dark-eyed Juncos and Hermit Thrushes was related positively to percent forb cover ($R^2 = 0.44$, df = 1,13, $P = 0.008$) and total conifer densities ($R^2 = 0.36$, df = 1,13, $P = 0.02$), respectively, while abundance of Fox Sparrows was related inversely to the number of gaps ($R^2 = 0.33$, df = 1,13, $P = 0.02$).

MEAN MONTHLY TEMPERATURES AND SNOW DEPTHS

Mean monthly temperatures recorded at the Ketchikan weather station over an 81-year period (1909–1990) were 2.1°C for December, 0.5°C for January, and 2.8°C for February. Monthly temperatures for December through February of 1991–1992 and 1992–1993 were only 1–4°C above and 1°C below the 81-year averages, respectively. However, mean snow depths differed between study years and among treatments ($P < 0.001$). In 1991–1992, snow depths ($\bar{x} \pm SE$, cm) did not differ ($Ps > 0.10$) among non-modified (2.5 ± 1.2), gapped (3.6 ± 1.9), thinned (1.8 ± 1.0), and old-growth (1.3 ± 0.7) treatments. In addition, snow depths during this winter ranged from 0–25 cm throughout the study area with snow present only during a six-day period in February. In contrast, in 1992–1993, snow depths in old growth (12.0 ± 2.1) were nearly ½ those in non-modified (21.2 ± 2.1, $P = 0.10$), gapped (23.3 ± 3.5, $P = 0.04$), and thinned (25.2 ± 2.5, $P = 0.01$) sites. Snow depths ranged from 12–89 cm throughout the study area and snow was present from January through mid-February.

WINTER BIRD ABUNDANCE

We recorded a total of 1,037 winter bird detections during 40 survey days (720-person hours) from December to February 1991–1993; 598 in 1991–1992 and 439 in 1992–1993. In general, three species accounted for most (81%) of the total detections during both winters: Golden-crowned Kinglets (52%), Winter Wrens (19%), and Chestnut-backed Chickadees (10%). Ten uncommon species accounted for 17% to 19% of the total detections each year (Appendix A).

Truncating avian detections at plot sizes of 40 m, 75 m, and 100 m had no discernible influence on our findings. Therefore, winter bird abundance was calculated using the 100-m radius plot size.

Young growth. Total abundance, species richness, and abundance of the three common bird species did not differ ($Ps > 0.10$) among young-growth treatments in either year (Table 3).

Young growth vs. old growth. Patterns of total abundance among treatments differed ($P < 0.001$) between winters (Table 3). In 1991–1992, total abundance did not differ ($Ps > 0.10$) between young- and old-growth treatments, but was 3 × greater ($Ps < 0.001$) in old- than in young-growth

TABLE 3. Mean[a] (± SE) numbers of detections (abundance) of common (≥ 30 detections/year) winter bird species, total abundance (all species combined), and species richness in non-modified, canopy gapped, and precommercially thinned young-growth (20 years) and old-growth (≥ 150 years) treatments ($n = 5$ sites/treatment) on Prince of Wales Island, southeast Alaska, during the winters of 1991–1992 and 1992–1993. Unless otherwise indicated, means across top rows are for 1991–1992; those across bottom rows are for 1992–1993.

	Treatment[b]			
Species	Non-modified	Gapped	Thinned	Old growth
Golden-crowned Kinglet	2.5 ± 0.2B	2.9 ± 0.2B	2.6 ± 0.7B	4.2 ± 0.7A
(*Regulus satrapa*)	1.8 ± 0.3B	2.0 ± 0.4B	2.9 ± 0.3B	7.9 ± 0.6A
Winter Wren	2.4 ± 0.2A	2.4 ± 0.4A	2.3 ± 0.2A	0.7 ± 0.2B
(*Troglodytes troglodytes*)	0.4 ± 0.1A	0.4 ± 0.1A	0.6 ± 0.2A	0.4 ± 0.2A
Chestnut-backed Chickadee	0.6 ± 0.2A	0.4 ± 0.2A	1.1 ± 0.5A	1.4 ± 0.4A
(*Parus rufescens*)	0.3 ± 0.1A	0.4 ± 0.2A	0.4 ± 0.2A	0.6 ± 0.2A
Total abundance	7.2 ± 0.9A	7.0 ± 0.4A	7.4 ± 1.0A	8.2 ± 0.7A
	3.0 ± 0.6B	3.5 ± 0.2B	4.5 ± 0.6B	10.8 ± 1.1A
Species richness[c]	4.1 ± 0.5B	4.8 ± 0.2B	4.5 ± 0.5B	6.5 ± 0.4A

[a] Abundance for each species was averaged across four site visits in each treatment.
[b] Means sharing the same letters do not differ (ANOVA and Least Squares Means Test, $P > 0.10$).
[c] Species richness was pooled between years due to lack of significant annual differences.

treatments in 1992–1993. Species richness was greater (Ps < 0.03) in old- than in young-growth treatments and this pattern was consistent ($P = 0.92$) between years. Old growth averaged at least two more species of birds than any of the young-growth treatments in each year. This difference was primarily attributed to greater use of old growth by some uncommon species (e.g., Brown Creeper, Appendix A). Brown Creepers occurred nearly exclusively (38 of 39 detections in both years) in old growth and the one creeper detected in young growth was within 100 m of an old growth site.

Differences in abundance of Golden-crowned Kinglets among treatments differed ($P = 0.001$) between winters. In 1991–1992, kinglet abundance was nearly 2 × greater in old growth than in young-growth treatments (Ps ≤ 0.07). In contrast, in 1992–1993, kinglet abundance was 4 × greater in old growth than in each of the young-growth treatments (Ps < 0.001).

Differences in abundance of Winter Wrens among treatments differed ($P = 0.003$) between winters. In 1991–1992, Winter Wrens were approximately 3 × as abundant in young- than in old-growth treatments (Ps < 0.001); however, in 1992–1993, wren abundance did not differ (Ps > 0.10) between young- and old-growth treatments.

Although abundance ($\bar{x}$ ± SE) of Chestnut-backed Chickadees was similar (Ps > 0.10) between old- and young-growth treatments during both winters, chickadees were twice as abundant ($P = 0.05$) in 1991–1992 (3.5 ± 0.7) than in 1992–1993 (1.8 ± 0.5).

DISCUSSION

We assumed that overall differences in vegetation characteristics, including old growth vs. young growth and silviculturally modified vs. non-modified young growth, did not influence our ability to detect birds and thus that differences in avian abundance among treatments were unrelated to differences in detectability. This assumption was supported by the similarities in mean detection distances and effective detection distances among treatments and the consistency in interpretation of treatment effects during the winter regardless of plot size selected for count point stations.

BREEDING BIRDS

Young growth. Most breeding bird species utilizing young-growth treatments in this study were habitat generalists that are widespread in coniferous forests of southeast Alaska (Kessler and Kogut 1985, Armstrong 1995) and the Pacific Northwest (Brown 1985). However, six of the 16 common breeding bird species were associated with at least one of the silvicultural modifications of young growth. Dark-eyed Juncos were positively associated with thinning, while Hermit Thrushes and Townsend's Warblers were negatively associated with thinning. American Robins were positively associated with gapping, while Fox Sparrows and Wilson's Warblers were negatively associated with gapping.

Our finding for juncos is consistent with that of Mannan and Meslow (1984) who reported higher numbers of this ground-nesting bird in thinned than in unthinned sites in northeast Oregon. Higher junco abundance in the thinned sites we studied was attributed to increased forb cover that was associated with reduced conifer densities and canopy cover caused by thinning. In contrast, Hermit Thrushes tend to nest in areas with dense conifers and understory vegetation (Mannan and Meslow 1984). Higher abundance of thrushes in gapped sites we studied was related to greater conifer densities relative to thinned sites. However, this pattern was not consistent for non-modified sites that had similar conifer densities as gapped sites. Therefore, thrushes may have been responding to the combination of dense conifers juxtaposed with canopy gaps that was unique to gapped sites. The reductions in canopy cover caused by thinning also may have limited nesting habitat for Townsend's Warblers, which typically nest in areas with dense canopy volume (Tobalske et al. 1991). Although we did not measure canopy volume in this study, thinned sites had the lowest canopy cover of any of the treatments and this difference was most pronounced between thinned and old-growth sites where differences in warbler numbers were greatest.

None of the vegetation variables we measured was correlated with the relatively high abundance of American Robins in gapped sites; however, our results were consistent with the high foraging use by robins of fire-created gaps in coniferous forests of the Sierra Nevada (Bock and Lynch 1970). The reasons for the apparent negative response of Fox Sparrows and Wilson's Warblers to gapping remain unclear. Both species nest and forage in deciduous shrubs and conifer saplings in young regenerating forests in southeast Alaska (Kessler and Kogut 1985) and are associated with forest edges and shrubby clearcuts (Tobalske et al. 1991). The effects of gapping or thinning on Winter Wren abundance could not be determined because responses were inconsistent between years. It is likely that this species was responding to factors unrelated to vegetation characteristics we measured. Low statistical power associated with tests among treatments for Song Sparrows, Varied Thrushes, Steller's Jays, and Chestnut-backed Chickadees also limited our ability to detect treatment effects.

Young growth vs. old growth. Although we did not measure abundance across a successional gradient following logging, and abundance is not always a reliable indicator of habitat quality (Van Horne 1983), three common and one uncommon species were positively associated with old growth: Golden-crowned Kinglets, Red-breasted Sapsuckers, Pacific-slope Flycatchers, and Brown Creepers. The Brown Creeper was included as an old-growth associate because of its exclusive use of old growth during both breeding seasons. Creepers also are uncommon elsewhere in southeast Alaska (Armstrong 1995) and nest primarily in old growth in southeast Alaska (Kessler and Kogut 1985) and the Pacific Northwest (Sakai and Noon 1991).

Each of the old-growth associated species in our study area is known to decline in abundance following clearcut logging (Franzreb and Ohmart 1978, Mannan and Meslow 1984, Kessler and Kogut 1985, Rosenberg and Raphael 1986, Manuwal and Huff 1987, Raphael et al. 1988, Sakai and Noon 1991) and is less abundant in intermediate age classes (75 years) than old-growth forests of southeast Alaska (Kessler and Kogut 1985). These species also tend to use specific structural attributes rarely present in managed young-growth forests in southeast Alaska, including large-diameter trees (Pacific-slope Flycatcher, Sakai and Noon 1991; Brown Creeper, Adams and Morrison 1993), snags (Red-breasted Sapsucker, Raphael and White 1984), and multilayered tree canopies (Golden-crowned Kinglet, Mannan and Meslow 1984). Such characteristics are unlikely to develop within the commercial forest rotation (Alaback 1982a, 1982b, Tappenier and Alaback 1989, McComb et al. 1993).

In contrast, four species, Orange-crowned Warblers, Swainson's Thrushes, Fox Sparrows, and Wilson's Warblers were negatively associated with old growth and may therefore benefit initially from clearcut logging and no silvicultural modification of young regenerating forest. Each of these species was abundant in non-modified young growth, nests or forages in dense understory vegetation, and is common in early forest seral stages in southeast Alaska (Kessler and Kogut 1985). Habitat for these species in southeast Alaska is temporarily increasing due to replacement of old-growth forests by young growth.

Our results may underestimate the influence of silvicultural modifications on overall composition of breeding bird communities because our data describe site use by species of birds with relatively small home ranges that breed in the coastal temperate rainforest of southeast Alaska. We did not collect information on site use by Northern Goshawk (*Accipiter gentilis*) and Marbled Murrelet (*Brachyramphus marmoratus*) that occupy relatively large home ranges and nest almost exclusively in old-growth forests (Crocker-Bedford 1990, Quinlan and Hughes 1990), nor for nocturnal species such as owls, or species associated with old-growth/saltwater edges (e.g., Vancouver Canada Goose *Branta canadensis fulva,* Lebeda and Ratti 1983). These species were only observed flying over our study area. Both Red Crossbills (Benkman 1987) and Pine Siskins (Bent 1968) typically occur in mixed species flocks that undergo periodic population irruptions in response to conifer-cone production. Such factors likely contributed to high interannual variation in abundance of these species and our limited ability to detect treatment effects.

WINTERING BIRDS

The wintering bird community we studied was characterized by few species having low abundances. In general, three species accounted for the majority of winter bird detections, with 10 other species occurring in low numbers. The northern location of our study area may have limited species richness and abundance of wintering birds particularly since the Island lies outside the most northern extent of the distribution of many forest bird species (Armstrong 1995).

Thinning and gapping of young growth had no detectable effect on site use by wintering birds regardless of winter conditions. This was attributed to similarities in snow depths among young-growth treatments. Numbers of winter bird detections, however, varied substantially between years and these differences appeared to be related to winter weather conditions that influenced use of young- and old-growth treatments by wintering birds. Rotenberry (1978) indicated that the number of frost-free days and days with snowpack indirectly influenced population levels of wintering birds. Others (Helms 1968, Grubb 1977, 1979) have attributed differences in habitat use by northern forest birds to climatic factors.

Because winter conditions at low elevation in southeast Alaska typically hover at or above freezing (based on 81-year Ketchikan weather station records), relatively small differences in mean monthly temperatures between years contribute to large differences in snowfall accumulation. The winter of 1991–1992 was characterized by mean monthly temperatures that were 1–4°C above the 81-year regional average and sparse snowfall. These conditions likely contributed to the relatively high numbers of wintering birds throughout the study area and high use of young growth by Winter Wrens. As was the case for all other species, Winter Wren abundance was relatively low during the second winter when snow levels were especially high in young-growth treatments. Greater snow depths during relatively harsh winters may force ground-foraging species like Winter Wrens to winter further south or in other habitats where snowpack is low. Schoen et al. (1988) also reported low Winter Wren abundance in young growth during periods of heavy snow accumulations in southeast Alaska. Notably, Winter Wren abundance in this study was highest in young growth during the winter of 1991–1992 and the breeding season of 1992. Thus, the milder winter of 1991–1992 may have contributed to greater overwintering survival of wrens in young growth and thus greater use of these treatments during the breeding season.

The winter of 1992–1993 was characterized by mean monthly temperatures that were 1°C below the 81-year regional average and greater snowfall than in 1991–1992. Harsher winter conditions in 1992–1993 than in 1991–1992 likely contributed to greater abundance of wintering birds in old growth relative to young growth and substantially higher use of old growth than young growth by Golden-crowned Kinglets. Manuwal and Huff (1987) attributed greater use by overwintering birds of Douglas-fir (*Pseudotsuga menziesii*) old-growth forests in the southern Washington Cascades to more favorable microclimate and better foraging conditions relative to young forests. Similarly, Morrison et al. (1986) reported overwintering birds in old growth, mixed-conifer forests of the western Sierra Nevada used areas characterized by high, heavy canopy cover that provided protection from wind and precipitation.

The snow intercept properties of old-growth forest canopies (Kirchhoff and Schoen 1987) may provide foraging sites free of snow for canopy-foraging species such as Golden-crowned Kinglets, especially during harsh winters. In particular, we observed low numbers of kinglets in young growth following storms that coated tree branches with ice and snow. Kinglets foraged in small flocks primarily in multi-layered tree canopies of old growth that appeared to have less snow covering branches than the uniform tree canopy of young growth. Moreover, because kinglets also nested in old growth in this study they may be particularly vulnerable to combined reductions in wintering and nesting habitat caused by timber harvest.

Old growth also provided wintering habitat for uncommon species like Brown Creepers regardless of winter weather conditions. Creepers roost in large snags during the winter (Walsberg 1986) and forage along the crevices of large tree boles and branches (Jackson 1979, Morrison et al. 1985, Adams and Morrison 1993). These structural features are lacking in managed young growth-forests, which may explain the creepers apparent affinity for old growth during both the wintering and breeding seasons.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

We suggest that land managers replace uniform thinning with variable-spaced thinning to create additional canopy layers for young-growth bird communities. Variable-spaced thinning would eventually produce two-storied tree canopies within even-aged sites, allowing for rapid growth by some trees (thinned areas) and reduced growth or death by others (unthinned areas) (McComb et al. 1993). Thinned areas in these sites would provide forb cover for Dark-eyed Juncos; unthinned areas would provide canopy cover for Townsend's Warblers. A two-storied tree canopy also may distribute snowfall unevenly across tree canopies and provide more snow-free tree branches than uniform tree canopies for canopy-foraging species like Golden-crowned Kinglets. However, thinned areas may initially accumulate snow in the understory until regenerating trees are tall enough to fill openings in the tree canopy created by thinning. Ground-foraging species, such as Winter Wrens, may still experience relatively deep snows during harsh winters at least until a secondary tree canopy develops.

The USDA Forest Service has temporarily abandoned its gapping program in the Forest because this treatment has had limited effects on availability of deer forage (DellaSala et al. 1994). Although we found only one species, American Robins, that was positively associated with gapping, our study reflected conditions in gapped sites only two to four years post-gapping. Thus, we recommend this sampling be replicated over a longer period to evaluate fully the effectiveness of the gapping program. Because variable-spaced thinning produces greater spacings between thinned and unthinned areas relative to uniform thinning, thinned areas may effectively function as gaps for gap-associated species like American Robins. Variable-spaced thinning also may provide a more suitable distribution of dense conifers and openings for Hermit Thrushes than uniform thinning. Costs of variable-spaced thinning are comparable to those for uniform-spaced thinning (A. Anderson, District Manager, Craig, AK, pers. comm.). However, because understory response to thinning (whether variable or uniform spacing) is limited to ≤ 10 years as tree canopies close (Alaback and Herman 1988), thinning would need to be repeated on 10-year intervals increasing the costs associated with extending such benefits through longer periods of the commercial rotation.

Combining variable-spaced thinning with retention of residual clumps of old growth may further reduce negative effects of thinning for bird species that are associated with forest canopies (e.g., Townsend's Warbler), increase the use of otherwise homogenous young growth by species associated with old growth (Wetmore et al. 1985, Raphael et al. 1988), and increase snow intercept properties of young forests to provide more snow-free habitat for wintering birds. The USDA Forest Service retains some residual old-growth trees following commercial logging activities as part of ecosystem management in the Forest (USDA Forest Service 1991). However, because of the relatively small size (0.05–1.3 ha) of residual clumps in this study, such clumps lack interior forest conditions and thus should not be viewed as mitigation for large-scale removal of contiguous forests. Furthermore, because residual clumps are subject to high-velocity winds that are a frequent disturbance in this region (Alaback 1991), they should be relatively large and positioned within topographically protected areas (away from ridge tops). Clumps also could be positioned along clearcut/old-growth forest edges to minimize abruptness and microclimatic effects associated with edges (e.g., increase wind velocities; Chen et al. 1992).

Our results are significant to regional conservation and management of old-growth associated species. Notably, there is only one published study of breeding bird communities (Kessler and Kogut 1985) and no published studies of wintering bird communities in young- and old-growth forests in southeast Alaska. Kessler and Kogut (1985) conducted their study during only one breeding season and without the benefit of replicated sites. In addition, both the Brown Creeper and Red-breasted Sapsucker are "management indicator species" in the Forest (USDA Forest Service 1991) and the Pacific-slope Flycatcher has been proposed for similar designation (DellaSala et al. 1994). The USDA Forest Service uses management indicator species to assess the effects of timber harvest on wildlife habitat. This study supports the use of these species as management indicators and suggests the addition of the Pacific-slope Flycatcher and Golden-crowned Kinglet.

Our findings also suggest that old growth provides important refugia for some breeding and wintering bird species, particularly during harsh winters. Although none of the species we studied is threatened or endangered in southeast Alaska and they were observed in young growth in reduced numbers, up to 70% of 286,000 ha of old growth on the Island and elsewhere in the region will be harvested by the year 2150 (USDA Forest Service 1991). We encourage managers to begin the development of monitoring and conservation planning early on to avoid the future need for more reactionary approaches such as those that have characterized the policy debate in Pacific Northwest where old growth has declined substantially and the economic and social costs of protecting what remains has escalated.

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APPENDIX A. Total detections of uncommon (< 30 total detections in either year) breeding and wintering bird species in non-modified, canopy gapped, and precommercially thinned young-growth (20 years) and old growth (≥ 150 years) treatments (n = 5 sites/treatment) on Prince of Wales Island, southeast Alaska. Breeding bird detections were summed counts over the 1991 and 1992 breeding seasons. Wintering bird detections across top rows are for 1991–1992; those across bottom rows are for 1992–1993.

	Treatment			
Species	Non-modified	Gapped	Thinned	Old growth
Uncommon Breeding Birds				
Red Crossbill (*Loxia curvirostra*)	23	12	7	46
Pine Siskin (*Carduelis pinus*)	22	10	5	43
Rufous Hummingbird (*Selasphorus rufus*)	9	7	1	4
Ruby-crowned Kinglet (*Regulus calendula*)	12	10	14	2
Brown Creeper (*Certhia americana*)	0	0	0	22
Tree Swallow (*Tachycineta bicolor*)	2	6	2	0
Lincoln's Sparrow (*Melospiza lincolnii*)	2	2	1	3
Hairy Woodpecker (*Picoides villosus*)	0	0	2	4
Common Raven (*Corvus corax*)	0	3	0	1
Purple Finch (*Carpodacus purpureus*)	0	1	1	2
Northern Flicker (*Colaptes auratus*)	1	1	2	0
Olive-side Flycatcher (*Contopus borealis*)	1	0	1	0
Totals	72	52	36	127
Uncommon Wintering Birds				
Red Crossbill (*Loxia curvirostra*)	18	4	11	1
	1	2	2	0
Brown Creeper (*Certhia americana*)	0	1	0	21
	0	0	0	17
Pine Grosbeak (*Pinecola enucleator*)	9	2	4	0
	7	7	6	2
Common Raven (*Corvus corax*)	0	2	1	5
	0	0	3	9
Steller's Jay (*Cyanocitta stelleri*)	1	7	1	2
	4	3	2	1
Red-breasted Sapsucker (*Sphyrapicus ruber*)	0	0	0	1
	0	0	0	7
Hairy Woodpecker (*Picoides villosus*)	0	2	0	1
	0	1	0	4
Song Sparrow (*Melospiza melodia*)	0	1	1	0
	0	1	2	0
Bald Eagle (*Haliaeetus leucocephalus*)	0	0	0	2
	1	1	0	0
Evening Grosbeak (*Coccothraustes vespertinus*)	0	0	0	2
	0	0	0	0
Totals	28	19	18	35
	13	15	40	40

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

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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 (Leighty 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 nootkatensis*) 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

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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 tending 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.

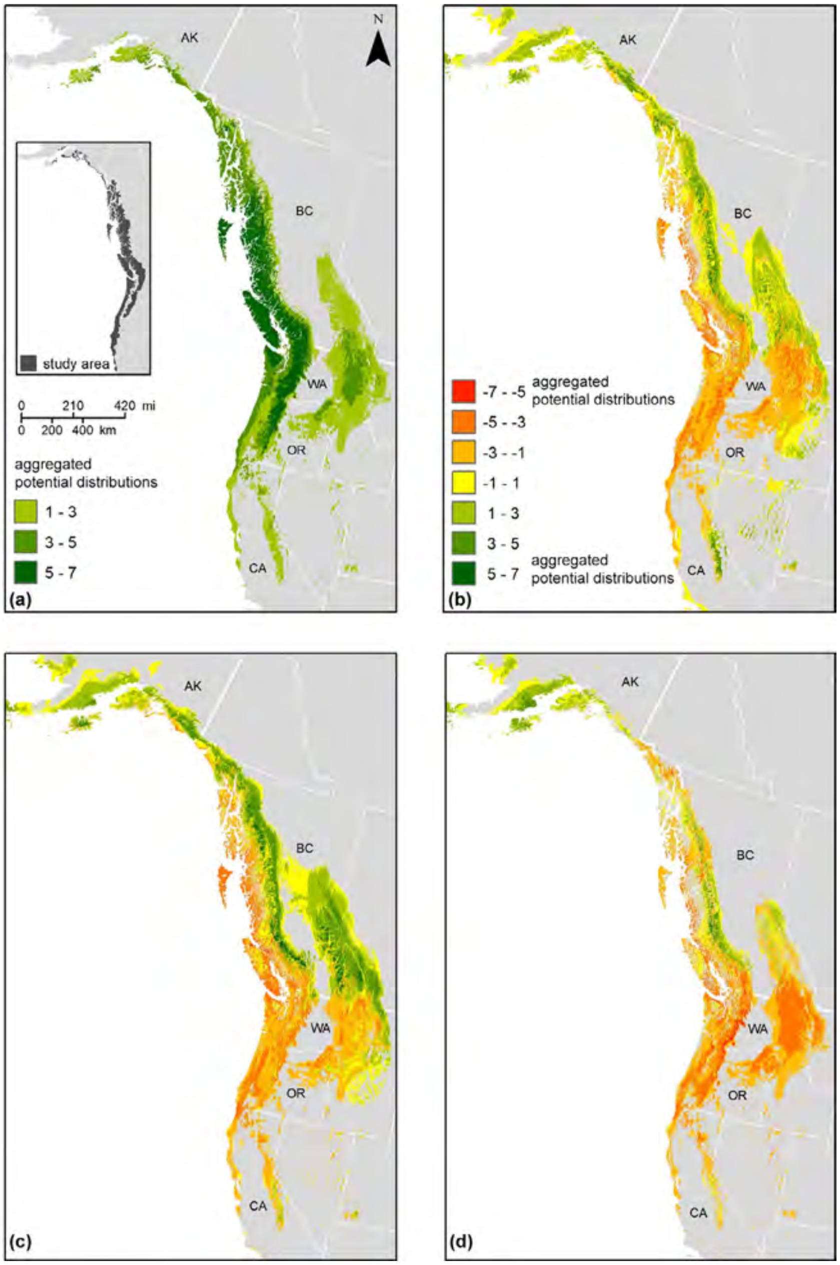

Figure 1 Aggregated potential distribution of eight focal conifer species (Pacific silver and grand fir, Alaska yellow-cedar, Sitka spruce, western red cedar, western and mountain hemlock, coast redwood) for the baseline period (a) and the richness changes for 2080s under scenario A2A ensemble-emissions 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°, 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)

Species	*Period*	*Loss (%)*	*Persistence (%)*	*Gain (%)*
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
Moutain hemlock	2050s	7	59	7
	2080s	15	33	4
Coast redwood	2050s	21	16	3
	2080s	23	1	0

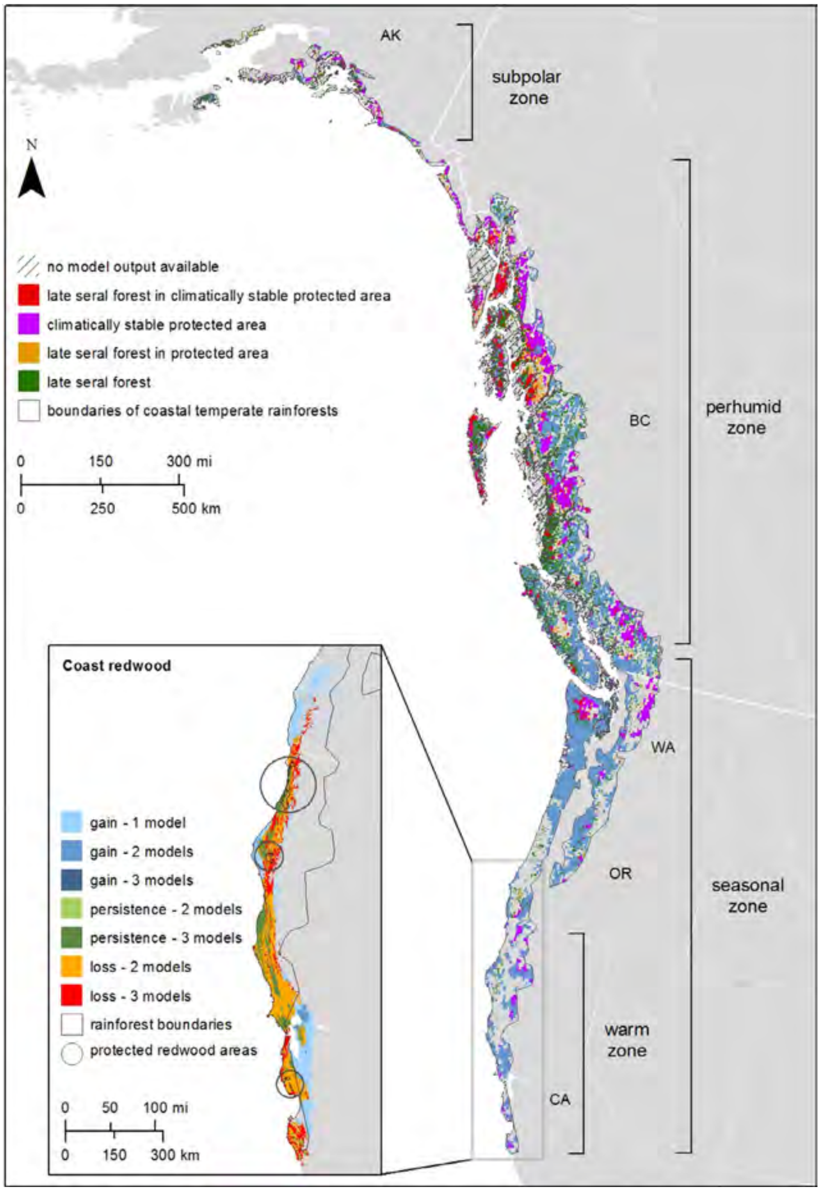

Figure 2 Predicted areas of vegetation stability (scenario A2, 2080s), protected areas, and late-seral forests in the Pacific coastal rainforests. Inset map shows potential distribution gain, persistence, and loss of coast redwood based on three GCMs (CSIRO, CCCMA, and HADCM3). The three circled areas 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.

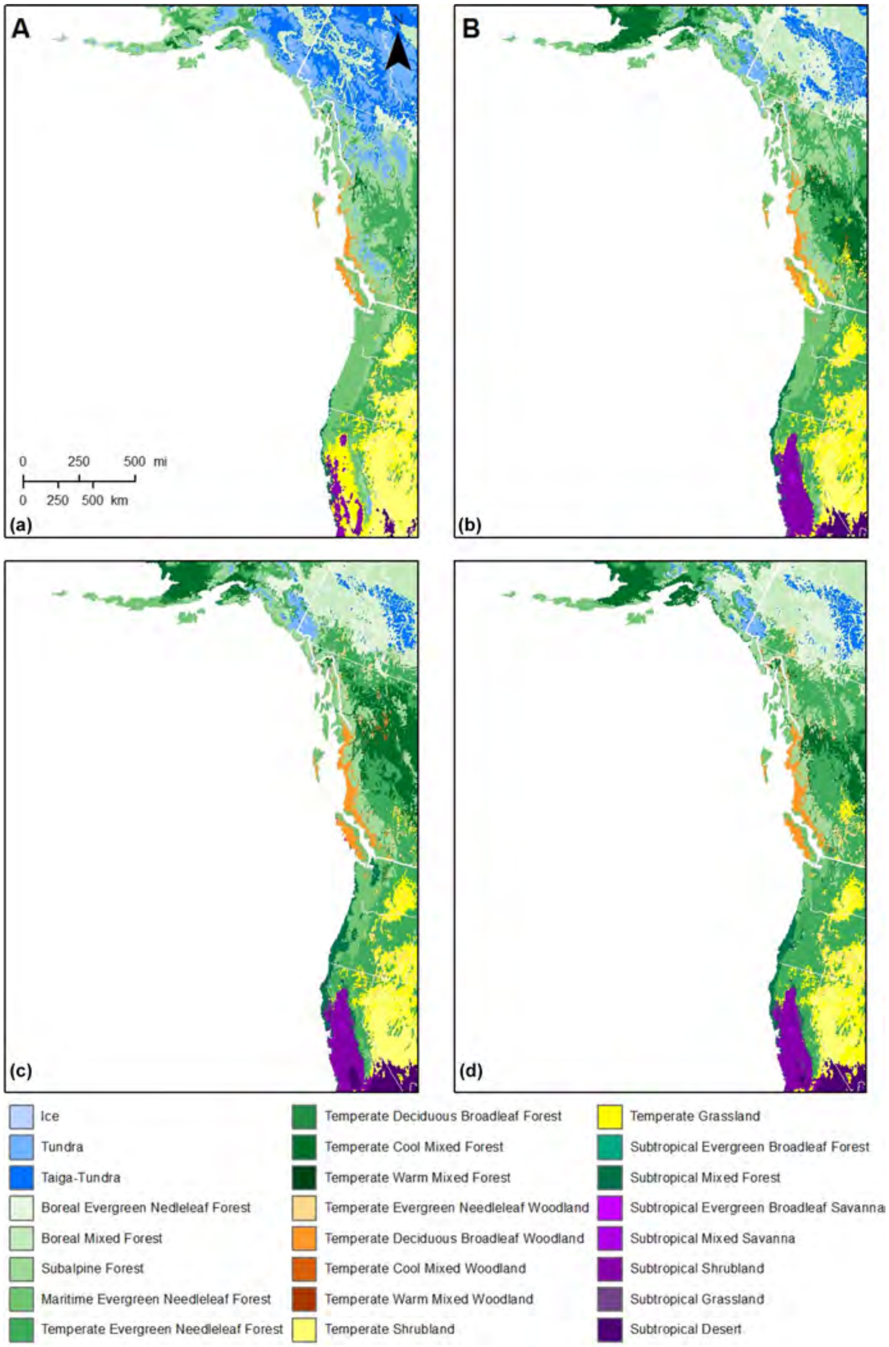

Figure 3 Outputs from MC1 functional vegetation model show baseline (a) and future dominant types of vegetation for 2080s (2075–85) based on three GCMs: CSIRO (b), MIROC (c), and HADCM3 (d).

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.

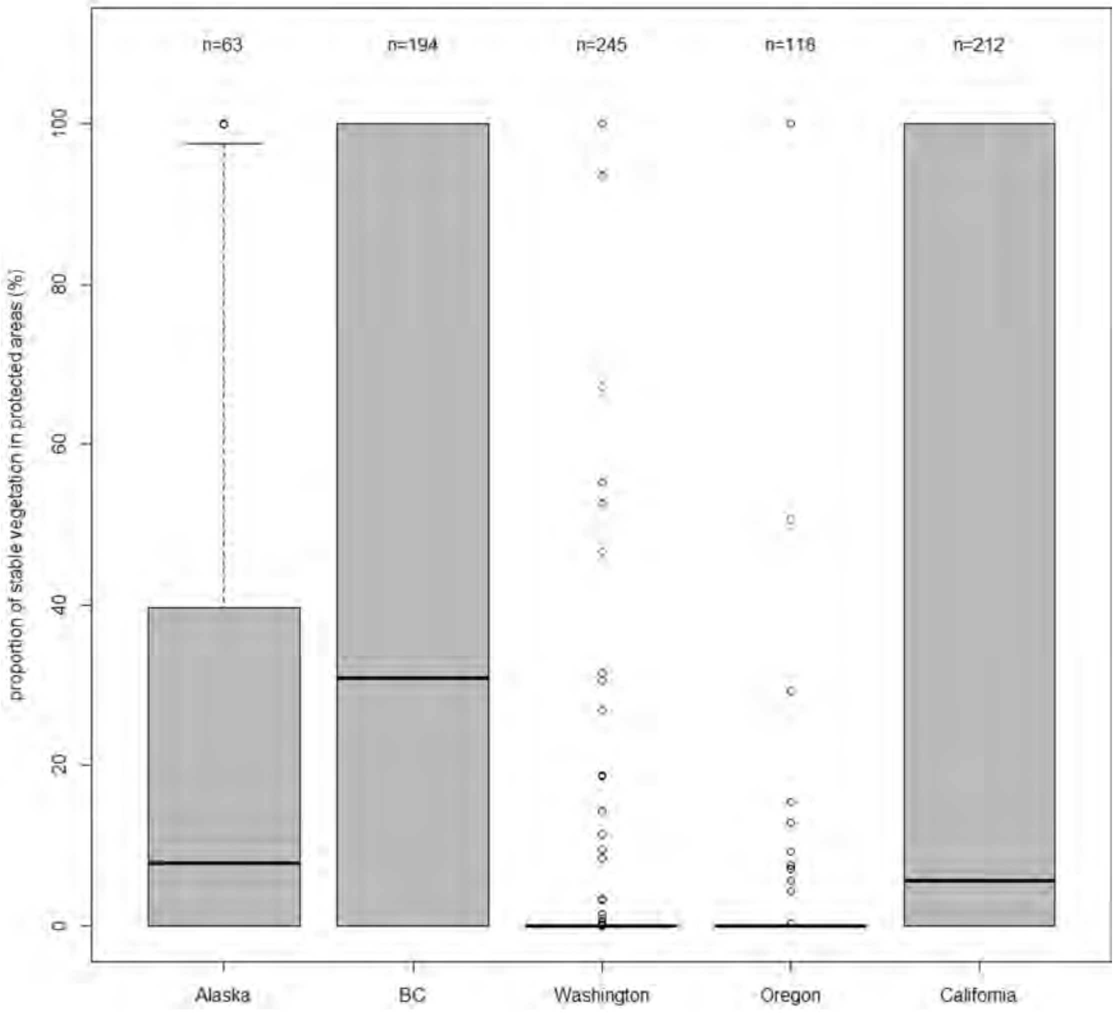

Figure 4 Predicted vegetation stability in protected areas per state or province derived from outputs of the MC1 model based on the agreement of three GCMs under the A2 scenario for 2080s (2075–85) (BC = British Columbia).

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 km^2) 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.

Acknowledgments

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

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ABSTRACT

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

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

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

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

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

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

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

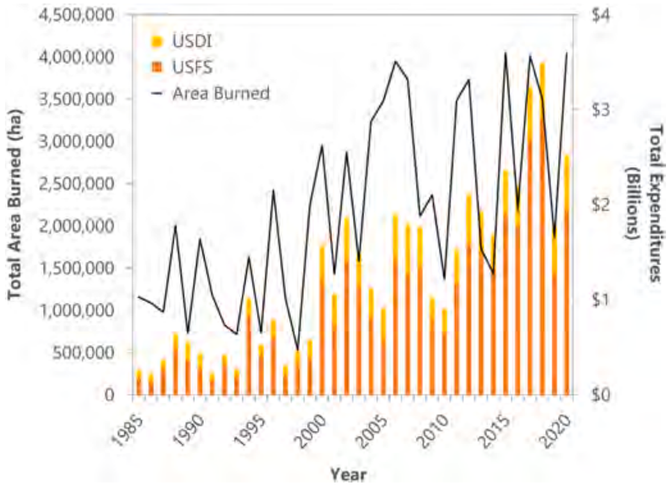

Fig. 1. Total area burned and wildfire suppression expenditures by federal land management agencies from 1985 to 2020. Data compiled from the National Interagency Fire Center suppression reports and from fiscal year agency budgets, with USDI mainly being National Park Service that since 1972 has been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

1.1. *Wildfire suppression*

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

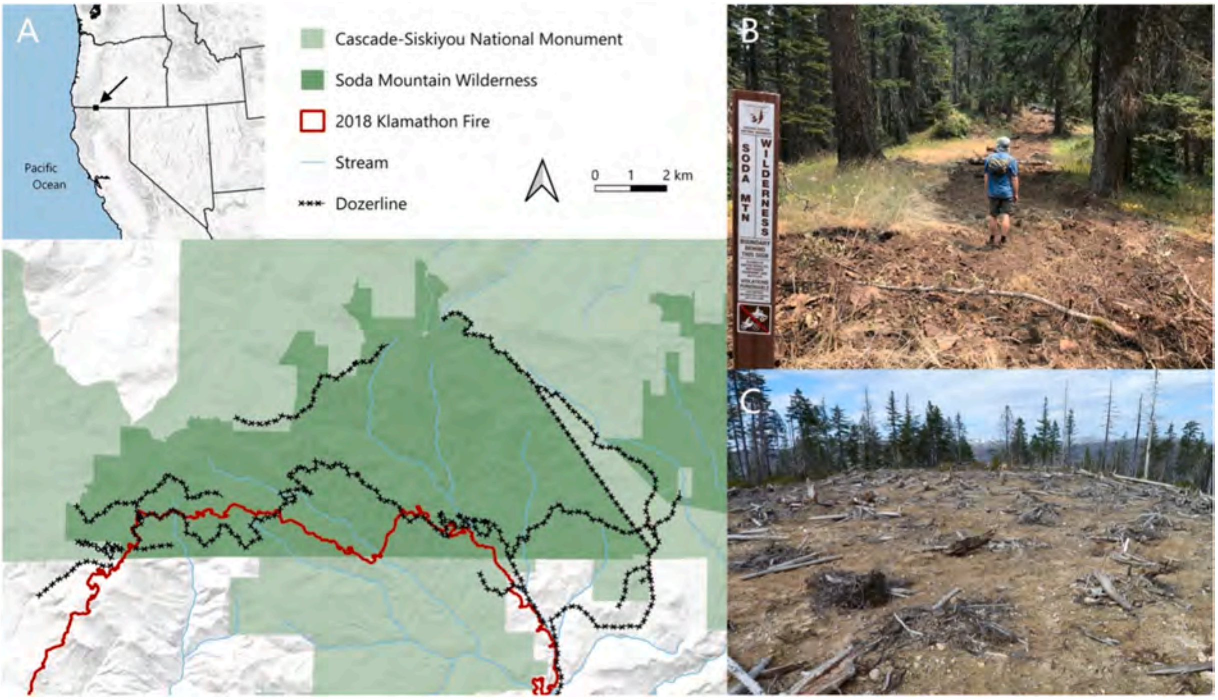

Fig. 2. (A). Extent of dozerlines built during the 2018 Klamathon fire in the Soda Mountain Wilderness within the Cascade-Siskiyou National Monument, southwest Oregon. (B) Close up of dozerline within the Soda Mountain Wilderness. The fire never reached this fireline because handlines built below were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

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

1.2. *Megafire active management approach*

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

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

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

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

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

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

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

2.1. High severity burn patches are biologically rich and undervalued

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

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

2.2. Good vs. bad fire terminology is subjectively misleading

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

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

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

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

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

2.4. High severity burn patches link successional processes

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

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

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

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

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

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

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

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

3.2. Snags are more than fuels

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

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

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

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

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

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

4.1. *Large trees are often removed in logging operations*

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

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

5. Do actively managed areas burn at lower severity?

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

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

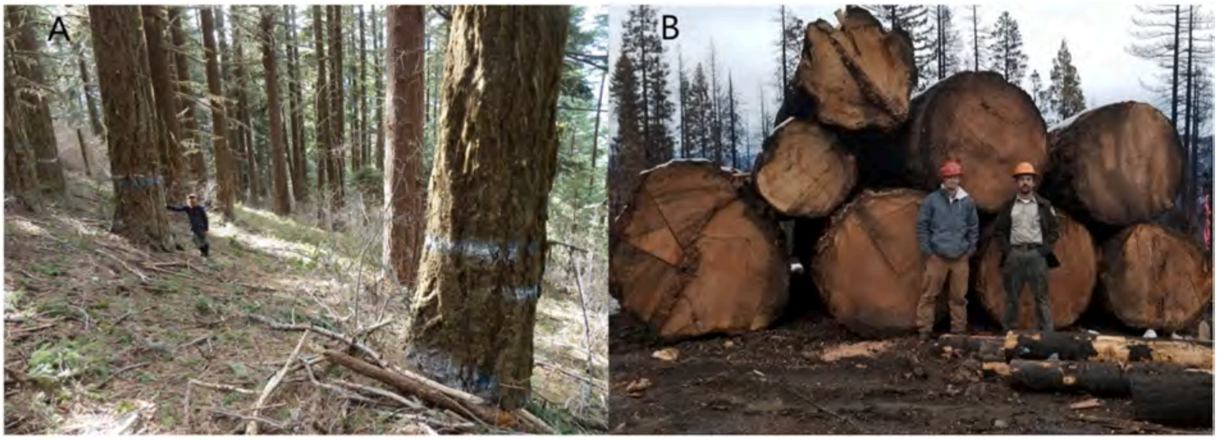

Fig. 3. (A) Nedsbar Timber Sale Medford District BLM Applegate Watershed (for “fuel reduction”) showing “take tree” markings. (B) Postfire logging on Takilma Happy Camp Road in response to the Slater fire, Rogue River-Siskiyou National Forest. These trees were regarded as fire hazards. Photos: L. Ruediger.

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

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

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

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

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

6. Is the precautionary principle constraining active management?

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

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

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

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

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

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

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

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

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

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

8. Redefining active management approaches

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

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

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

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

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

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

CRediT authorship contribution statement

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

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Declaration of competing interest

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Appendix A. Supplementary data

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

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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

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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 km^2, and only 7 % of which were > 100 km^2. 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

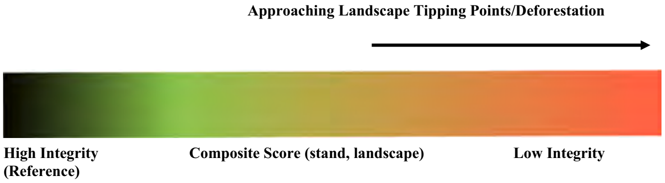

Fig. 1. Ecosystem integrity composite factors based on principles, criteria, indicators, and verifiers, as adapted from Mackey et al., 2024 and displayed in Table 1. Each of the factors in Table 1 can receive a scoring based on comparisons to reference conditions and site or regionally specific literature 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 Carbon stock levels (Mg/ha) all pools and by age classes Tree heights, canopy layering, biomass
	Ecosystem processes	Natural disturbances	Degree of altered fire and other disturbance regimes
		Nutrient cycling	Coarse woody Soil compaction Soil productivity Mycorrhizae functionality
		Optimal hydro-ecology	Unlogged watersheds Road-stream intersections Water quality limited streams Surface runoff Evapotranspiration rates
	Ecological composition	Ecosystem stability	Carbon stock (Mg/ha, all pools) average and range relative to reference Exotic vs native species (ratio)
		Adaptive potential	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)
	Ecosystem functionality (e.g., see Freudenberger et al., 2012)	Ecosystem complexity	Vegetation density, topographical heterogeneity, carbon storage, species richness of vascular plants, tree height, plant functional richness
		Climate buffering	Temperature remote-sensed data of forest patches (e.g., see Mann et al., 2023)
	Landscape characteristics	Spatial extent	High conservation value forests (e.g., https://www.hcvnetwork.org/hcv-approach; accessed December 11, 2024) Forest seral stages, especially old growth Patch sizes and distributions, especially large ones (total roadless area) Gamma diversity
		Spatial configuration	Barriers to wildlife movements Road density, mean/median roadless areas size (e.g., Ibisch et al., 2016) Intra-patch connectivity/fragmentation
		Temporal extent	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 proports 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 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).

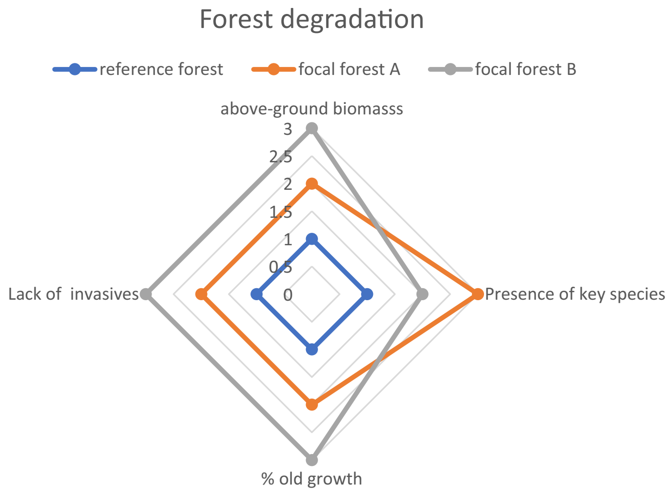

Fig. 3. Spiderweb schematic illustrating how the departure in integrity between two focal forests and a hypothetical reference condition can be scored (i.e., in comparison to primary forests, near-natural forest). The higher the overall score, the more significant the forest degradation. Statistical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

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).

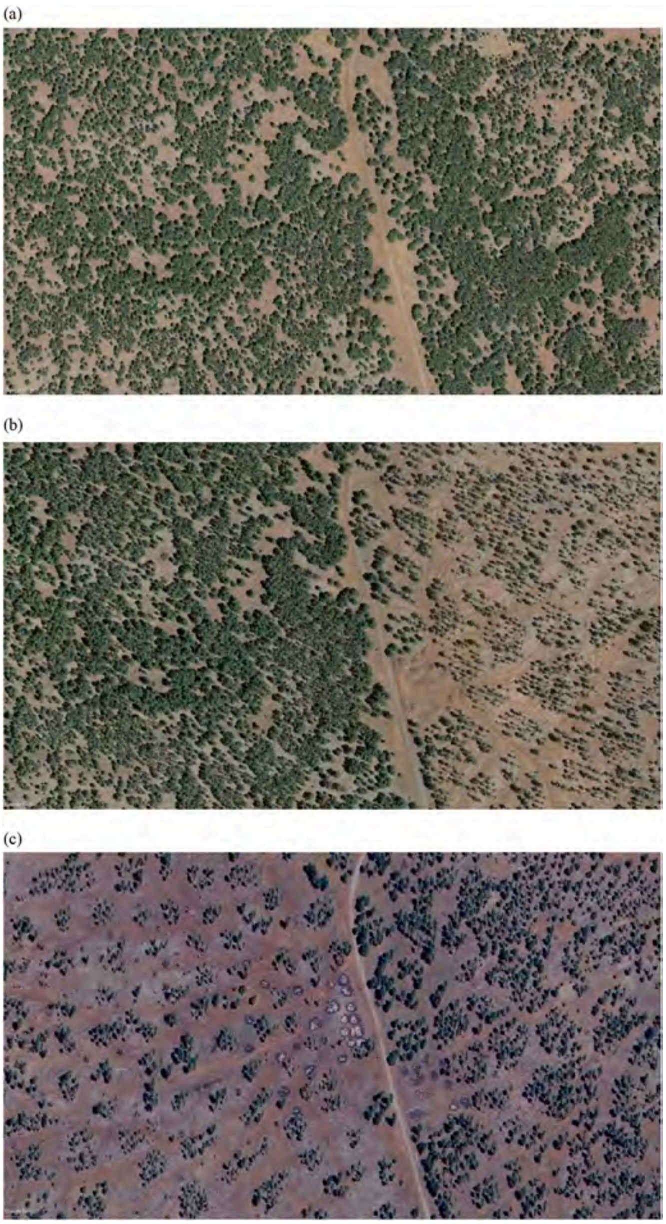

Fig. 5. Google Earth imagery of excessive fuel treatments on the Coconino National Forest, Arizona illustrating landscape scale changes (Table 1: landscape characteristics) showing (a) pre-treatment (2017); (b) commercial thinning (right side) in 2021; and (c) commercial thin (right) and group-selection (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 $<1\text{km}^2$, 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-Belarussian 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

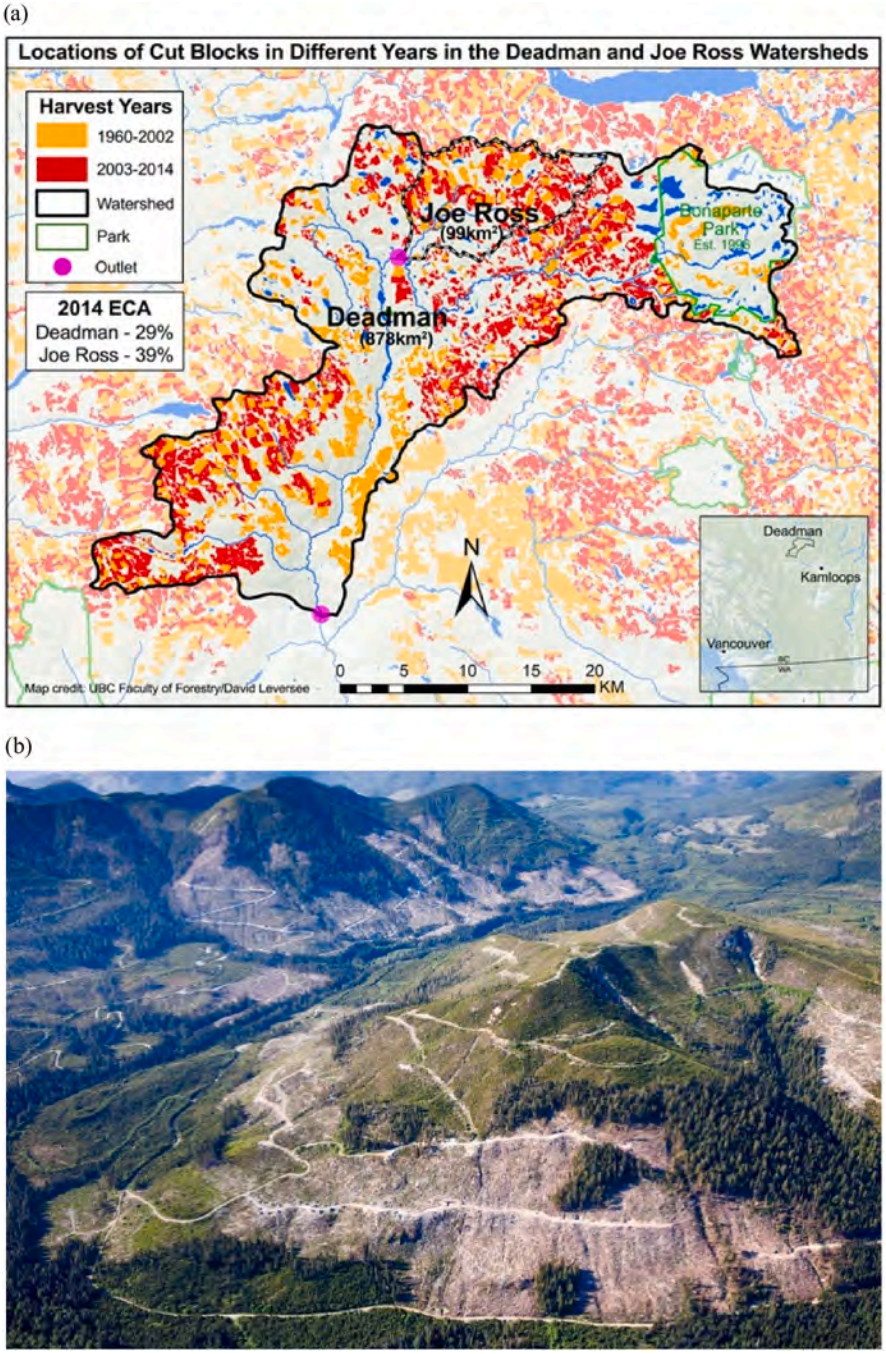

Fig. 6. (a) Extensive clearcutting with impacts that accumulate at the landscape scale, increasing the risk of extreme flooding and mass-wasting events (Table 1: ecosystem processes-hydrology; landscape characteristics). The equivalent clearcut area (ECA) is the area that has been clearcut with a reduction 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-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).

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.

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. **Julee 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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Data availability

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

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Article

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

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

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

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1. Introduction

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

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

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

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

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

2. Methods

2.1. Study Area

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

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

The Koppen Climate Classification subtype for the southeast Alaska region of our study area is "Dfc" (Continental Subarctic Climate). Mean precipitation during the winter is 642 mm (125 mm to 1473 mm range) and mean temperature in the summer is 12.5 °C (9.9° to 17.9 °C range), which is on the wetter, cooler side of temperate rainforests globally [3].

Due to the northern latitude and short growing seasons, treeline on the TNF is generally 300 m, declining northward. Old-growth forests are characterized by multi-layered forest canopies mainly of western hemlock (*Tsuga heterophylla*), yellow-cedar (*Calliptropsis nootkatensis*), mountain hemlock (*T. mertensiana*), Sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*), and low growing shore pine (*Pinus contorta*) on wetter sites such as muskegs. Rainforest understories are rich in forbs and shrubs [20,21] with dense mats of oceanic lichens and bryophytes that carpet the ground and extend into the overstory canopy.

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

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

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

2.2. Timber Sale Datasets

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

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

2.3. Carbon Datasets

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

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

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

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

2.4. GIS Overlays

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

2.5. Evaluating At-Risk IRA and POG Scenarios

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

2.6. Estimating Emissions from Harvested Wood Products

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

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

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

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

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

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

3. Results

3.1. Young vs. Productive Old Growth Forests

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

3.2. Timber Volume Sold by Time Period

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

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

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

3.3. Carbon Stocks

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

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

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

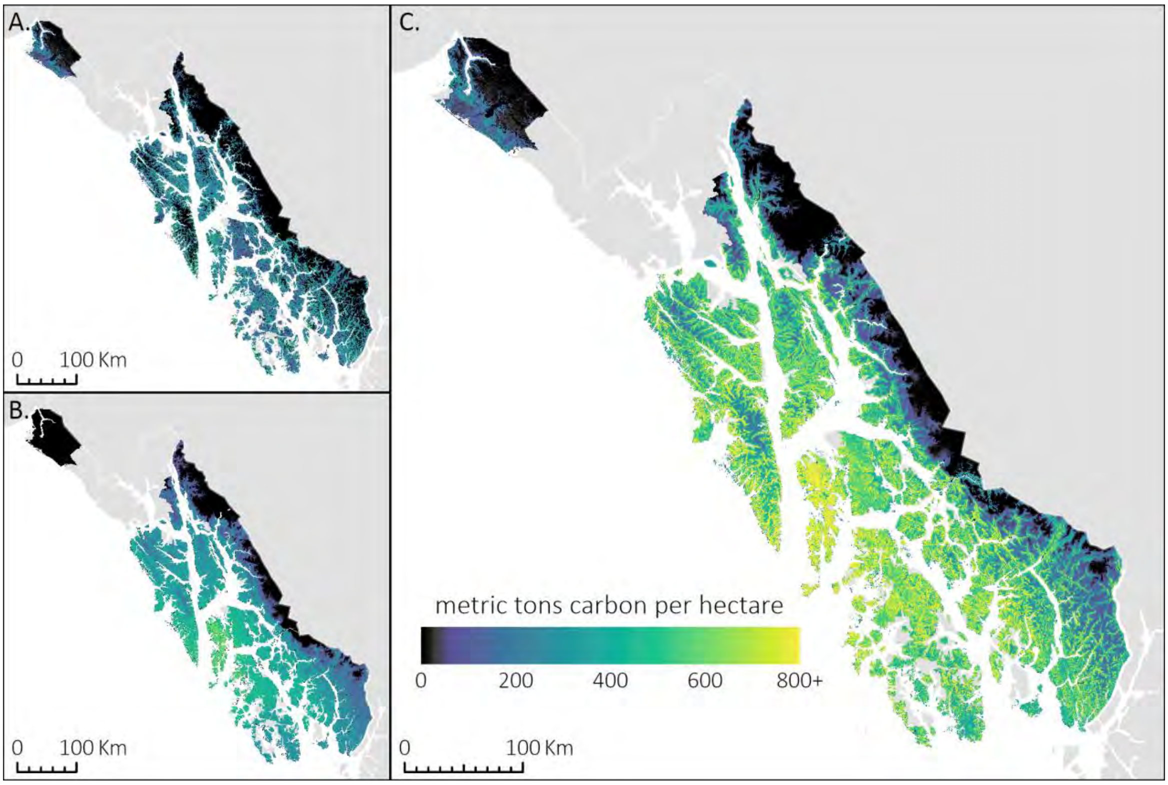

Figure 2. Spatial distribution of carbon (metric tons ha^{-1}) stored in (**A**) woody plant biomass (carbon pools include trees, roots, woody debris, seedlings/saplings, snags, and understory vegetation), (**B**) soil organic matter (top 1 m of mineral soil plus surface organic horizons), and (**C**)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

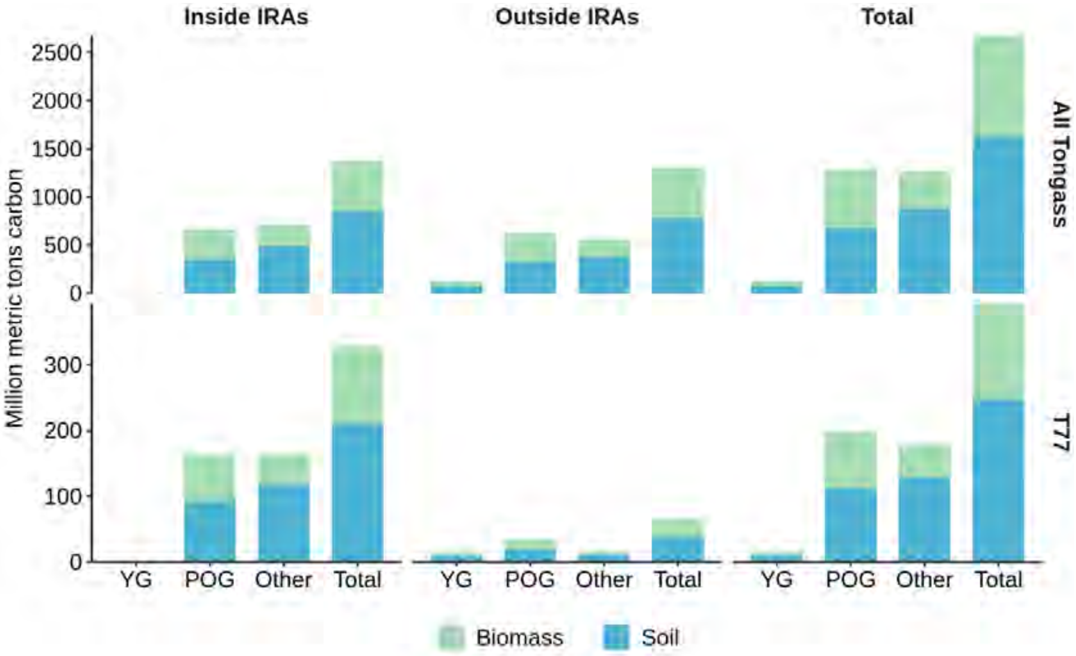

Figure 3. Carbon (million metric tons) stored in woody plant biomass and soil by forest age class (YG = young growth; POG = productive old growth) both inside and outside of Inventoried Roadless Areas (IRAs) and inside Tongass 77 watersheds (T77; bottom row) on the Tongass National Forest (top).

3.4. At-Risk Scenarios

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

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

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

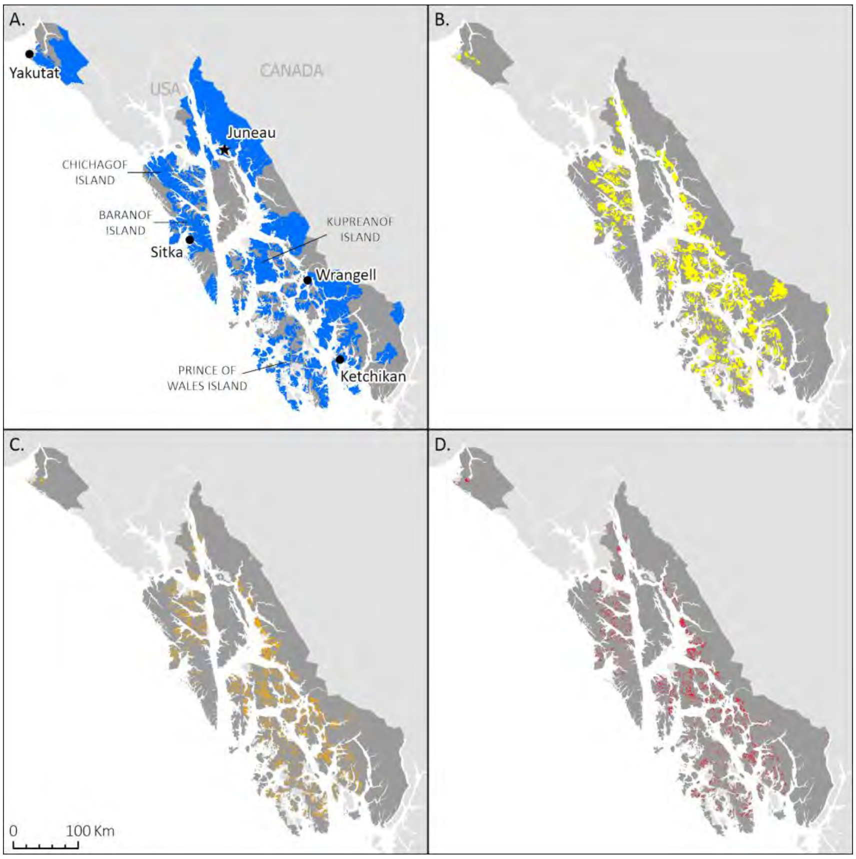

Figure 4. Spatial distribution of inventoried roadless areas based on: (**A**) all roadless areas (blue), (**B**) scenario 1 (yellow), (**C**) scenario 2 (orange), and (**D**) scenario 3 (red). Study area shown in gray. See Section 2.5. for description of scenarios.

3.5. Estimated Carbon Emissions

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

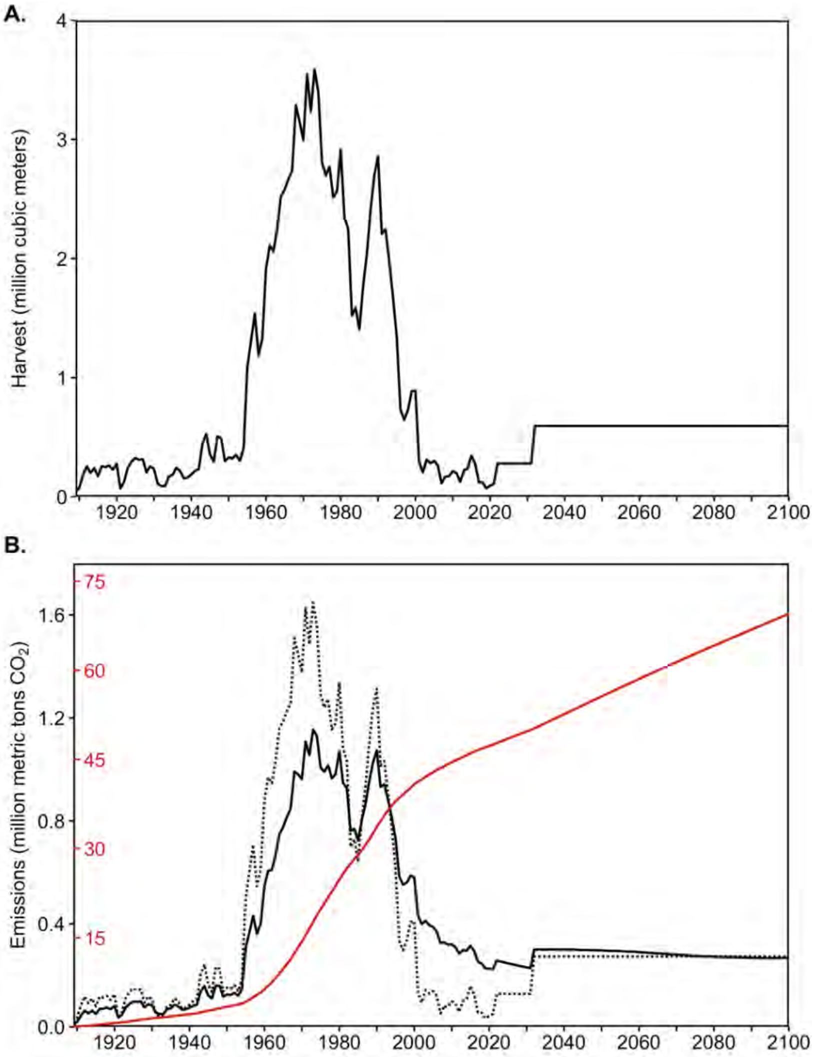

Figure 5. (**A**) Historic (1909–2021) and projected (2022–2100) annual harvest volumes (million cubic meters) for the Tongass National Forest. (**B**) Estimated 100-yr emissions from harvested wood products

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

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

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

4. Discussion

4.1. Timber Volume and Associated Impacts

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

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

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

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

4.2. Carbon Stock (Carbon Reservoir)

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

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

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

4.3. Importance of IRAs and Tongass 77 Watersheds

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

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

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

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

4.4. Stock Change Due to Logging

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

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

5. Conclusions

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

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

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

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

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

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

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

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

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

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Can Young-Growth Forests Save the Tongass Rainforest in Southeast Alaska?

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Abstract

The Tongass National Forest in southeast Alaska is one of the last relatively intact temperate rainforests in the world. Due to public controversy over old-growth logging, the USDA Forest Service finalized a plan in 2016 to transition out of old-growth logging but not until 2032 as the agency claims it needs to log ∼17,000 ha of old growth as "bridge timber" until some 114,000 ha of young growth regenerating from prior clearcut logging is readily available. Transitioning out of old growth logging faster than proposed by the Forest Service would maintain fish, wildlife, and climate benefits along with timber industry needs more aligned with the limits of what the Tongass rainforest can sustain. Recent young growth (mainly 55-year old precommercially thinned stands) inventories on the Tongass suggest that the Forest Service can begin a transition out of old-growth logging within 5 years and on a much smaller (∼50,000 ha) and predominately young growth land base than the agency proposes in its transition plan, if certain conditions are met.

> "The Tongass National Forest is a national treasure. Today, I am outlining a series of actions by USDA and the Forest Service that will protect the old-growth forests of the Tongass while preserving forest jobs in southeast Alaska. I am asking the Forest Service to immediately begin planning for the transition to harvesting second growth timber while reducing old-growth harvesting over time."
>
> July 3, 2013 Press Release, USDA Secretary Tom Vilsack

Tongass as a World Class Temperate Rainforest

At 6.8 million hectares, the Tongass National Forest in southeast Alaska is the largest national forest in the United States and one of the world's last relatively intact temperate rainforests (DellaSala, 2011). This national forest is hemmed in by glaciated Coast Mountains to the east and numerous near-shore islands to the west ranging from the Yakutat Forelands in the north to Prince of Wales Island south (one of the largest islands in North America) (**Fig. 1**).

Some 90% (>2 million ha) of forests on the Tongass is considered "productive" old growth, consisting of structurally complex, multilayered forests with trees >150 years (Schoen and Orians, 2013, also see **Fig. 1**). Old-growth Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forests on the Tongass are global carbon sinks (Leighty et al., 2006) that store atmospheric carbon for centuries primarily because the maritime climate limits fire occurrence. The region's relatively intact watersheds provide ideal conditions (compared to the lower 48 states) for five species of salmonids (*Oncorhynchus* spp.), a principal food source for grizzly bears (*Ursus arctos*), wolves (*Canis lupus ligoni*, unique subspecies), and bald eagles (*Haliaeetus leucocephalus*).

In spite of its global significance, the Tongass is the only national forest in the nation that still clearcuts (clear-fells) old growth on an industrial scale. Old-growth logging began in earnest in the 1950s with peak logging levels achieved in the 1960s–80s (**Fig. 2**). At the time, "high-grading" of the largest trees was a common practice that concentrated logging in low-elevation systems and on productive karst (limestone base) topography (Schoen and Orians, 2013).

The Tongass is now at a critical juncture regarding its status as a global carbon sink and relatively intact rainforest. Compared to the Pacific Northwest, which overcut old growth decades ago resulting in a shutdown of federal lands logging due to litigation over the imperiled Northern Spotted Owl (*Strix occidentalis caurina*), the Tongass currently has no endangered species. Therefore, there is a unique opportunity to transition out of old-growth logging to avoid future controversial listings.

In 2016, the USDA Forest Service finalized an amendment to the Tongass land use plan to transition out of old-growth logging if certain conditions were met. The transition would provide a potential means to end decades of controversy where the choices were limited to either protect some or clearcut much of the old growth (**Fig. 3**). A transition would present a third option that would eventually rely mostly on limiting logging to young forests regenerating from prior clearcut logging.

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Data sources: NACP Aboveground Biomass and Carbon Baseline Data (NBCD 2000), Aboveground forest biomass for Alaska, USDA-FS FIA & RSAC (from Data Basin by the Conservation Biology Institute

Fig. 1 Tongass National Forest, southeast Alaska. Map provided by J. Leonard, Geos Institute. Dark green shows forests exceptionally high carbon-biomass important in climate regulation and climate refugia (DellaSala, 2011).

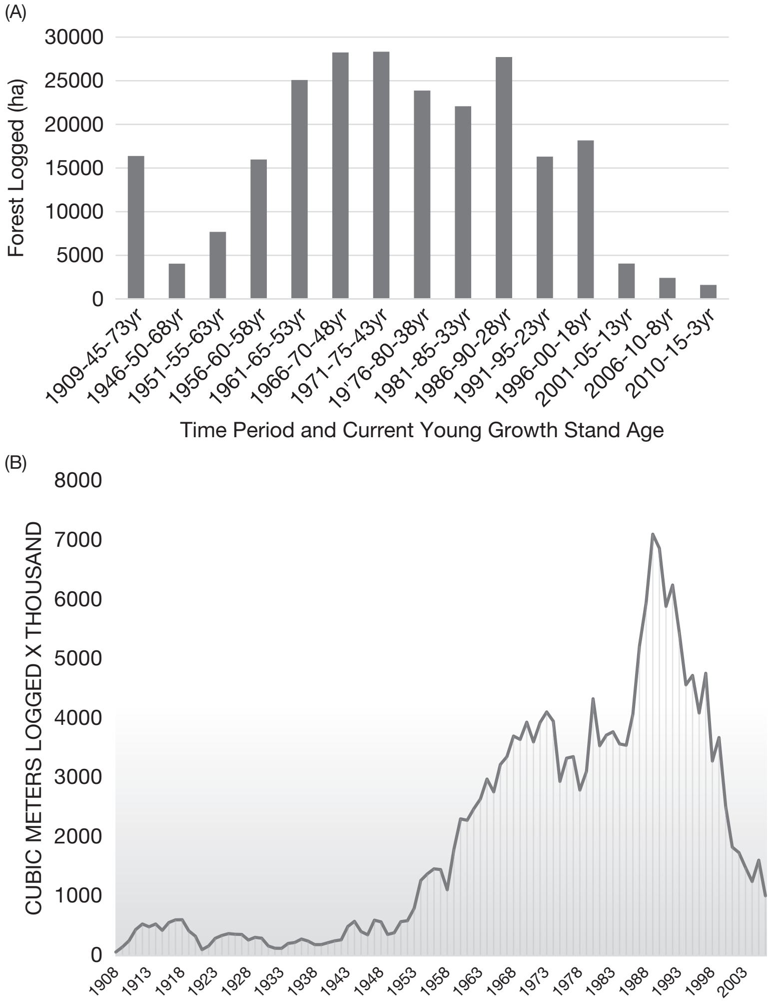

Fig. 2 (A) Tongass National Forest old-growth forest logged from 1909 to 2015 and current (2018) age of logged young stands. (B) Timber volume logged from 1908 to 2006 on the Tongass National Forest. Volume calculations (cubic meters) are based on green and rough sawn at 1 full inch containing ~2.4 cubic meters of usable material. Actual recovery of lumber is greater than estimated long log scale and therefore a conversion factor of 6.25 was used to express the data in cubic meters. Data for both figures were extracted from available timber harvest records courtesy of A. Brackley, USDA Forest Service, Pacific Northwest Research Station, Sitka, AK, United States.

To achieve its transition, the Forest Service specified that it would need to log another ~17,000 ha of old growth during the next 16 years (presumably to 2032) before getting to ~114,000 ha of young growth needed to sustain industry over a 100-year period at a projected volume of 287.5 million cubic meters annually.

Setting a Transition Timeline: Young Growth Volume

Determining when to transition out of old growth centers on how much young growth is available now and into the future and the commercial viability of young trees (i.e., can industry make a profit?). Only the volume necessary to meet a transition timeline is estimated herein. More detailed timber volume estimates and a study of economic value of young growth trees are currently in progress.

Adjusting Cumulative Mean Annual Increment (CMAI)—young growth stands on the Tongass must reach 95% of CMAI, generally the time at which annual growth of trees begins to level off before a regeneration (clearcut) harvest is attempted (~80–90 years, pers. commun. A. Brackley). However, the Forest Service can relax this requirement if logging is deemed consistent with other plan components of its land management plan, which, in this case, is a transition out of old-growth logging. Shorter rotation ages allow capture of timber volume in younger age stands. We argue that a rotation age of 55-years can be used to achieve transition quickly, as this age class corresponds to the oldest young growth stands currently available on the Tongass (Fig. 2) and the average quartile mean diameter-at-breast-height of 28 cm, which is currently being exported on private lands in the region.

Fig. 3 Three choices on the Tongass rainforest: (A) protect some of the old growth for ecological, cultural, and climate benefits; (B) log most of the accessible old growth and convert it to commercially producing plantations; and (C) transition into previously logged and now regenerated young growth (D. DellaSala). Note on the Tongass, regeneration following clearcut logging is via natural seed source. No planting is necessary.

Ecological and Operability Constraints on Young Growth Logging—Based on Forest Service inventories, the Tongass has over 173,000 ha of young growth of varying ages (mostly <50 years; Fig. 2); 71% of this is within roaded and development land-use designations and technically within the timber base (USDA Forest Service 2014). Notably, the Forest Service uses the most current and complete data available on young growth, which provided a foundation for a faster transition (http://databasin.org/maps/d4ee7a0d9662463289b17bf429f6a0ff/active).

For this estimate, we included young stands (55 years) within 240 m of operable roads that were either precommercially thinned (PCT) or commercially thinned (CT), on slopes <72% (based on prior Forest Service analysis), and not within ecologically sensitive areas (Table 1). Precommercial thinning on the Tongass is designed to reduce competition among densely packed young trees (speeding up growth rates) and usually occurs 15–30 years after stand initiation. A second entry via commercial thinning typically occurs at ~60 years with extraction of commercial product.

Young Growth Timber Volume Projections—Based on the logging constraints proposed, sufficient young growth timber volume would be readily available on the Tongass to meet transition requirements (~287 million cubic meters annually) beginning as soon as 2020 (Table 2). Obtaining young growth volume from these stands would reduce the timber land base by >60% of the Forest Service's transition footprint. In sum, ~50,000 ha of predominately young growth PCT and CT stands within five Ranger Districts closest to milling operations could support a more rapid transition with reduced insert "environmental" conflicts.

Young Growth Economics: The Bottom Line

Determining the market potential of young growth on the Tongass is in early stages but initial results are promising (Fig. 4). For instance, a commercial thinning project ("Dragon Point commercial thin") in 70-year old young growth offered by the Forest Service yielded 28.1 million cubic meters with an appraised value of $440,035. All four timber sale bids received by the agency were above appraised value and one was 81% above appraisal (http://sitkawild.org/2014/06/dargon-point-timber-sale-local-wood-local-benefits/). The private sector (mainly Sealaska Native Corporation) also exports Sitka spruce round logs from 50 to 70-year-old young growth in the region.

Table 1 Ecological and operability constraints for a 55-year old young growth timber base within five Tongass Ranger Districts (Thorne Bay, Craig, Petersburg, Wrangell, Ketchikan) closet to timber mills

	Importance
Ecological constraint	
Karst topography	Known to be highly productive and likely to become future old growth via restoration (also the terrain tends to be unstable due to physical and chemical weathering of the bedrock geology
Wilderness, land-use II designations, national monuments, inventoried roadless areas	High ecological values, mostly old growth, mostly off-limits to logging (out of the timber base)
Beach fringe, riparian buffers	Highly productive ecotones for salmon, bears, eagles, and other wildlife and where logging is restricted via forest plan standards and guidelines
Slopes $>72\%$	Unstable and erosive
Natural disturbances	To allow for development of complex early seral forests and succession to old growth
Not in the suitable harvest base	Already restricted due to environmental concerns
Operability constraint	
5 Ranger districts with prior log sourcing	Hauling distance
Precommercially thinned within 240 m of operable roads (as determined by the Forest Service)	Already productive with road access
Precommercially thinned with at least partial overlap with a 240-m road access buffer	May have access problems given part of the stand lies outside the 240-m buffer
Commercially thinned stands within 240 m of road access	Additional young growth sites for volume estimates

Table 2 Timber volume scenarios within five Tongass ranger districts (Craig, Wrangell, Ketchikan, Thorne Bay, Petersburg) projected over a six-decade period using precommercially thinned (PCT) stands within ~240 m of operable roads. Carryover volumes are based on harvest levels remaining consistent for each of the scenarios with the carryover from prior periods being used to supplement the harvest base such that there are no rolling green outs

Time period	*Annual cubic meters × thousand*	*Annual carryover/deficit cubic meters × thousand*	*Additive annual carryover/deficit cubic meters × thousand*
2015–19	142,512	−4362	
2020–24	524,968	290,594	290,593
2025–29	520,119	285,744	576,338
2030–34	475,569	241,194	817,531
2035–39	394,338	159,962	977,494
2040–44	299,850	65,475	1,042,969
2045–49	205,206	−29,169	1,013,800
2050–54	42,881	−191,494	822,306
2055–59	194	−234,181	588,125
2060–64	0	−234,375	353,750
2065–69	0	−234,375	119,375
2070–74[a]	142,512	−91,862	27,521
2075–79	524,969	290,594	318,106

[a] Re-harvest of 2015–19 units begins.

As an important next step to securing a rapid transition, an economic study is needed to determine lumber grade of 55-year old logs, in consultation with experts from the timber industry and Forest Service. Recently proposed on the Tongass, a wood products study would allow mills to sort young growth by "value-added" lumber and determine market response, securing the best possible information on young growth log and lumber recovery, young growth value-added grade recovery, and market response to young-growth wood products.

Climate Benefits of a Rapid Transition

Tongass rainforests not only store more carbon than any national forest in the United States, but also may function as a critically important climate refuge (i.e., first line of defense) given maritime influences that moderate more extreme climate events anticipated for interior Alaska and temperate regions further south (DellaSala et al., 2017). Relatively intact watersheds also provide refuge for old-growth dependent species (including many that are important to subsistence needs), while buffering salmon from cumulative effects of climate change and more extensive logging in the surroundings (especially on private lands) (Watson et al., 2013).

Notably, prior estimates of carbon flux from logging scenarios on the Tongass indicate that *only a no-logging scenario* maintains carbon stores over time. Carbon also has future economic value in terms of avoided costs from global warming pollution and development of carbon-offset markets. For instance, if carbon were stored long-term in old-growth forests instead of being released to the atmosphere by logging, estimated annual economic value of stored carbon would be comparable to revenue generated from Tongass timber sales should carbon markets mature (Leighty et al., 2006). Importantly, an Interagency Working Group on Social Cost of Carbon estimated that the costs of carbon from global warming effects would be $27–221 per ton by 2050. Recent evidence suggests the costs may be much higher, including large demographic displacements of human settlements along coastlines (Pizer et al., 2014).

Soon after logging old growth, carbon is emitted to the atmosphere via decomposition of logging slash, fossil-fuel emissions from transport and wood processing (e.g., up to 50% of Tongass logs can be shipped overseas), and decay or combustion (within 40–50 years) of forest products in landfills. Planting or growing young trees or storing carbon in wood products does not make up for emissions released from a logged forest, especially one on short timber rotations ($<$100 years compared to old-growth forests that store carbon for centuries). Indeed, after an old forest is clearcut, the young forest remains a net CO_2 emitter for 5–50 years, depending on site productivity (see Harmon et al., 1990; Law and Harmon, 2011) (**Fig. 5**).

Globally, deforestation (8%–15%) and forest degradation (6%–13%) contribute more greenhouse gas pollution than the world's entire transportation network (Estimates are conservative as they were mainly derived from the tropics where the majority

Fig. 4 (A) Young trees on a log deck awaiting processing. (B) Milled beams processed by local Alaskan mill (D. DellaSala).

Fig. 5 Logging on the Tongass National Forest contributes greenhouse gas emissions while depleting fish and wildlife habitat (D. DellaSala).

of forest losses occur—boreal and temperate losses are not available at this time (Intergovernmental Panel on Climate Change, 2007; Houghton et al., 2012). Recognizing the importance of unlogged forests as carbon sinks, scientists have repeatedly called for protecting carbon stored in primary forests as integral to stabilizing global climate change (Mackey et al., 2014), which is why countries have committed to reducing emissions and protecting forest sinks (COP 21 climate agreements).

Tongass Climate Change Refuge: Uncertainties and Risks

Follow Up Research and Monitoring—reliably estimating carbon flux under different transition scenarios requires comprehensive carbon assessment tools. Without the benefit of such analysis, however, the Forest Service claims that logging old-growth forests "could result in *either a net loss or gain* of carbon" (emphasis added) depending on logging practices used even though clearcut logging (a substantial emissions source) is the method of choice on the Tongass (some young tree retentions and small (<4 ha) clearcuts are proposed in young forests within Old Growth Reserves and Beach buffers by the agency). Follow up work, ideally conducted by the Forest Service, in consultation with carbon scientists, is needed to determine logging emissions; however, in prior simulations (as noted), only a no-logging alternative results in continued long-term carbon storage (Leighty et al., 2006).

Climate Shift Happens—effects of climate change on forest productivity represent significant and costly risks to the Tongass' global status. As the climate warms, other vegetation types may replace carbon-dense conifer forests on the Tongass that evolved during a cooler climate (DellaSala et al., 2017). For instance, during the Miocene millions of years ago, Alaska was a much warmer place dominated by hardwood forests. As current climate change accelerates, it could lower carbon storage potential of conifer forests as hardwoods gradually replaces conifers and some conifers die off (thereby emitting CO_2 as is currently happening with an extensive die-off of Alaska yellow cedar *Cupressus nootkatensis*; Hennon et al., 2012). However, the maritime climate of the Tongass also might ameliorate some of climate-mediated impacts compared to more extreme changes for interior Alaska and temperate rainforests to the south, but only if old-growth forests are intact (DellaSala et al., 2017) (**Fig. 6**).

In sum, the Tongass is a global carbon sink; however, this sink may increasingly become an emissions source due to old-growth logging (DellaSala, 2011). Choosing a climate responsible and rapid transition for the Tongass would better safeguard Alaska's climate, comply with the COP 21 Paris climate change agreements and the global pledge by governments and entities to end global deforestation.

> "We share the vision of slowing, halting, and reversing global forest loss while simultaneously enhancing food security for all. Reducing emissions from deforestation and increasing forest restoration will be extremely important in limiting global warming to 2°C." United Nations Climate Summit New York Declaration on Forests (agreed to by 157 governments, including the United States, indigenous groups, corporations, NGOs, and others).

Fig. 6 Relatively intact forest landscape (potential climate refuge) within Mendenhall Glacier National Park near Juneau, Alaska (A. DellaSala).

Conclusions

The Tongass is one of the last places on Earth where primary forests (unlogged) are still relatively abundant but declining. This critically important rainforest provides Alaskans with unparalleled economic (e.g., recreation and tourism economies greatly exceed logging related jobs and revenue), ecological, and climate benefits (Schoen and Orians, 2013). Using Forest Service inventories, a rapid transition could (1) begin in 2020 as 55-year stands become increasingly available compared to the agency's 2032 transition that relies mostly on old growth logging to get to a transition stage; (2) achieved on a much smaller land base ($\sim$50,000 ha of young growth vs. a mix of 114,000 ha of young growth and 17,000 ha of old growth); and (3) result in substantially less carbon emissions along with ecological and cultural benefits sustained over time. Under a rapid transition, logging would occur within areas of relatively low controversy, reducing litigation costs and uncertainty of timber supply to local mills. An economic assessment of young growth is needed to fully assess viability of young trees.

The Tongass is the only national forest still clear cutting old growth on an industrial scale. Other national forests such as the Siuslaw in Oregon are generating young growth timber volume as part of a 1990s-transition due to policy reforms enacted. The time for the Tongass to make a transition is rapidly approaching if the Forest Service will act while there is still significant old growth remaining to conserve and without the controversy of future endangered species listings and ongoing timber wars.

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LETTER

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

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Supplementary material for this article is available online

Abstract

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

Introduction

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

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

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

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

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

Methods

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

Displacement decline

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

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

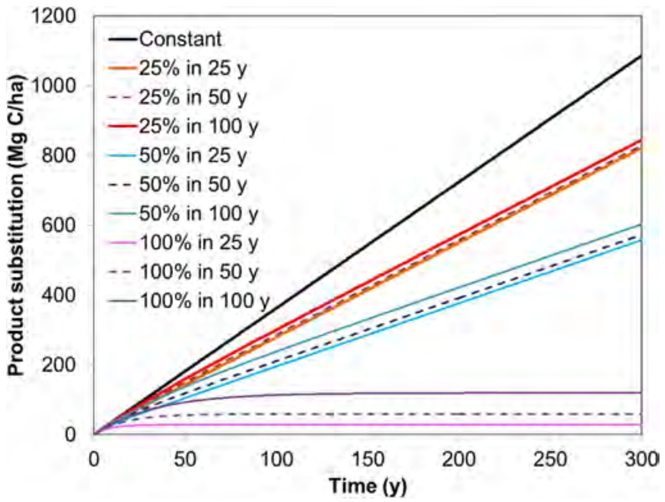

Figure 1. Accumulation of product substitution carbon when displacement is reduced 25%–100% over a 25–100 year period for a 50 year clear-cut harvest interval. For these simulations losses via leakage and replacement were zero[3].

Leakage losses

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

Replacement losses

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

Overall effect

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

Results

Displacement decline

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

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

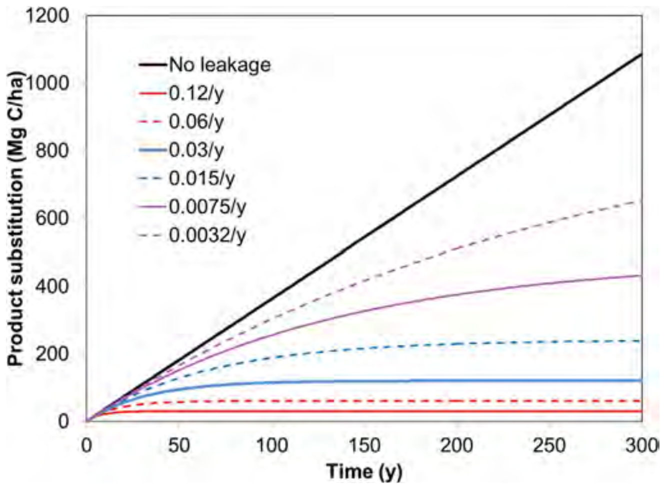

Figure 2. Accumulation of product substitution carbon when the time for displacement to be lost via leakage varies from 25 to 800 years for a 50 year clear-cut harvest interval. Displacement was assumed constant and replacement losses zero[3].

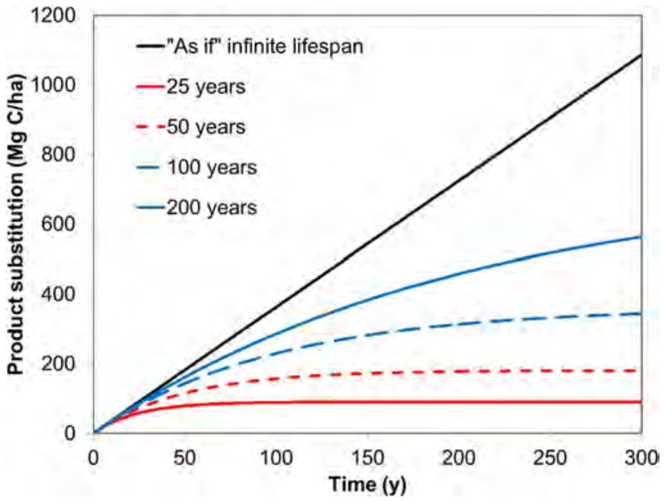

Figure 3. Accumulation of product substitution carbon when the average longevity of building varies for a 50 year clear-cut harvest interval. For these simulations displacement was constant and there were no leakage losses[3].

Leakage losses

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

Replacement losses

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

Overall effect

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

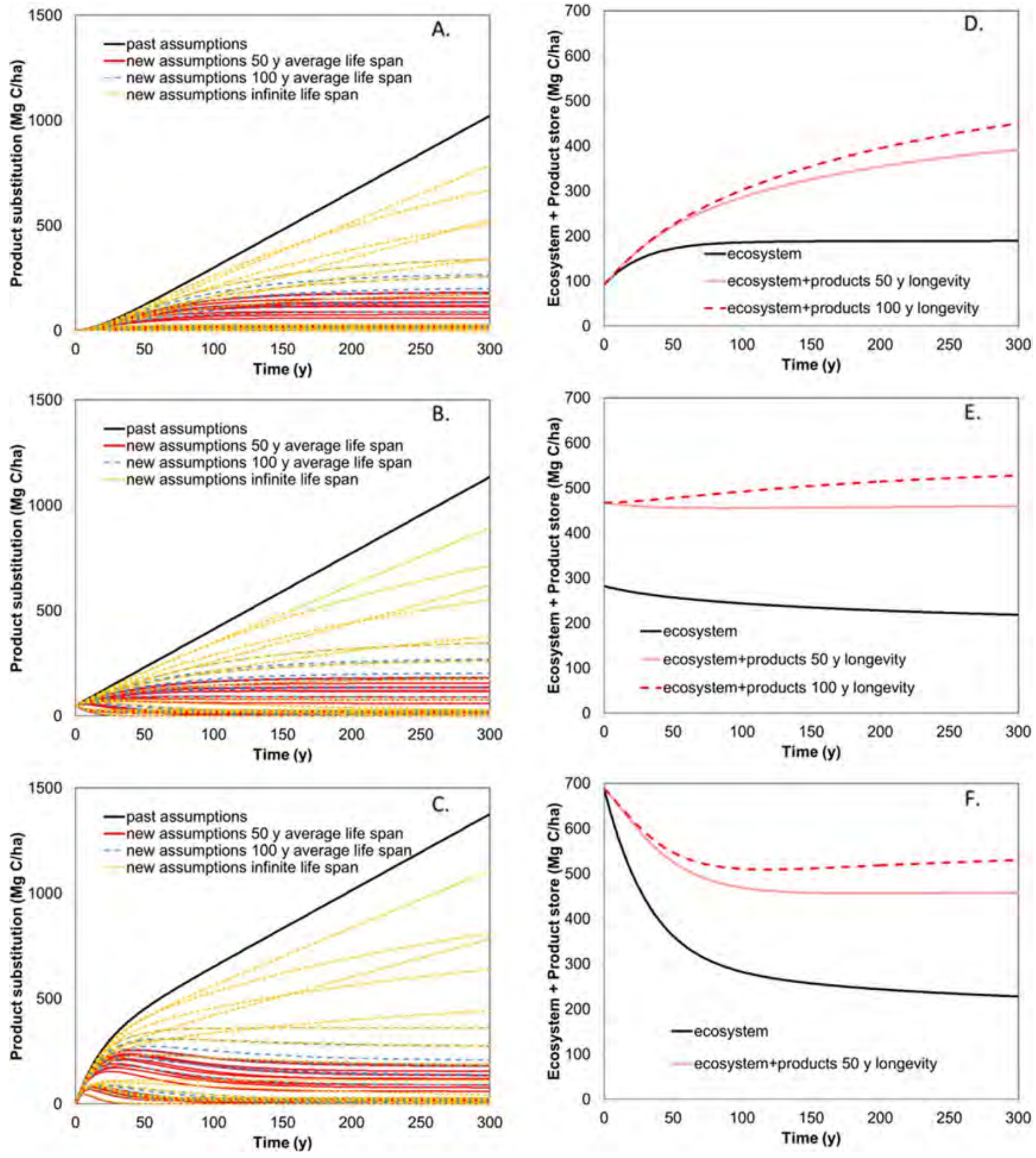

Figure 4. Accumulation of ecosystem, products in-use and disposed, and product substitution carbon stores for a 50 year clear-cut harvest interval in the Pacific Northwest for three possible scenarios: a plantation forest established on an agricultural field (A), (D); a production forest system that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

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

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

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

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

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

Discussion

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

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

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

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

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

Conclusions

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

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LETTER

Meeting GHG reduction targets requires accounting for all forest sector emissions

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Keywords: carbon, forests, wood products, climate mitigation, GHG mandates

Supplementary material for this article is available online

Abstract

Atmospheric greenhouse gases (GHGs) must be reduced to avoid an unsustainable climate. Because carbon dioxide is removed from the atmosphere and sequestered in forests and wood products, mitigation strategies to sustain and increase forest carbon sequestration are being developed. These strategies require full accounting of forest sector GHG budgets. Here, we describe a rigorous approach using over one million observations from forest inventory data and a regionally calibrated life-cycle assessment for calculating cradle-to-grave forest sector emissions and sequestration. We find that Western US forests are net sinks because there is a positive net balance of forest carbon uptake exceeding losses due to harvesting, wood product use, and combustion by wildfire. However, over 100 years of wood product usage is reducing the potential annual sink by an average of 21%, suggesting forest carbon storage can become more effective in climate mitigation through reduction in harvest, longer rotations, or more efficient wood product usage. Of the ~10 700 million metric tonnes of carbon dioxide equivalents removed from west coast forests since 1900, 81% of it has been returned to the atmosphere or deposited in landfills. Moreover, state and federal reporting have erroneously excluded some product-related emissions, resulting in 25%–55% underestimation of state total CO_2 emissions. For states seeking to reach GHG reduction mandates by 2030, it is important that state CO_2 budgets are effectively determined or claimed reductions will be insufficient to mitigate climate change.

Introduction

Heat trapping greenhouse gases (GHGs) are being added to the atmosphere at an accelerating rate by fossil fuel combustion and land use change. Climate change consequences were recently described by the Intergovernmental Panel on Climate Change (IPCC) and the United States National Climate Assessment (USGCRP 2018). The IPCC Special Report (IPCC 2018), Global Warming of 1.5 °C, concludes that to keep global average temperature below 1.5 °C by 2100, it is essential to reduce fossil fuel emissions by 45% by 2030, while substantially increasing the removal of atmospheric CO_2. Both reports emphasize the need to increase atmospheric CO_2 removal strategies by forests in addition to sustaining current forest carbon uptake (Houghton and Nassikas 2018). Some states in the US have set targets for reducing GHGs that include forest climate mitigation options (Anderson *et al* 2017, Law *et al* 2018), yet consistent, rigorous accounting methods are required for evaluating options. Challenges include determining the extent that forests, harvest operations, and wood products affect GHG budgets and emissions accountability.

The most recent global carbon budget estimate indicates that land-based sinks remove 29% of anthropogenic emissions (including land use change) with a significant contribution from forests (Le Quéré *et al* 2018). However, none of the agreements or policies (IPCC 2006, NRCS 2010, Brown *et al* 2014, Doe 2017, EPA 2017, Duncan 2017) provides clear and consistent procedures for quantitatively assessing the extent forests and forest products are increasing or reducing carbon dioxide concentrations in the atmosphere. Assessments are challenging because they involve components that require multiple types of expertise and accounting methods (i.e. forest ecosystem processes, wood products, and inherently uncertain substitution credits). Methods are often in disagreement over the wood product Life Cycle Assessment (LCA) assumption of *a priori* carbon neutrality, where biogenic emissions from the combustion and decomposition of wood is ignored because the carbon released from wood is assumed to be replaced by subsequent tree growth in the following decades (EPA 2016). Despite a multitude of analyses that recognize that the assumption is fundamentally flawed (Harmon *et al* 1996, Gunn *et al* 2011, Haberl *et al* 2012, Schulze *et al* 2012, Buchholz *et al* 2016, Booth 2018), it continues to be used in mitigation analyses, particularly for wood bioenergy.

Forests are sustainable *net* sinks as long as forest carbon uptake from the atmosphere exceeds emissions from harvesting, wood product use and decomposition, and wildfire. Wood products ultimately release CO_2 to the atmosphere as they are manufactured, disposed of, and decompose or are burned. However, because of concerns about double-counting, significant emissions associated with harvest and wood product use have not been counted for any sector (EPA 2018). These emissions are often not included in state CO_2 budget estimates (Brown *et al* 2014, Oregon Global Warming Commission 2017), even when they are included in national budgets (EPA 2017) (table S1 is available online at stacks.iop.org/ERL/14/095005/mmedia). If US states intend to use forests for mitigation strategies, they must account for all contributing sources and sinks of forests and forest-derived products (Stockmann *et al* 2012, IPCC 2014).

By focusing on a region with sufficient information to conduct a meaningful LCA, we demonstrate how a quantitative assessment of forests, management practices and wood products can assess the actual role played by forests and forestry practices in managing atmospheric CO_2. We calculate the regional forest carbon balance (from 2001 to 2016) using observations from over 24 000 forest inventory plots in Washington, Oregon, and California (states with GHG reduction mandates). Net forest sector carbon balance is quantified using an improved LCA including harvest, transportation, manufacturing, wood product pool storage and decay, emissions associated with fire, and substitution for both building construction and energy production. We specifically consider global warming potential associated with carbon dioxide and do not include additional GHGs such as nitrous oxide and methane. Our aim is to provide an accurate cradle-to-grave, transparent and transferable accounting method of all forest-derived carbon for other states and countries with GHG reduction mandates (figure 1; box 1; figure S1; tables S2–S6).

Results

Western US forest ecosystem CO_2 balance (2001–2016)

Forest carbon uptake and release (net ecosystem production (NEP); figure 1(a)) controlled by ecosystem biological processes is calculated as the balance between forest carbon uptake (net primary production (NPP)) and forest carbon release through the decomposition of dead organic matter (heterotrophic respiration; R_h). In this study, a negative number indicates a net carbon sink (removal from the atmosphere) and a positive number indicates a net carbon source (addition to the atmosphere). The coastal Western US states together are a strong forest carbon sink with NEP of −292 ± 36 million metric tonnes (MMT) CO_2e per year (−857 g CO_2e m^{-2} yr^{-1}) (table 1; table S1), and account for approximately 60% of total Western US forest NEP (coastal, southwestern, and intermountain regions).

In addition to NEP, disturbances from harvest and wildfire influence estimates of net ecosystem carbon balance (NECB = NEP minus losses Chapin *et al* 2006; figure 1(a)). In the Western US states, the significant carbon losses from the forest are primarily from removals of wood through harvest, decomposition or burning of aboveground and belowground harvest residues, and wildfire (Law and Waring 2015). Significant harvest has been occurring in the western US since the early 20th century (figure S2). Up to 40% of the harvested wood does not become a product and the products themselves decay over time, resulting in product accumulation much smaller than the total amount harvested (figure 2(a); solid line) (Harmon *et al* 1996, Dymond 2012, Williams *et al* 2016, EPA 2017). Emissions include combustion of wood that does not become a product, combustion for energy, decomposition and/or combustion at end-of-life (table 1; rows 5, 6, 9, and 10). When these carbon losses are accounted for, these forests remain significant carbon sinks at −187 ± 33 MMT CO_2e per year (−551 g CO_2e m^{-2} yr^{-1}), with the largest sink in California (40%) followed by Oregon (33%) and Washington (27%). Despite California having twice the fire emissions of the other states (~10 versus ~5 MMT CO_2e yr^{-1} per state) the ranking is due to much lower harvest removals in California (~12 MMT CO_2e yr^{-1}) compared to almost double in

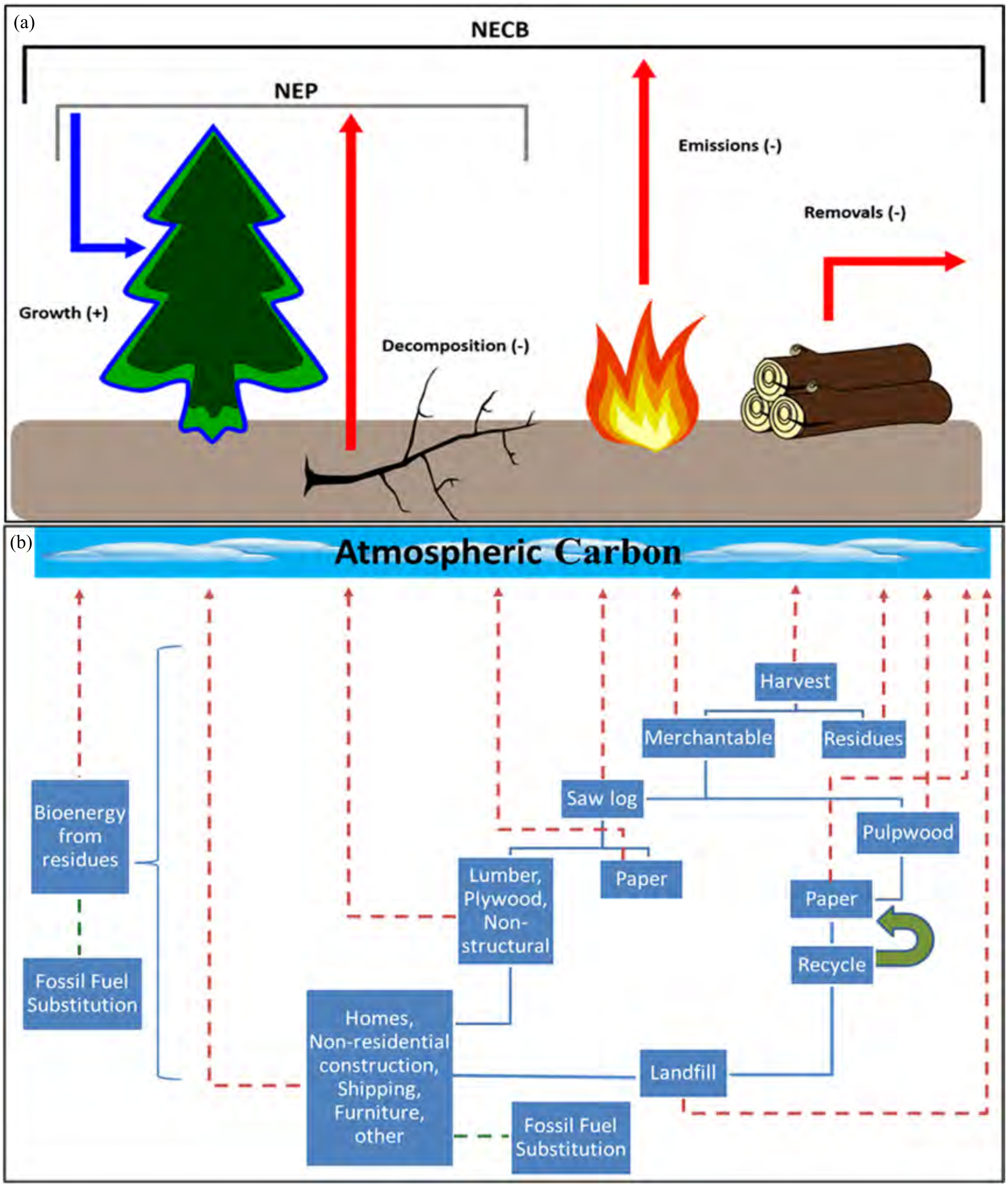

Figure 1. Conceptual diagram of Forest-GHG (a) describes the natural, land-based forest carbon sink where the net of growth and decomposition is net ecosystem production (NEP), and after accounting for removals from fire and harvest, the balance is net ecosystem carbon balance (NECB), (b) describes the cascade of wood products until eventual deposition in landfills or the atmosphere and shows the pathway of emissions.

Washington (~20 MMT $CO_2e\ yr^{-1}$) and triple in Oregon (~31 MMT $CO_2e\ yr^{-1}$). Fire emissions are a third of harvest removals region-wide.

Building on our earlier work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2018), we developed a modified cradle-to-grave model (Forest-GHG) for combining the balance of carbon captured in forest ecosystems, wood product use, lifetime emissions, and eventual return to the atmosphere or long-term storage in landfills. Forest-GHG tracks emissions associated with harvest of wood and manufacturing, transport and use of wood products. Harvest removals result in immediate (combustion of residues on-site or as mill residues with and without energy recapture), fast (short-lived products such as paper), decadal (long-lived products such as wood) and centuries-long (older buildings and land-filled) timeframes before emissions are released back to the atmosphere (figures 1(b) and S1). Our model includes seven product pools and temporally dynamic recycling and landfill rates. Most importantly, we now include a more mechanistic representation of longer-term structural wood in buildings, by moving beyond a simple half-life with exponential decay (figure 3 and SI methods and SI tables 2–6). Our new building cohort-component method tracks decay of short- and

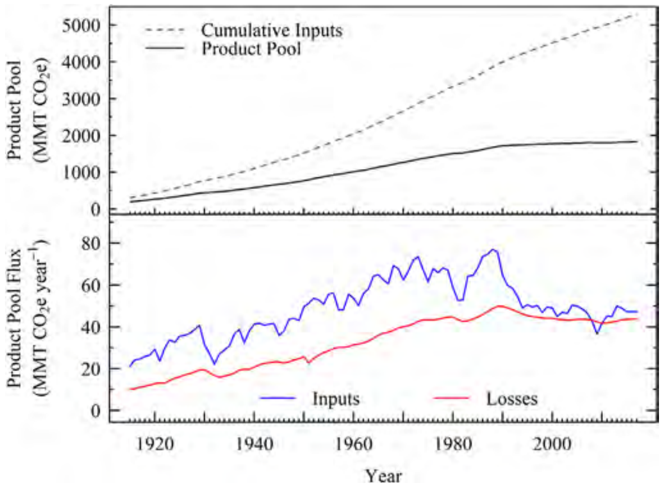

Figure 2. Wood product inputs and outputs from 1900 to 2016 for Washington, Oregon, and California. (A) Cumulative production in MMT CO$_2$e per year assuming no losses over time (dotted grey line) versus the realized in-use wood product pool over time after accounting for decay (losses). (B) Yearly product inputs over time (blue line) that represents the fraction of harvest (removed wood) that becomes a product versus the decay emissions from the pool over time (red line).

Table 1. Average annual total fluxes by state and region from 2001 to 2016. All units are in million MT CO$_2$e. Negative numbers indicate a carbon sink (CO$_2$ is being removed from the atmosphere). The more negative the number, the stronger the sink. Grey shading is used to indicate net values that represent carbon sink strength both before and after removals are accounted for.

Ecosystem	Washington	Oregon	California	Total
1. Forested area (million hectares)	9.7	12.4	11.9	34.0
2. Net ecosystem production (NEP)	**−89.9**	**−102.0**	**−99.8**	**−291.6**
3. Fire emissions	5.1	5.3	10.3	20.7
4. Harvest removals	18.5	30.5	11.5	60.5
Net ecosystem carbon balance (NECB) (sum of rows 1 through 4)	**− 66.4**	**−66.2**	**−78.0**	**−210.5**
Forest industry	**Washington**	**Oregon**	**California**	**Total**
5. Harvest residue combustion (onsite)	3.9	6.5	2.5	12.9
6. Harvest, transportation, manufacturing (FFE emissions)	2.8	4.6	1.6	9.0
7. Wood product pool annual inputs	−18.5	−30.5	−11.5	−60.5
8. Landfill annual inputs (from products)	−6.8	−11.9	−4.2	−22.9
9. Wood manufacturing losses	3.9	6.5	3.9	14.3
10. Wood product and landfill decomposition	21.4	36.2	13.3	71.0
Net forest sector carbon balance (NECB + sum of rows 5 through 10)	**−59.5**	**−54.7**	**−72.4**	**−186.6**
11. Wood product substitution (wood)	−3.0	−4.9	−1.6	−9.4
12. Wood product substitution (energy)	−1.8	−3.0	−1.8	−6.6
Net forest sector carbon balance (with credits; NECB + sum of rows 5 through 12)	**−64.3**	**−62.6**	**−75.8**	**−202.7**

long-lived building components annually, and the lag time associated with these losses (figure S3). Our wood bioenergy substitution credits (Sathre and O'Connor 2010) include wood waste from harvest, mill residues, and wood products displacement of more fossil fuel intensive materials.

Using our component tracking LCA, we found that of the ~10 700 MMT CO$_2$e of wood harvested in all three states since 1900 (figure 2), only 2028 MMT CO$_2$e are currently stored in wood products with half stored in Oregon (1043 MMT CO$_2$e). In just over 100 years, Oregon has removed the equivalent of all live trees in the state's Coast Range forests (Law *et al* 2018), and returned 65% to the atmosphere and transferred 16% to landfills. Even though these are some of the most productive and carbon dense forests in the world (Hudiburg *et al* 2009), the carbon accumulated in much of the removed biomass took up to 800 years to accumulate—and cannot be recovered if current management practices continue.

Forest harvest-related emissions have averaged 107 MMT CO$_2$e annually from 2001 to 2016 (table 1; row 5, 6, 9, and 10). Emissions are highest from decay of the wood product pool that has been accumulating for over 100 years (table 1 row 10; figures 3 and S3). This is after accounting for recycling and semi-permanent storage in landfills. Structural wood product decay for long- and short-term components (wood in buildings; figure 3) account for about 30%–35% of wood product and landfill decomposition while paper and non-building wood products account for about 65%–70%. Under this complete accounting, the

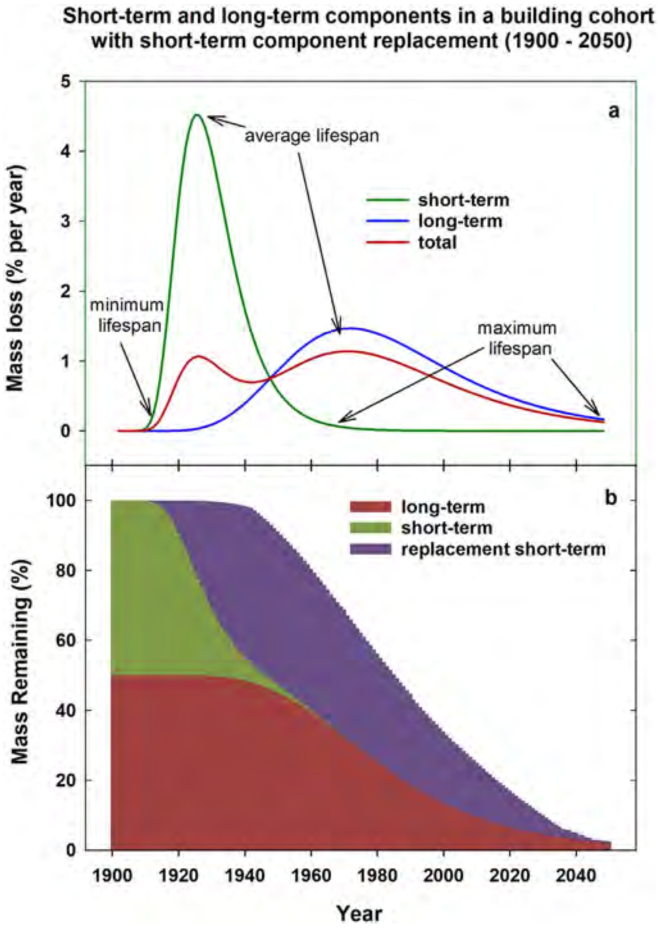

Figure 3. Conceptual models of the Forest-GHG cohort-component method for: (a) mass loss in a cohort of buildings with a 75 year average life span that accounts for the short and long-term portions of buildings and (b) mass remaining in a single building cohort over time (with replacement). Data presented is based on the 1900 cohort of single-family homes built in Oregon.

lowest contribution to overall emissions is from fossil fuel usage during harvest, transportation, and manufacturing, i.e. less than 10% of total wood product-related emissions in the three states.

We found that wood-related substitution for construction materials (0.54 fossil fuel carbon emissions avoided per unit carbon of wood; table 1 row 11) and energy (0.68 fossil fuel carbon emissions avoided; table 1 row 12) may offset 18% of forest industry emissions. This assumes 50% of wood-derived construction products are substituted for a non-wood product and that 75% of mill residues are substituted for fossil fuel energy (Berg *et al* 2016).

We varied the maximum average life spans of the wood products used in construction (e.g. buildings) to examine its effect on emissions estimates. Emissions are minimally reduced by 2%–4% in each state when a longer average maximum lifespan is used (100 years) for the long-term building components and minimally increased by 2%–3% when a shorter average maximum lifespan is used (50 years, which is the mean lifetime of buildings in the US EPA 2013).

Combined, the US west coast state forest sector (cradle-to-grave) is a net carbon sink, removing ~187 MMT CO_2e annually from the atmosphere and potentially reducing fossil fuel emissions by up to another 20 MMT CO_2e through product and energy substitution. Harvest-related emissions reduce the natural sink (NEP—Fire) by 34, 46, and 27% for Washington, Oregon, and California, respectively. When substitution credits are included, this changes to reductions of 27%, 37%, and 23%. Harvest rates have been highest in Oregon (table 1), contributing to increasing wood product emissions and the largest reductions to forest sink capacity.

Discussion

NECB is a good estimate of ecosystem carbon uptake, e.g. for carbon offsets programs (Anderson *et al* 2017), and can be compared spatially with changing environmental conditions or disturbances, but is an incomplete calculation of the entire forest sector emissions. It does not include emissions from wood products caused by machinery, transport, manufacturing and losses—emissions that can equal up to 85% of the total versus 15% from fire, insects, and land use change (Williams *et al* 2016). Nor does it account for the storage and subsequent release of carbon in varying end uses with varied product lifetimes. Given that not all harvested wood is an immediate source to the atmosphere and very little harvested wood is stored in perpetuity, it is essential to track associated emissions over time. For state- or region-level carbon budgets, a cradle-to-grave carbon LCA should be combined with the ecosystem carbon balance (NEP and NECB) to account for how much the forestry sector is contributing to or offsetting total carbon emissions.

If wood buildings are replaced by wood buildings, substitution is not occurring, and because wood is preferred for construction of single-family housing in North America, some of our substitution values are overestimated (Sathre and O'Connor 2010). Wood products store carbon temporarily, and a larger wood product pool increases decomposition emissions over time (figure 3). This emphasizes that increasing the wood product carbon sink will require shifts in product allocation from short-term to long-term pools such as reclaimed (re-used) wood products from demolition of buildings, and reduction of product manufacturing losses (EPA 2016). Clearly, there is potential for climate mitigation by using forests to sequester carbon in biomass and reduce losses associated with the wood product chain (Law *et al* 2018).

It is argued that there may be reductions in fossil carbon emissions when wood is substituted for more fossil fuel intensive building materials (e.g. steel or concrete) or used as an alternative energy source (Butarbutar *et al* 2016). Substitution is a one-time credit in the year of the input. Studies have reported a range of substitution displacement factors (from negative to positive displacement; Sathre and O'Connor 2010, Smyth *et al* 2017), but we found no study that has tracked the actual amount of construction product substitution that is occurring or has occurred in the past in the United States. This makes substitution one of the most uncertain parts of this carbon budget. It may be more easily tracked in the fossil fuel sector through a decrease in emissions because of reduction in product supply, in which case it would be double counting to then include it as a credit for the forest sector. We show results with and without the substitution credit (a decrease in forest sector emissions) because it cannot be verified. We show the potential impact it has on the overall forest sector carbon sink, even though the displacement factor may be unrealistically high (Smyth *et al* 2017, Dugan *et al* 2018). For forest sector emissions assessments, the uncertainty suggests exclusion of the credit.

Currently, state's GHG accounting budgets are incorrect because they are not full cradle-to-grave estimates of all CO_2 emissions associated with forest natural processes and human influences. For accurate GHG accounting, these emissions should be included in the forestry sector as they are not accounted for by state's energy and transportation sectors (IPCC 2006) (table S1). The US EPA reported average fossil fuel CO_2 emissions of 491 MMT CO_2e yr^{-1} for the three states combined (2013–2016). Forest industry harvest, transportation, and manufacturing fossil fuel emissions are included in this total. However, it is unclear to what extent wood product decay and combustion emissions are also counted in state budgets. In Oregon, they are not included at all, resulting in state CO_2 emissions that have been underestimated by up to 55% (Oregon Global Warming Commission 2017, Law *et al* 2018). Washington includes combustion emissions from the current year's harvest (table 1; Manufacturing losses; row 9), but not from wood product decay, resulting in up to a 25% underestimation of state CO_2 emissions. Because California's emissions from other sectors are so high (76% of regional total), and harvest rates have been historically lower than in Oregon and Washington, the impact of not including these emissions is very small as a proportion of the total. Although fire in California has received much attention, it only accounts for 3% of the state's total fossil fuel CO_2 emissions.

These underestimates are especially alarming for Oregon where GHG reduction targets are to be 10% below 1990 levels by 2020 and at least 75% below 1990 levels by 2050 (Pietz and Gregor 2014). California and Washington emissions are to be reduced to 1990 levels by 2020 (Nunez 2006), and 80% and 50% below 1990 levels by 2050 (Washington State 2008), respectively.

In contrast, the US EPA reports emissions from wood product decay and landfills (EPA 2017) per the IPCC guidelines (IPCC 2006) (table S1). However, combustion emissions from logging and mill residues are not reported (EPA 2017). Moreover, ecosystem carbon losses are indirectly estimated through changes in biomass pools with measurement uncertainty that can be greater than the change (Ferster *et al* 2015). So even at the national level, emissions (as a fraction of fossil fuel emissions) would be underestimated by 10% and 24% in Washington and Oregon, respectively. Undoubtedly, there are implications for reduction mandates when the magnitude of emissions themselves are incorrect.

Conclusions

The goal for all societies and governments as stated in Article 2 of the *United Nations Framework Convention on Climate* Change (Oppenheimer and Petsonk 2005) should be '…stabilization of GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system.' The Paris Climate Agreement (UNFCCC 2015) aims to keep global average temperature from rising by no more than 2 °C above preindustrial levels, and if possible no more than 1.5 °C. Forests are identified as part of the strategy (UNFCCC 2015).

Although some US states have attempted to quantify a portion of forest-related emissions, improved estimates are essential to track emissions to meet reduction goals. We identified the main components that should be part of the forest sector state estimates. We found that emissions have been underestimated by up to 55% in Oregon and 25% in Washington, and that at present, these emissions are not reported in state GHG reporting guidelines. The accuracy of forest sector emissions estimates can be improved with sub-regional data on residential and commercial building lifespans, recycling, verifiable substitution benefits and accurate monitoring of growth rates of forests. However, verifiable substitution of one material for another may be more readily quantified in the fossil fuel sector.

The 2006 IPCC GHG guidelines provide three different approaches for calculating emissions from harvested wood products (IPCC 2006) (including reporting 'zero') and reporting of this component is not required by UNFCCC. To complicate accounting further, several studies have shown that using the different recommended approaches results in emissions that differ by over 100% (Green *et al* 2006, Dias *et al* 2007). Moreover, according to IPCC and UNFCCC, emissions of CO_2 from forest bioenergy are to be counted under land use change and not counted in the energy sector to avoid double counting. However, this provides a 'loophole' leading to their not being counted at all.

The United States government currently requires all federal agencies to count forest bioenergy as carbon neutral because the EPA assumes replacement by future regrowth of forests somewhere that may take several decades or longer (EPA 2018). While it is theoretically possible that a replacement forest will grow and absorb a like amount of CO_2 to that emitted decades or a century before, there is no guarantee that this will happen, and the enforcement is transferred to future generations. In any rational economic analysis, a benefit in the distant future must be discounted against the immediate damage associated with emissions during combustion. Furthermore, the goal for climate protection is not climate neutrality, but rather reduction of net GHGs emissions to the atmosphere to avoid dangerous interference with the climate system. Allowing forests to reach their biological potential for growth and sequestration, maintaining large trees (Lutz *et al* 2018), reforesting recently cut lands, and afforestation of suitable areas will remove additional CO_2 from the atmosphere. Global vegetation stores of carbon are 50% of their potential including western forests because of harvest activities (Erb *et al* 2017). Clearly, western forests could do more to address climate change through carbon sequestration if allowed to grow longer.

Since it is now clear that both CO_2 emissions and removal rates are essential to meet temperature limitation goals and prevent irreversible climate change, each should be counted and reported. We recommend that international agreements and states utilize a consistent and transparent carbon LCA that explicitly accounts for all forest and wood product storage and emissions to determine compliance with goals to lower atmospheric GHGs. Only by using a full accounting of GHGs can the world manage its emissions of heat trapping gases to achieve concentrations in the atmosphere that will support a stable climate.

Materials and methods

We calculated the 2001 to 2016 average net forestry sector emissions from cradle-to-grave, accounting for all carbon captured in biomass and released through decomposition by forest ecosystems and wood products industry in Washington, Oregon, and California. Building on our previous work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2013, Law *et al* 2018), we developed a modified and expanded LCA method to combine with our ecosystem carbon balance, now called Forest-GHG (version 1.0; figure 1 and box 1). We accounted for all carbon removed from forests through fire and harvest. All harvested carbon was tracked until it either was returned to the atmosphere through wood product decomposition/combustion or decomposition in landfills, minus the amount semi-permanently stored in landfills (buried). This required calculating the carbon removed by harvest operations starting in 1900 to present day because a portion of the wood removed in the past century is still in-use or decomposing. In addition to carbon in biomass, we also accounted for all carbon emissions associated with harvest (equipment fuel, transportation, manufacturing inputs). Moreover, our wood product life-cycle assessment includes pathways for recycling and deposition in landfills. Finally, we give substitution credits for not using more fossil fuel intensive materials than wood used in construction of buildings and energy production.

Observed carbon stocks and fluxes (ecosystem carbon balance)

Carbon stock and flux estimates were calculated from over 30 000 forest inventory plots (FIA) containing over 1 million tree records in the region following methods developed in previous studies (Law *et al* 2018) (SI Methods). Flux calculations include NPP (Clark *et al* 2001) NEP, and NECB. The NECB represents the net rate of carbon accumulation in or loss from ecosystems.

Off-site emissions associated with harvest (LCA)

Decomposition of wood through the product cycle was computed using a LCA (Harmon and Marks 2002, Law *et al* 2018). A 117 year wood products pool (1900–2016) was simulated using reported harvest rates from 1900 to 2016 for Oregon and Washington (Harmon *et al* 1996, DNR 2017, Oregon Department of Forestry 2017) and from the California State Board of Equalization (CA 2018). Harvest was converted to

Box 1. Terminology and Flux Definitions for table 1

1. Forest Area = sum of all forest area in each state derived from US Forest Service forest area map (30 m resolution). Includes all ownerships.

1. NEP = Net Primary Production—heterotrophic respiration; microbial respiration as they decompose dead organic matter in an ecosystem.

1. Fire emissions = the emissions associated with *combustion* of organic matter at the time of the fire. Most of what burns is fine surface fuels, averaging 5% of aboveground biomass in mixed severity fires of Oregon and Northern California.

1. Harvest removals = Wood actually removed from the forest (not the total aboveground biomass killed). Removals are not equal to emissions but are the removed carbon from the forests at the time of harvest. This is subtracted from NEP along with fire emissions to calculate the net forest carbon balance from the viewpoint of the forest ecosystem.

NECB = NEP + Fire Emissions + Harvest Removals. The term is the simplest expression of forest carbon balance without tracking wood through the product life cycle. Although not all of the harvest removals will result in instant or near-term emissions, NECB still captures the impact of the removed carbon on the forest ecosystem carbon balance, and is consistent with international agreements (REDD+, conservation).

1. Harvest Residue Combustion = the emissions associated with combustion of slash piles; the branches, foliage, and non-merchantable wood left after harvest operations (remains in the forest) and burned onsite (assumed to be 50% of slash).

1. Harvest, Transportation, Manufacturing (FFE emissions) = the fossil fuel emissions associated with harvest (skidding, sawing, etc), transportation of logs to mills, manufacturing of wood and paper products, and transportation of products to stores (see table S5 for coefficients).

1. Wood Product Pool Annual Inputs = Harvest removals

1. Landfill Annual Inputs (from products) = The amount of wood and paper that is sent to landfills at end of life. In Forest-GHG, this occurs incrementally from 1950 to 1960 and then in 1961 is assumed to be constant at the current rate.

1. Wood Manufacturing Losses = fraction of wood that is lost at the mill (sawdust, etc) and is assumed to be returned to the atmosphere within one year through combustion (with 75% energy recapture) or decomposition.

1. Wood Product and Landfill Decomposition = fraction of the total wood product and non-permanent landfill carbon pools that is returned to the atmosphere annually.

Net Forest Sector Carbon Balance = sum of NECB and rows 5 through 10. Emission sources are rows 5, 6, 9, and 10. Sinks are rows 7 and 8.

1. Wood product substitution (Wood) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for a fossil fuel derived product in buildings (e.g. concrete or steel). We assume 0.54 g C fossil fuel emissions avoided per g of C of wood biomass used.

Box 1. (Continued.)

1. Wood product substitution (Energy) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for energy. In the Oregon, Washington, and California this primarily a mix of natural gas and coal. We include the biogenic emissions from combustion of forest-derived woody biomass and include an energy substitution credit if it is combusted with energy recapture.

Net Forest Sector Carbon Balance (with substitution credit) = sum of NECB and rows 5 through 12.

total aboveground biomass using methods from (Law *et al* 2018). The carbon emissions to the atmosphere from harvest were calculated annually over the timeframe of the analysis (1900–2016).

The coefficients and sources for the Forest-GHG LCA (figures 1(b) and S1) are included in table S1 through S6 with all units expressed as a function of the wood biomass being cut, transported, manufactured, burned, etc. We accounted for the fossil fuel emissions that occur during harvest (fuel for equipment) and the fossil fuel emissions associated with transport of wood to mills. Then, we accounted for the fossil fuel emissions associated with manufacturing of products followed by a second transportation emission for delivery of products to stores and warehouses. Wood that is not made into a wood or paper product (e.g. waste) is assumed to be combusted onsite at the mill (with 50% energy recapture as combined heat and power) or used in a product that will return the carbon to the atmosphere within one year (table 1 and box 1; Wood Manufacturing Losses).

Wood products are divided into varying product pools and are then tracked through the wood product cascade until end of life (figure 1(b)). Wood products are split into seven product pools: single-family homes, multi-family homes, mobile homes, non-residential construction, furniture and manufacturing, shipping, and other wood. We simulated wood product storage and emissions to 2050 for display purposes in the figures assuming a constant harvest rate after 2016.

We estimate the carbon pools and fluxes associated with buildings by separating buildings into components with different life spans (figures 3 and S3). This allows components and buildings to have a lag time before significant losses occur, and recognizes the difference between building life span and the residence time of carbon in a building. This also allows capacity for Forest-GHG to have component and building life spans evolve over time as construction practices and the environment (including biophysical, economic, and social drivers) change.

In Forest-GHG, a fraction of each year's new harvest is allocated to residential (single-family, multi-family, and mobile homes) and non-residential construction (Smith *et al* 2006). This fraction is further divided into the short-term (23%) and long-term (77%) components. The resulting pools are tracked independently, quantifying losses through decay and demolition from the year they start until then end of the simulation.

All the components created in a given year are considered a building cohort that is also tracked separately each year. All components are summed to give the total amount of building carbon remaining in a cohort at a given time (figure S3). For each year, the amount lost to the atmosphere or to the landfills through demolition, is simply the current year's total wood product carbon pool plus the current years inputs and minus last year's total wood product carbon pool.

Substitution

We calculated wood product substitution for fossil fuel derived products (concrete, steel and energy). The displacement value for product substitution was assumed to be 0.54 Mg fossil C/Mg C (Smyth *et al* 2017, Dugan *et al* 2018) wood use in long-term structures (Sathre and O'Connor 2010). Although the displacement value likely fluctuates over time, we assumed it was constant for the simulation period. We accounted for losses in product substitution associated with building replacement (Harmon *et al* 2009), but ignored the leakage effect related to fossil C use by other sectors. We assumed 75% of 'waste wood' was used for fuelwood in homes or at mills (wood manufacturing losses in table 1). We accounted for displacement of fossil fuel energy sources using a displacement factor of 0.68 assuming a mix of coal and natural gas replacement (Smyth *et al* 2017, Dugan *et al* 2018).

Uncertainty estimates and sensitivity analysis

We calculate a combined uncertainty estimate for NEP and NECB using the uncertainty in the observations and input datasets (climate, land cover, harvest amounts). For the biomass and NPP observations, we performed Monte Carlo simulations of the mean and standard deviations for NPP (Hudiburg *et al* 2011) derived for each plot using three alternative sets of allometric equations. Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest removals (7%), and land cover estimates (10%) using the propagation of error approach. Sensitivity analysis was only used for the long-term wood product pool by varying the average life spans of buildings by ±25 years in our new cohort component method. Our estimates varied by 7%. This was combined with the uncertainty in NECB to calculate total uncertainty on the net forest sector carbon balance.

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Perspective

Creating Strategic Reserves to Protect Forest Carbon and Reduce Biodiversity Losses in the United States

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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 (CO_2).

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 policymakers 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 km^2 Tongass National Forest in southeast Alaska, of which about 20,000 km^2 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 CO_2 removal options that finds the potential for afforestation and reforestation in limiting atmospheric CO_2 to be modest [23].

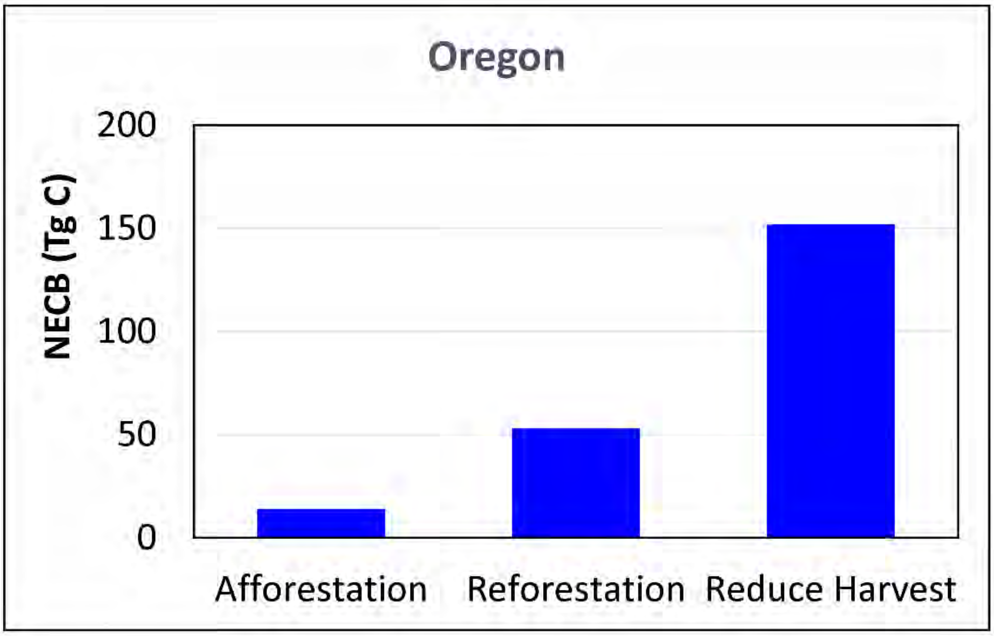

Figure 1. Land-use strategies to mitigate climate change across Oregon. Values on *y*-axis are cumulative change in net ecosystem carbon balance (NECB) from 2015 to 2100. Reduced harvest is a combination of restricted harvest by half on federal lands, and increased harvest intervals to 80 years on private 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).

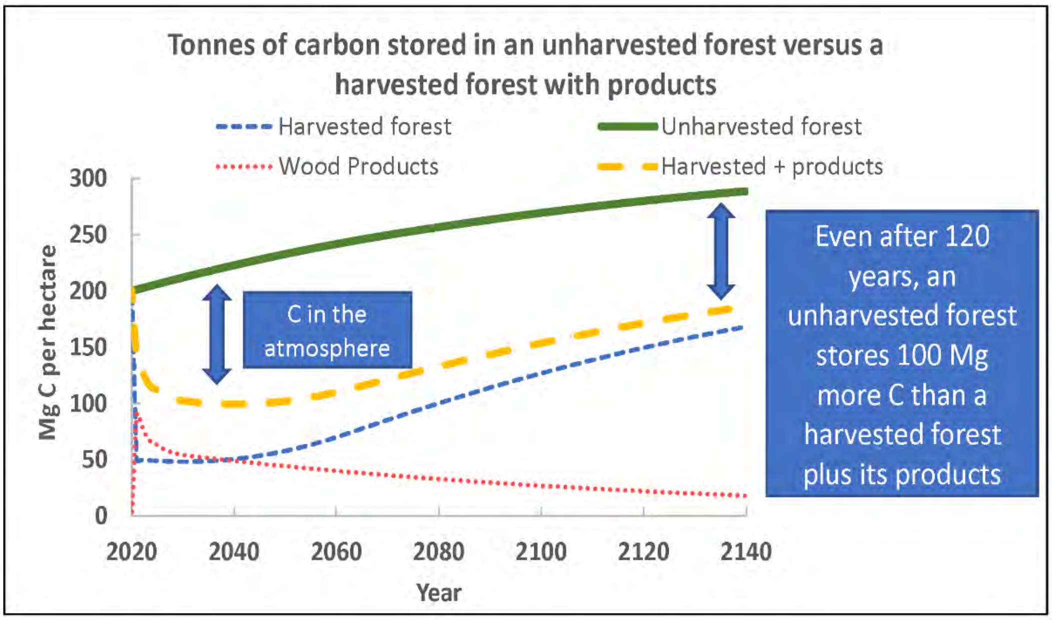

Figure 2. A mature forest with a carbon density of 200 tons of carbon per hectare (green line) is harvested (blue line) in 2020. This results in an immediate reduction of live tree carbon stocks. Approximately half of the aboveground carbon is removed and taken to the mills (as wood) while the other 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* CO_2 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 CO_2-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 CO_2 per unit of primary energy than fuel oil, and about 75% more CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2. 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 Broadscale 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 km^2 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].

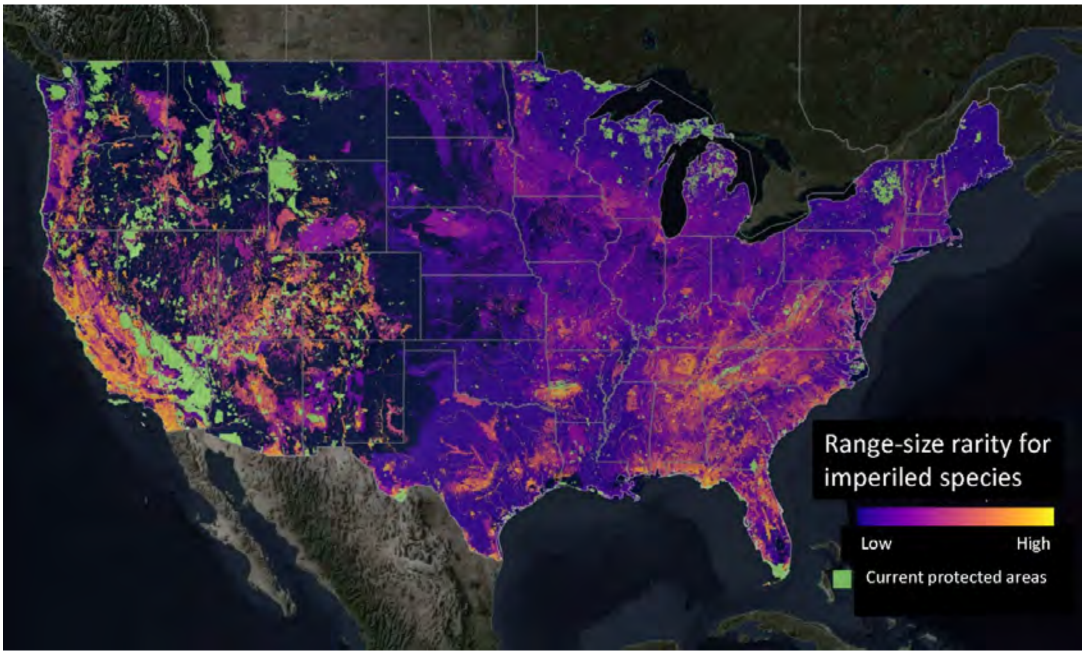

Figure 3. Summed range-size rarity of forest and non-forest species in the lower 48 states that are protected by the Endangered Species Act and/or considered to be in danger of extinction. Species include vertebrates (birds, mammals, amphibians, reptiles, freshwater fishes), freshwater invertebrates, 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 CO_2 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.

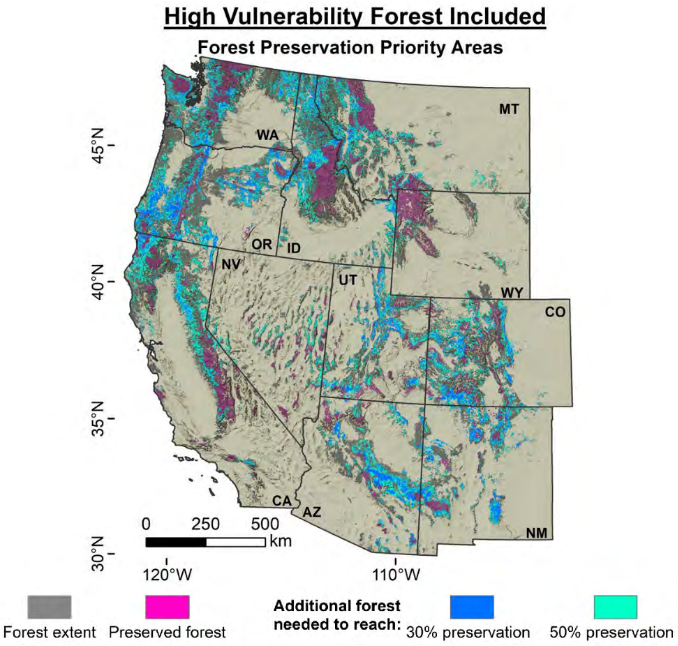

Figure 4. Forestlands that are currently preserved, and additional areas identified as high priority for protection of biodiversity and forest carbon for climate mitigation across the western U.S. Adapted from [5].

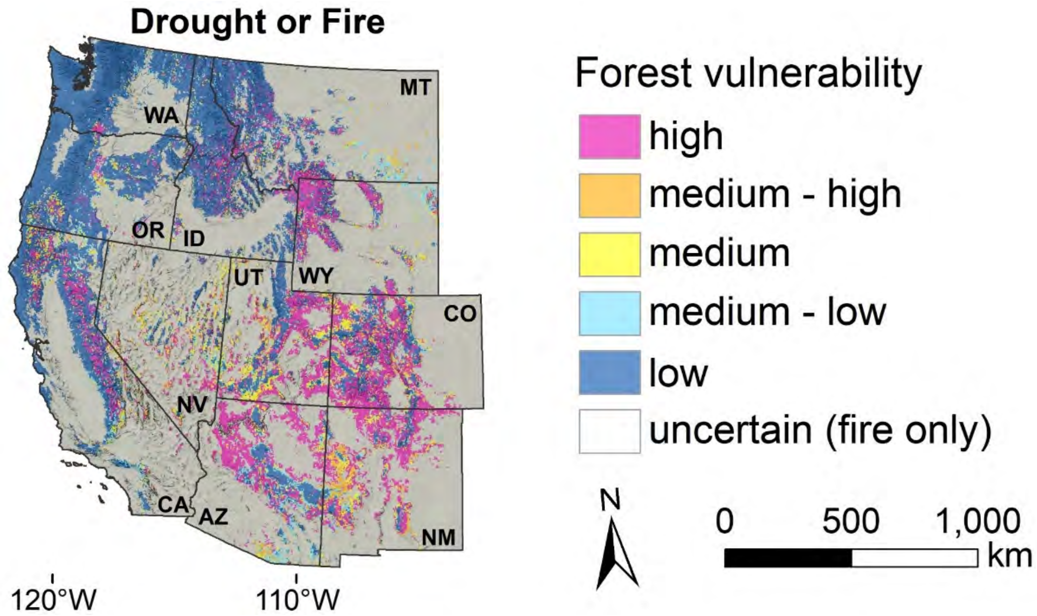

Figure 5. Vulnerability of forestlands to either drought or fire under future climate scenarios to year 2050. Adapted from [83].

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 CO_2 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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RESEARCH ARTICLE

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Southern Alaska's Forest Landscape Integrity, Habitat, and Carbon Are Critical for Meeting Climate and Conservation Goals

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Key Points:

- The Tongass and Chugach are the largest and most intact of all US National Forests, with key bald eagle, brown bear, and gray wolf habitat
- The Tongass and Chugach are cool and wet with forest carbon stocks minimally impacted by wildfire and likely to increase with climate change
- The Tongass, Chugach and Pacific Northwest's National Forests are high priority for protection to meet climate and biodiversity goals

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract The interdependent crises of climate change and biodiversity losses require strategic policies to protect, manage, and restore essential ecosystems. Here, we evaluate the relative importance of US national forests (NFs) for protection and conservation as natural climate and biodiversity solutions. We compared landscape integrity (degree of modification by humans), habitat for three keystone species, forest carbon density, accumulation, and total biomass carbon stocks across 154 NFs in the United States. Southern Alaska's Tongass and Chugach NFs hold disproportionally large amounts of high landscape integrity area among all NFs with 25.3% and 5.6% (total 30.9%) of all high (≥9.6) landscape integrity found on NF lands. The Tongass and Chugach store approximately 33% and 3% of all biomass carbon stocks that occur in NFs with high landscape integrity. These two NFs together account for about 49%, 37%, and 18% of all bald eagle, brown bear, and gray wolf habitat found on NF lands. Gray wolf habitat extent was 4% of the total or less on remaining NFs. The Tongass and Chugach were historically wetter and cooler among NFs, and are projected to experience much larger increases in precipitation and much lower increases in maximum temperatures over the coming century. Combined with relatively low recent occurrence of wildfire, this makes permanence more likely. The Tongass and Chugach forests, along with the Pacific Northwest's high carbon density forests should be a high priority for protection and conservation to meet climate and biodiversity goals given their landscape-scale scarcity and high value.

Plain Language Summary Permanent protection of forests with relatively high carbon stocks, landscape integrity, and habitat extent would contribute substantially to climate mitigation and species adaptation. The Tongass and Chugach National Forests in southern Alaska rank highest among U.S. National Forests in all three areas. These forests also have relatively low near-term vulnerability to wildfire and climate, higher connectivity for animal movement, and lower human impacts, making permanence more likely.

1. Introduction

Forests play crucial roles for mitigating climate change and supporting biodiversity, thus making it important to identify and protect the most vital forests (IPCC, 2022; Law et al., 2021). Terrestrial ecosystems have been removing about 30% of global anthropogenic CO_2 emissions from the atmosphere each year for the past 60 years and most of the removal is by forests (Friedlingstein et al., 2022). Climate impacts would be even more severe without this ecosystem service. Yet intact forests with high carbon density and biodiversity are disappearing at an alarming rate (Potapov et al., 2017), such as in the Brazilian Amazon and Canadian British Columbia, which have become net carbon sources (Gatti et al., 2021; Government of British Columbia, 2022; Harris et al., 2021; Qin et al., 2021). Concerningly, current national climate pledges will increase greenhouse gas emissions by 16% from 2010 to 2030, indicating that the planned emissions reductions and increased removals from the atmosphere by the biosphere need to be much more aggressive (UNFCCC, 2021).

Nature-based Climate Solutions (NbCSs) are essential for protecting interdependent forest carbon and biodiversity (Dinerstein et al., 2020), leading to calls for conservation of 30%–50% of Earth's surface in the coming decades (IPCC, 2022). NbCSs allow ecosystems to continue to store and accumulate carbon from the atmosphere, provide habitat for plant and animal species, and protect watersheds. Intact forests are crucial for supporting wildlife, fish, clean water, carbon sequestration, and other ecosystem services (Grantham et al., 2020; Watson et al., 2018). Protected public lands (e.g., Wilderness Areas, National Parks) provide important NbCSs (Law

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et al., 2021, 2022), in part because they likely afford greater permanence of carbon storage than private lands (Anderegg, 2021). In the United States (US), there are 154 National Forests (NFs) that account for 76% of all federal forest land (590,240 km^2 of 773,620 km^2) (Smith et al., 2019). Logging and other extractive activities are allowed throughout most NF forest lands, with only about 19% classified as "reserved" from timber production (Smith et al., 2019), albeit with varying levels of biodiversity and logging protection. Consequently, there is a substantial gap between current conservation of NF forest lands and conservation targets focused on protecting biodiversity and carbon stocks.

Federal lands managed by the U.S. Forest Service (FS), the National Forest System (NFS), and the Bureau of Land Management are managed under a multiple use—sustained yield model (US Congress, 1960, 1976). The statute directs the agencies to "balance multiple uses of their lands and ensure a sustained yield of those uses in perpetuity" (Riddle, 2022). The balance of multiple uses on federal lands has been an ongoing point of contention (Riddle, 2022), with many concerned that conservation isn't a higher priority given the critical need for meeting conservation targets for climate mitigation and adaptation. Forest management activities, particularly harvest, appear to be in conflict with the intertwined goals of protecting forest carbon and biodiversity for climate mitigation and adaptation. NFs in the conterminous US particularly in the West have experienced increasing incidence of wildfire, insects, and drought, yet still represent the majority of late mature and old-growth forest area remaining, which imparts a unique role in protecting these areas for biodiversity and climate change. Research studies have shown that older forests containing large trees are more resilient and have greater ecosystem integrity than younger forests (Rogers et al., 2022).

The coastal rainforests of southern Alaska are unique ecosystems that could help fill the conservation gap on NF forest lands (DellaSala et al., 2022; Vynne et al., 2021). Two NFs in the region are the Tongass and Chugach NFs (Figure 1). In addition to storing a large amount of carbon (Barrett, 2014; DellaSala et al., 2022), these coastal rainforests have extensive intact forests, complete wildlife assemblages, and are strongholds for wild salmon and other fish (Vynne et al., 2021). Unlike much of the conterminous US, this region still has substantial populations of large carnivores including bald eagle (*Haliaeetus leucocephalus*), brown bear (*Ursus arctos*), and gray wolf (*Canis lupus*). Therefore, to guide conservation planning it is important to understand current forest integrity and protection status in these coastal rainforests, as well as how they compare with other US NFs.

Recently developed spatial data sets can provide valuable insights into current forest integrity and other forest bioclimatic characteristics that are important to consider in conservation planning. For instance, the new forest landscape integrity index (FLII) characterizes the level of forest landscape degradation from human activities in a consistent manner worldwide (Grantham et al., 2020). Other large-scale spatial data sets provide detailed information on forest biomass carbon stocks (Spawn et al., 2020), wildlife habitat (USGS GAP, 2022), and fire activity (Giglio et al., 2018), as well as current and potential future climate (Brun et al., 2022a, 2022b). Forest carbon stocks and wildlife habitat can be eroded by high fire activity and climatic changes that lead to hotter and drier conditions (Buotte et al., 2019). Together, these data sets provide new opportunities to characterize forest bioclimatic conditions across coastal rainforests in southern Alaska and to understand how these rainforests compare with forest lands in other US NFs.

To better understand potential conservation benefits of preserving forest lands in the Tongass and Chugach NFs (Figure 1), we compared forest bioclimatic attributes of these NFs with all other NFs in the conterminous US. We focus on the need to retain large tracts of intact forest landscapes that help mitigate climate change and protect biodiversity as part of a "Strategic Forest Reserve" system emphasizing NbCSs on federal lands in the US. Our objectives are:

1. Compare forest area, landscape integrity, and biomass carbon among NFs;
2. Determine and compare the areal extent of habitat for bald eagle (*Haliaeetus leucocephalus*), brown bear (*Ursus arctos*), and gray wolf (*Canis lupus*) among NFs;
3. Compare recent and projected climate conditions and wildfire occurrence among NFs to determine risk.

Our analysis was based on spatial data sets primarily derived from satellite remote sensing and geospatial modeling (Giglio et al., 2018; Grantham et al., 2020; Hansen et al., 2013; Spawn et al., 2020), though also included future climate projections from CMIP6 (Brun et al., 2022a, 2022b) and current preservation status from the Protected Areas Database of the United States (PAD-US version 3) produced by the US Geological Survey (USGS) Gap Analysis Project (GAP; USGS GAP, 2018). These spatial data sets enable consistent analysis of

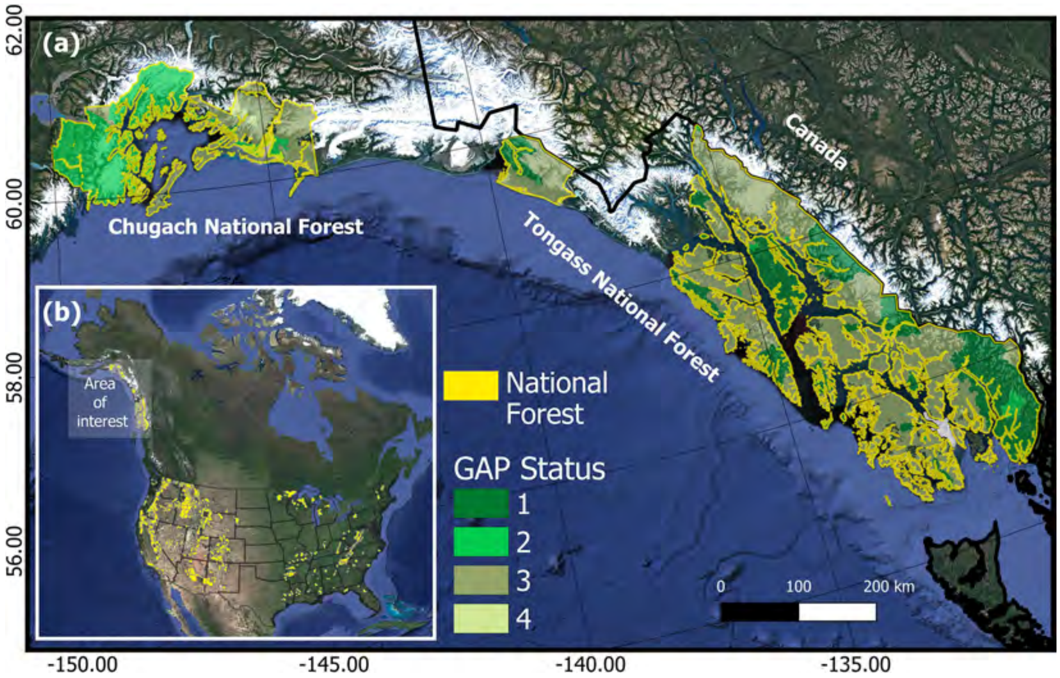

Figure 1. Administrative boundaries of the (a) Tongass and Chugach National Forests in southern Alaska and (b) National Forests throughout the USA. Also shown (a) are the current GAP Status of lands in the Tongass and Chugach National Forests. GAP 1 and GAP 2 lands are managed for biodiversity, GAP 3 lands are managed for multiple uses including mining, logging, and off highway vehicle use, and GAP 4 lands are those with no known mandate for protection. GAP Status data were from the Protected Area Database of the US (PAD-US version 3; USGS GAP, 2022). Basemap from Google Satellite © 2021 Google.

forest attributes across all US NFs. Our analysis highlights unique bioclimatic characteristics of coastal rainforests in southern Alaska that prioritize increased protection for forests in the region.

2. Materials and Methods

2.1. General Approach

We analyzed and ranked forest attributes among NFs using existing spatial data sets related to forest extent, landscape integrity, carbon, biodiversity, wildfires, and climate. Specifically, we focused on federally managed lands within the administrative boundary of each NF, with management type determined based on a spatial overlay with the PAD-US (USGS, 2022). Therefore, our analysis does not include inholdings within NF administrative boundaries, such as lands managed by local or state governments or Alaska Native Corporations. Our analysis also does not include the El Yunque National Forest in Puerto Rico due to data limitations. Most of the spatial data sets had a spatial resolution of ~300 m, therefore we chose to conduct the analysis using a common 300 m resolution grid in an Albers Equal Area projection. We reprojected categorical data sets using nearest neighbor resampling and continuous numeric data sets using bilinear interpolation. We analyzed and visualized data using the R software (version 4.2) (R Core Team, 2021) with the libraries *terra* (Hijmans, 2022), *raster* (Hijmans, 2019), *sf* (Pebesma, 2018), *data.table* (Dowle & Srinivasan, 2021), and *ggplot2* (Wickham, 2016). We created the maps using open-source software QGIS (v3.20; QGIS.org, 2021).

2.1.1. Forest Extent

We quantified the areal extent of forest within each NF using a global tree canopy cover data set (Hansen et al., 2013). This spatial data set provides per pixel estimates of tree canopy cover (0%–100%) at 30 m resolution for peak growing season circa 2010 based on Landsat 7 satellite imagery and regression tree modeling. We mean resampled these data from 30 to 300 m spatial resolution and then identified forestlands as areas with tree canopy cover ≥10%. We determined the total area of forestlands within each NF and used this layer to mask other spatial data sets to forestlands. Supplemental analysis showed a strong linear relationship between estimates of total forest area at 30 versus 300 m spatial resolution across NFs ($r^2 = 0.996$, $y = -219 + 0.946\,x$).

2.1.2. Forest Landscape Integrity

We assessed forest ecological integrity across each NF using the forest landscape integrity index (FLII; Grantham et al., 2020). This spatial data set describes the degree of modification of forests by humans and is derived from observed human pressures (infrastructure, agriculture, tree cover loss), inferred human pressure based on proximity to the observed pressures, and loss of forest connectivity (ratio of current to potential connectivity) (Grantham et al., 2020). The anthropogenically disturbed nature of many areas with temporary tree cover loss and recovery is reflected in scoring within the index, because temporary tree cover loss in the categories of shifting cultivation or rotational forestry is treated as an observed pressure. It does not treat tree cover loss associated with wildfire as an observed pressure because fires are often the result of natural processes. The FLII ranges from 0 to 10, with higher scores describing more intact forest landscapes that have ecosystem functions (e.g., carbon storage, biodiversity, watershed protection) closer to natural levels barring potential impacts of climate change. Scores are divided into three levels of integrity, low (≤6.0), medium (>6.0 and <9.6), and high (≥9.6) and were identified by the data creators (Grantham et al., 2020). Forests with scores ≥9.6 are considered to have high integrity based on inspection of benchmark locations (Grantham et al., 2020). The FLII was mapped globally at 300 m resolution using spatial data from 2000 to 2019 and can be applied at subnational to global scales. We computed the average and standard deviation of the FLII across each NF, as well as the total areal extent of high integrity forest (FLII ≥ 9.6) within each NF.

2.1.3. Forest Carbon

We quantified tree carbon stocks using harmonized global maps of above and belowground biomass carbon density in the year 2010 at 300 m spatial resolution (Spawn et al., 2020). The data set provides estimates of carbon storage in live tree aboveground (i.e., stems, branches, twigs, and bark) and belowground (i.e., roots) biomass for stems greater than 10 cm diameter at breast height. The data set was derived from remotely sensed measurements of tree aboveground biomass density combined with measurements of biomass carbon content and root to shoot ratios (Spawn et al., 2020). An accuracy assessment showed that estimates of total state-wide tree carbon stocks for states in the conterminous USA were very similar whether derived from the harmonized maps or independent USFS forest inventory data ($r^2 = 0.96$, slope = 1.17, $n = 48$; Spawn et al., 2020). We masked this data set to forestlands and then computed average and standard deviation of tree carbon density (Mg C ha^{-1}) for each NF, as well as total tree carbon stock (Tg C) in each NF.

2.1.4. Forest Wildlife Habitat for Keystone Species

We assessed the current areal extent of habitat for bald eagle (*Haliaeetus leucocephalus*), brown bear (*Ursus arctos*), and gray wolf (*Canis lupus*) across each NF using species distribution data sets produced by the USGS Gap Analysis Project (GAP) (Gotthardt et al., 2014; USGS, 2018). These species are important apex predators that can trigger trophic cascades (Ripple et al., 2014) and were historically ubiquitous in much of North America. Moreover, these top predators may function as umbrella species, hence conserving them could offer broader biodiversity benefits (Sergio et al., 2006). The GAP project produced separate species distribution models for Alaska (Gotthardt et al., 2014) and the continental US (USGS, 2018) at 60 and 30 m spatial resolution, respectively. Each species' distribution was predicted using models that linked occurrence records with geospatial data sets related to soil, hydrologic, topographic, land cover, development, disturbance climate, and ecological conditions. For each species, we reprojected data sets onto the common 60 m resolution grid and then quantified the areal extent of contemporary habitat that occurred within the boundaries of each NF.

2.1.5. Climate Data

We characterized historical climate conditions and potential future climate change across forestlands in each NF using two bioclimatic variables from the CHELSA-BIOCLIM + data set (Brun et al., 2022a, 2022b). This data set included climatologies for historical (1981–2010) and future (2071–2100) periods that were mechanistically downscaled to 1 km spatial resolution. For future conditions, we examined climatic changes predicted by an ensemble of five earth system models (ESMs) that were run as part of the Coupled Model Intercomparison Project Phase 6 (CMIP6) following a high-carbon emission shared socioeconomic pathway scenario (SSPS585). We focused on mean daily maximum temperature of the warmest month (hereafter *maximum temperature*, °C) and annual precipitation (mm), which are derived bioclimate variables that provide insight into ecosystem energy and moisture limitations. We reprojected these data onto the common 300 m resolution grid and masked out non-forest areas (e.g., icefields in the Tongass NF). For each grid cell, we computed the projected climatic changes from historical to future periods (i.e., 2071–2100 minus 1981–2010) using each climatology from the five ESMs. Next, we calculated the spatial average and standard deviation of historical and future climate and climatic changes for forestlands in each NF. For each NF, we focused on the ensemble median change predicted in spatially-averaged climate across the five ESMs, and also computed the minimum and maximum changes across the ensemble.

2.1.6. Wildfire Data

We quantified forest area burned in recent decades across each NF using the MODIS satellite burned area data set (MCD64A1 version 6; Giglio et al., 2018). This data set provides burned area extent every month across the world at 500 m spatial resolution. We accessed these data using Google Earth Engine (GEE; Gorelick et al., 2017) and for each grid cell determined whether it had burned from 2001 through 2020. We exported these data from GEE, resampled them to 300 m resolution to match the forest cover data set, and then computed total forest area burned for each NF, as well as the percentage of forest area that burned during these two decades.

2.1.7. Protected Area Data

We identified federally managed lands and evaluated the current extent of forest protection in the Tongass and Chugach NFs using the Protected Area Database of the United States (PAD-US version 3.0) produced by the United States Geological Survey Gap Analysis Project (USGS GAP, 2022). This spatial data set is the official inventory of protected areas across the nation (USGS GAP, 2022). Protected status is characterized by GAP status codes that describe management intent to preserve biodiversity following guidelines from the International Union for the Conservation of Nature (IUCN). GAP 1 and GAP 2 lands are managed for biodiversity, GAP 3 lands are managed for multiple uses including mining, logging, and off highway vehicle use, and GAP 4 lands are those with no known mandate for protection. GAP 1 typically aligns with IUCN Categories Ia, Ib, and II and is the only designation that protects all ecological functions and limits firefighting yet does allow hunting in Alaska. GAP 2 typically aligns with IUCN Categories III through VI and aims to maintain a "primarily" natural state but may receive uses or management that degrades the quality of existing natural communities, including suppression of natural disturbance. We rasterized land ownership and GAP status codes at 300 m spatial resolution, selecting the lowest GAP status if a land had multiple designations. We then masked all analyses to federally managed lands (i.e., excluded inholdings) and calculated total area and carbon stocks of forestlands falling under each GAP status code.

3. Results

3.1. Forest Area and Landscape Integrity

The Tongass and Chugach are among the few national forests (NFs) with high landscape integrity, and the Tongass has by far the largest forest area of all 154 NFs in the country (Figure 2). The Tongass and Chugach comprise 9.4% and 2.0% (total 11.4%) of all federally managed forest area on NF lands (~539,850 km^2 total) and are ranked first and second out of all NFs in terms of their forest area. Moreover, the Tongass and Chugach have mean (±1SD) FLII values of 9.8 ± 0.5 out of 10, respectively comprising 25.3% and 5.6% (total 30.9%) of all high (≥9.6) integrity forest landscapes found in the NFS, where FLII averages 8.0 ± 2.3. Other NFs with high mean forest landscape integrity (≥9.6) but less area include Challis NF in Idaho and Humboldt NF in California, which comprise 0.8% and 0.5% of all forest area on NF lands (Table S1 in Supporting Information S1). Compared to other NFs, the Tongass and Chugach are thus unique not only because of their extensive forest area but also their high forest landscape integrity.

3.2. Forest Carbon

Mean tree carbon densities are higher-than-average on the Tongass NF, but quite low on the Chugach NF (Figure 3a). The mean (±1SD) tree carbon density on the Tongass (88 ± 45 Mg C ha^{-1}) and Chugach (35 ± 25 Mg C ha^{-1}) are about ~10% higher and ~56% lower, respectively, than that of all forestlands in the National Forest System (61 ± 46 Mg C ha^{-1}; Figure 3a). The top 5 NFs with the highest mean tree carbon density (141–170 Mg C ha^{-1})

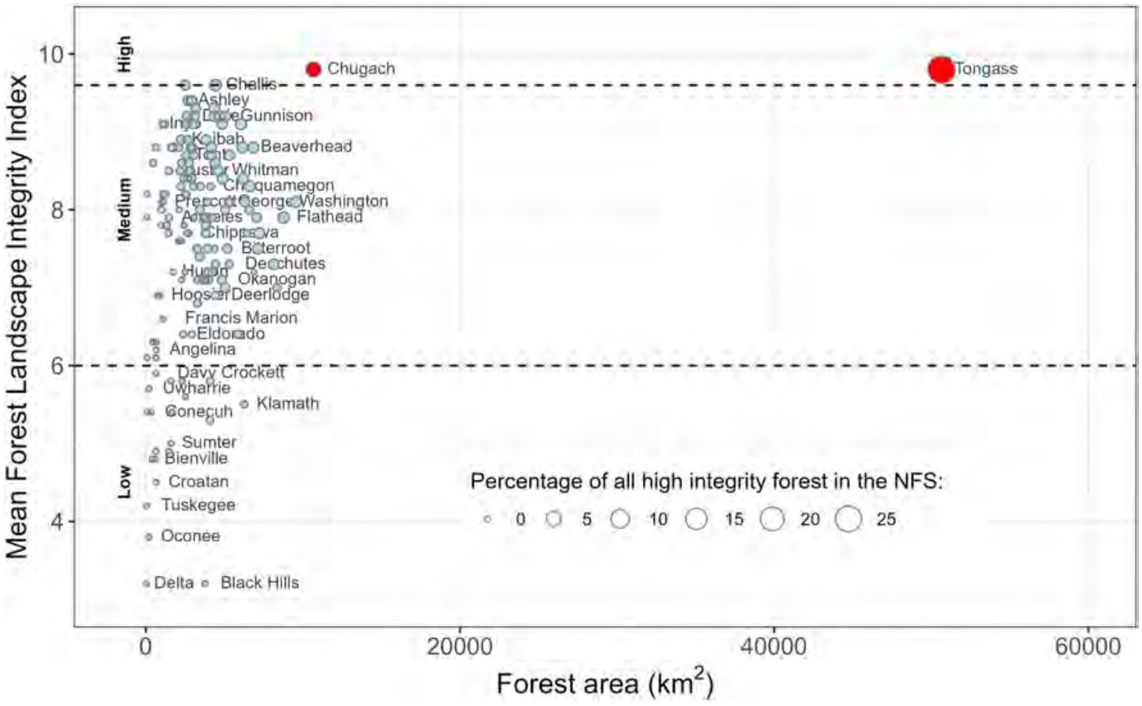

Figure 2. Forest area (km^2) and mean forest landscape integrity (unitless) for each national forest in the US National Forest System. The forest landscape integrity index ranges from 0 (lowest integrity) to 10 (highest integrity). Low (≤6.0), medium (>6.0 and <9.6), and high (≥9.6) forest integrity are identified using thresholds from the data creators (Grantham et al., 2020). The plotting character for each national forest is scaled by its relative holding of all high integrity forest in the National Forest System. Note the exceptional forest area and integrity of the Tongass and Chugach National Forests (red points).

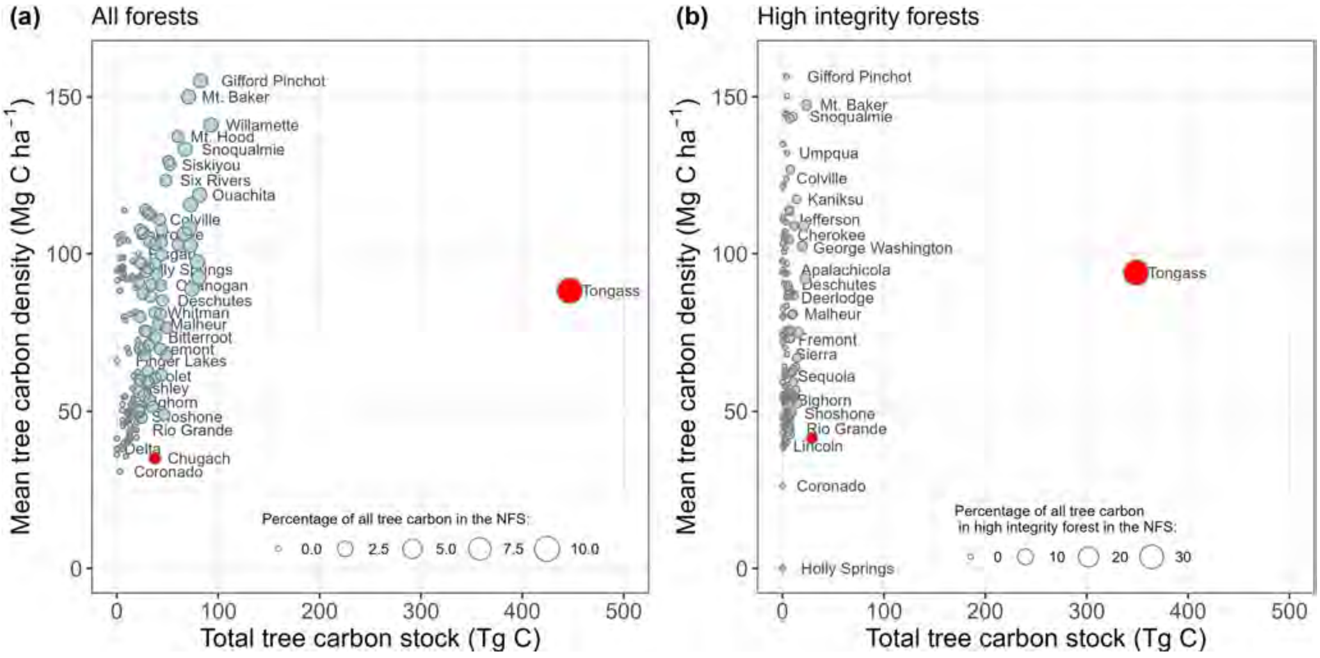

Figure 3. Mean tree carbon density (Mg C ha^{-1}) and total tree carbon stock (Tg C) for each national forest in the National Forest System (NFS). Summaries are provided for (a) all forests and (b) high integrity forests within each national forest. Tree carbon includes live aboveground and belowground biomass. The plotting character for each national forest is scaled by its overall contribution to total tree carbon stocks across (a) all forests and (b) high integrity forests in the NFS. Forests were considered high integrity if the forest landscape integrity index was ≥9.6 out of 10 (Grantham et al., 2020). There were 25 national forests without any high integrity forest, so in (b) these are plotted at the origin (0,0). The Tongass and Chugach National Forests are plotted as red points. Note the exceptionally large tree carbon stock of the Tongass and the much smaller carbon stock on the Chugach (red points).

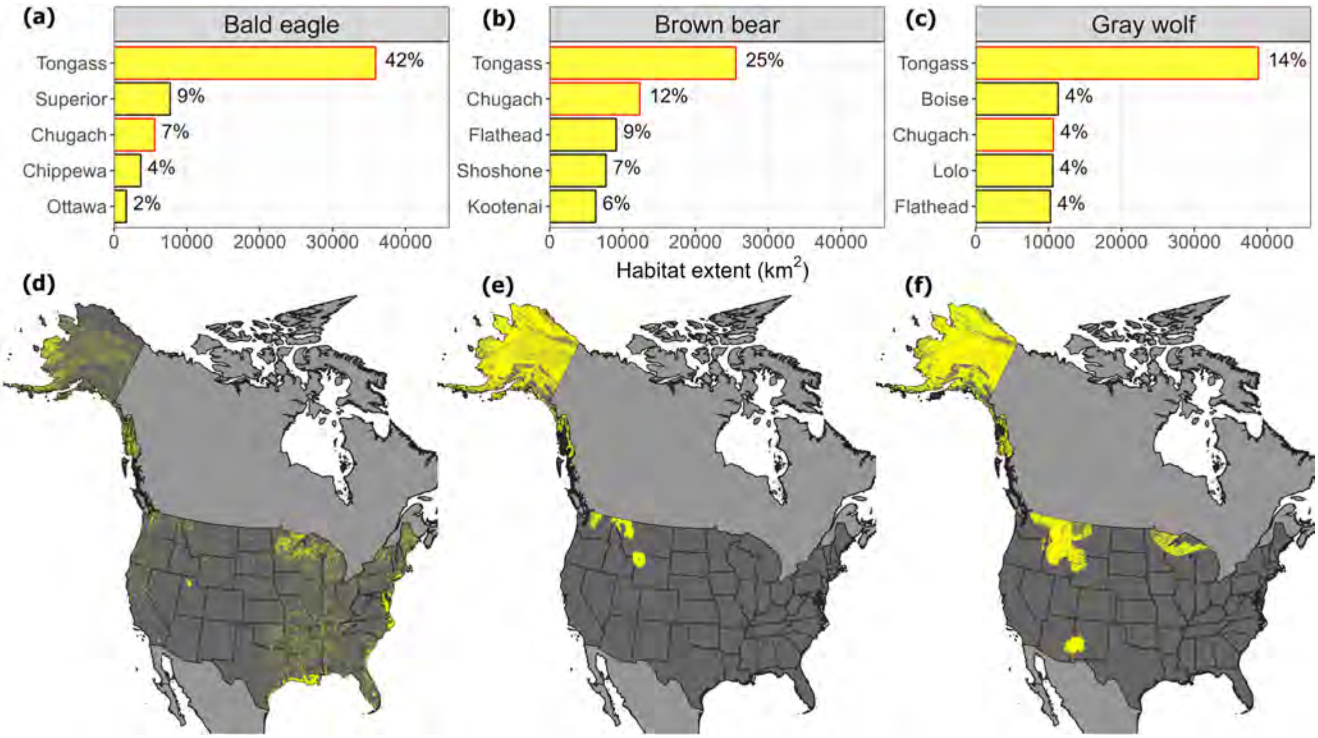

Figure 4. Current areal extent of bald eagle, brown bear, and gray wolf habitat in the (a–c) five national forests with the most habitat for each species and (d–f) the overall USA. In panels (a–c), the percentages denote the extent of species habitat within each national forest relative to the total extent of species habitat on all national forest lands. Species habitat distribution data sets generated as part of the USGS GAP (Gotthardt et al., 2014; USGS, 2018).

are the Siuslaw, Olympic, Gifford Pinchot, Mt. Baker, and Willamette, which all occur in either the Coast Range or Cascade Range of western Oregon and Washington (Table S2 in Supporting Information S1).

The Tongass and Chugach store approximately 10.4% and 0.9% (total 11.3%) of all tree carbon stocks that occur on NF lands (~4,305 Tg C total) and are ranked 1st and 40th out of all NFs in terms of their total tree carbon stocks (Figure 3a). Furthermore, the Tongass and Chugach store approximately 33% and 3% of all tree carbon stocks that occur in forests with high landscape integrity (FLII ≥9.6), placing them first and second among all NFs in this regard (Figure 3b; Table S2 in Supporting Information S1). Notably, the Tongass tree carbon stock (~447 Tg C) is nearly five time larger than that of the second ranked NF (Willamette). The top 5 NFs with the highest tree carbon stocks also include Ouachita, Flathead, and Gifford Pinchot, which is the only NF that also makes the top 5 for highest tree carbon densities.

3.3. Forest Wildlife Habitat

The Tongass provides substantially more habitat for bald eagles, brown bears, and gray wolves than any other NF, while the Chugach provides the second or third most habitat depending on species (Figure 4a). These two NFs together account for about 49%, 37%, and 18% of all bald eagle, brown bear, and gray wolf habitat found on NF lands, respectively. Other NFs important for bald eagles include Superior, Chippewa, and Ottawa in the upper Midwest (Figure 5), though the Tongass provides nearly three times as much habitat as all of these combined. While brown bears and gray wolves are found throughout much of Alaska, their current distributions in the continental US are restricted to the Northwest and, in case of gray wolves, to small areas in the Southwest and upper Midwest (Figure 4b).

3.4. Climate and Wildfire Risk

The Tongass and Chugach historically (i.e., 1981–2010) had the highest annual precipitation and lowest maximum temperature of all NFs (Figure 5a), as well as the largest projected increases in annual precipitation and among

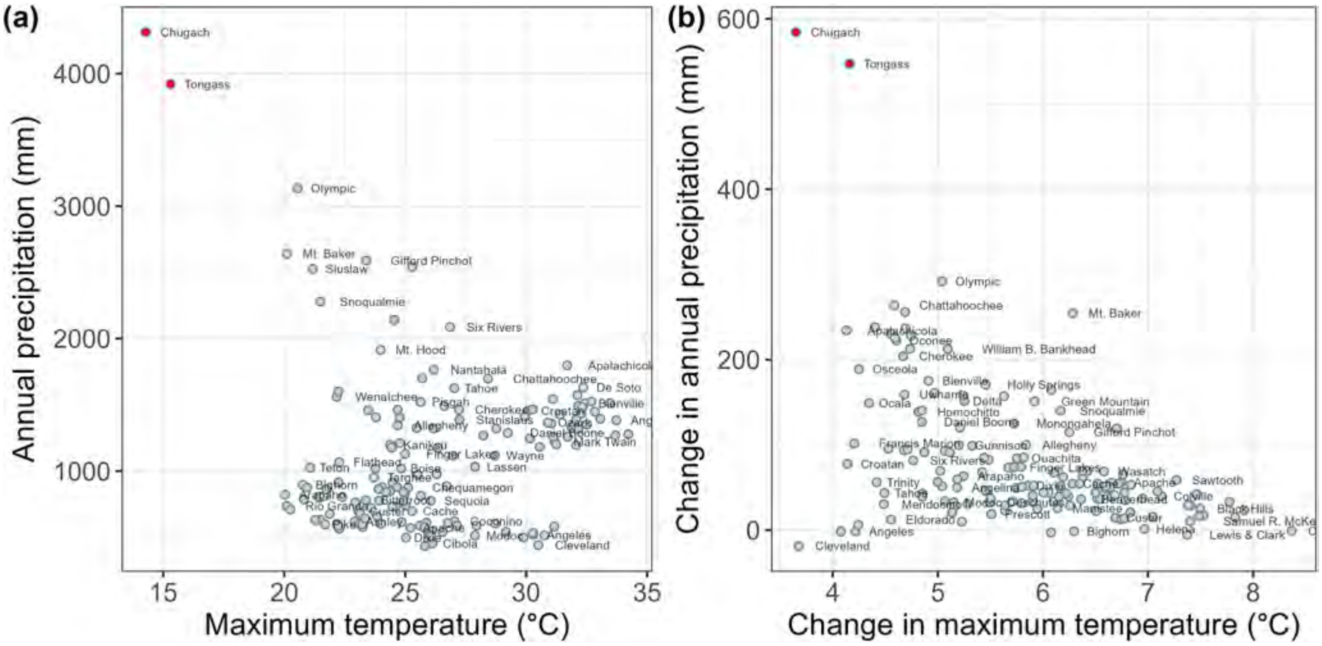

Figure 5. Historical climate (1981–2010) and future climate changes (2071–2100 minus 1981–2010) for each National Forest. (a) Climate variables include annual precipitation and mean daily maximum temperature of the warmest month (i.e., maximum temperature, °C). Climate data were spatially averaged across forestlands in each NF. (b) Climatic changes were derived from the ensemble median of predictions from five CMIP6 Earth system models driven by a high-carbon emission shared socioeconomic pathway scenario (SSPS585). Climate data were from the CHELSA-BIOCLIM + data set (Brun et al., 2022a, 2022b).

the lowest projected increases in maximum temperature over the coming century (i.e., 2071–2100; Figure 5b). Across forestlands in the Tongass and Chugach, annual precipitation historically averaged 3,920 ± 890 mm and 4,310 ± 1,390 mm, respectively, and is projected to increase 547 [195, 700] mm and 584 [413, 855] mm by the end of 21st century. Not only have the Tongass and Chugach historically been far wetter than any other NF, but future changes in annual precipitation are projected to be nearly two times larger than any other NF. Similarly, across forestlands in the Tongass and Chugach, maximum temperatures historically averaged 15.3 ± 2.1°C and 14.3 ± 1.6°C, respectively, and are projected to increase by 4.2 [3.5, 9.9] °C and 3.6 [2.5, 11.5] °C by the end of the century. The Tongass and Chugach historically had maximum temperatures that were about 5°C lower than any other NF, with rates of future warming that are the lowest to sixth lowest of any NF. Overall, the Tongass and Chugach were historically much colder and wetter than any other NF and are projected to experience much larger increases in precipitation and much lower increases in maximum temperatures over the coming century.

Satellite data showed fires burned a minuscule amount of forest area in the Tongass and Chugach from 2001 through 2020 (Figure 6). In total, forest fires burned about 70,251 km^2 (13.0%) of NF lands during the last two decades. The Tongass and Chugach together accounted for merely 0.1% of total forest burn area on NF lands but comprised about 11.4% of total forest area. During this period, forest fires burned a total of 61 km^2 (0.1%) and 27 km^2 (0.2%) in the Tongass and Chugach, respectively. These two NFs ranked near the bottom (144th and 140th) of all NFs in terms of their percent of forest area that burned in recent decades, in contrast with Mendocino and Angeles NFs where 66%–90% of forest area burned. Forests that burned multiple times (i.e., reburns) during this period are only counted once. Overall, forest fires were very uncommon during recent decades in Alaska's coastal rainforests.

3.5. Protected Areas

The forest area currently protected at GAP 1 or 2 levels sums to 17,983 km^2 on the Tongass (35.5% of the NF area) and 6,150 km^2 on the Chugach (57.6% of the NF area) (Figure 1, Table 1). The Tongass protected area is primarily GAP 1 status, mostly due to the six wilderness areas. The Chugach has no GAP 1 protected areas, with most protected areas designated as GAP 2 because of wilderness study and national heritage areas designated within its boundaries. GAP 3 areas are managed for multiple uses but also contain roadless areas which would be good candidates for higher levels of protection.

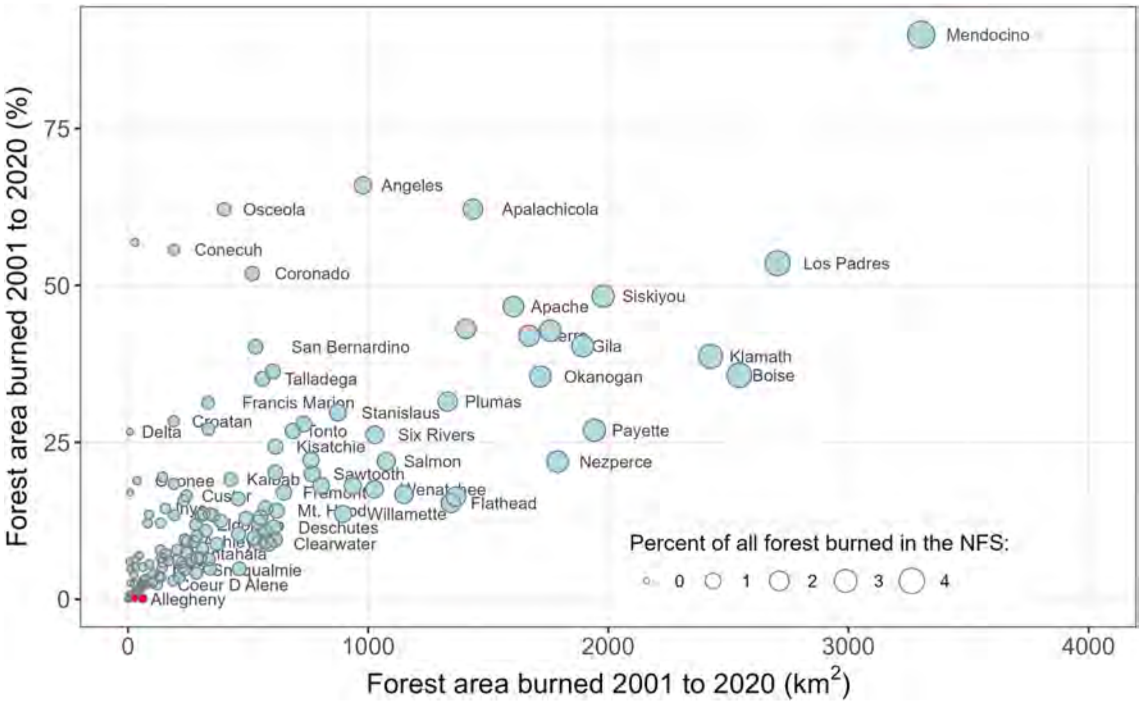

Figure 6. Absolute and relative forest area burned from 2001 to 2020 for each national forest in the US National Forest System. The plotting character for each national forest is scaled by its overall contribution to total forest burned area across all national forests. Note the exceptionally low absolute and relative forest burned areas of the Tongass and Chugach (small red points in bottom left). Burn area was derived from MODIS satellite data (Giglio et al., 2018).

4. Discussion

Severe ecological disruption is expected to occur over the next 10–30 years as the climate rapidly warms, hence immediate actions are needed to mitigate climate change and protect biodiversity (IPCC, 2018, 2021). These actions include effective conservation of 30%–50% of Earth's land, freshwater and ocean areas, including current near-natural ecosystems (IPCC, 2022). To better understand potential conservation benefits of preserving forestlands in the Tongass and Chugach NFs, we compared forest bioclimatic attributes of these NFs with all other NFs in the conterminous US. We focus on forests because of their significant carbon storage and accumulation of carbon over decades to centuries. Actions that support biodiversity also support ecosystem resilience in the long term (Oliver et al., 2015). Thus, our analysis compares landscape integrity among national forests, as well as tree biomass carbon stocks and habitat extent for keystone species while accounting for projected climate conditions that may impact some forests more than others. Current protected areas at GAP 1 and 2 levels can help to identify NFs where additional areas could be moved into these levels of protection with some changes in management, although there are some preexisting stipulations and allowances for other uses in Alaska. Our analysis highlights the Tongass and Chugach are exceptionally large and intact forests that provide important habitat and carbon sequestration that are buffered against fires and future climate disturbance.

Table 1
Current Extent of Land and Forest Protection Under Federal Management in the Chugach and Tongass National Forests in Southern Alaska

National Forest	GAP status	All lands		Forest lands		Forest carbon	
		km^2	%	km^2	%	Tg C	%
Chugach	1	0	0	0	0	0	0
	2	13,733	60.9	6,150	57.6	353	58.4
	3	8,821	39.1	4,520	42.3	251	41.6
	4	12	0.1	11	0.1	0	0
Tongass	1	23,421	34.3	17,267	34.1	1,005	33.3
	2	836	1.2	716	1.4	42	1.4
	3	43,986	64.5	32,667	64.5	1,974	65.3
	4	1	0	1	0	0	0

4.1. Forest Landscape Integrity

We found the Tongass and Chugach NFs have the highest forest landscape integrity of all NFs, and are ranked first and second in their forest area, making them high priority areas for protecting forest landscape integrity. Large contiguous tracks of intact forest landscape are important for biodiversity, carbon sequestration, water regulation, indigenous culture, and human health (Grantham et al., 2020; Potapov et al., 2017; Watson et al., 2018). However, globally, the extent of intact forest landscapes declined ~7% from

Table 2
Estimated Accumulation Rate of CO_2 by National Forest Region

National Forest region	Net change in stock ($Mg\ CO_2/yr$)	Area (ha)	Accumulation ($MgCO_2/ha/yr$)
Alaska	4.0	3,057,631	1.3
Eastern	11.5	4,767,960	2.4
Intermountain	−11.5	9,051,830	−1.3
Northern	−0.9	8,889,956	−0.1
Pacific Northwest	28.3	9,041,109	3.1
Pacific Southwest	5.7	5,994,752	1.0
Rocky Mountain	−12.2	6,118,661	−2.0
Southern	25.5	5,321,390	4.8
Southwestern	−6.9	6,164,438	−1.1
All Regions	43.5	58,407,728	0.7

Note. Net change in C stock from Domke et al. (2023). Area estimates are from the FIA database. Negative numbers mean CO_2 stocks are declining.

2000 to 2013 (Potapov et al., 2017), with overall forest landscape integrity also declining such that now only ~40% of forest area has high landscape integrity (Grantham et al., 2020). Moreover, just 27% of high-integrity forestland is designated as protected and, within the protected areas, slightly more than half of forestlands are considered high integrity (Grantham et al., 2020). Therefore, there is a pressing need to conserve the remaining large tracts of forest with high landscape integrity. There was extensive industrial logging in parts of southeastern Alaska during the second half of the twentieth century (DellaSala et al., 2022), yet our analysis underscores that the Tongass and Chugach NFs still have exceptionally large and intact forests compared to other NFs. Nevertheless, most NFs (83%) have at least some high integrity forests. Future analyses could identify conservation priorities within individual NFs by determining where contiguous tracts of intact forests occur using existing spatial data sets (e.g., Grantham et al., 2020).

4.2. Forest Carbon

Alaska's coastal rainforests have accumulated vast amounts of carbon for hundreds to thousands of years, keeping it out of the atmosphere (Smith et al., 2019). Drawing on a satellite-derived data set (Spawn et al., 2020), our results showed that the Tongass had higher and the Chugach had lower than average biomass density over all NFs. But because of the large area of these two forests, we estimated that the total live tree biomass in the Tongass and Chugach amounted to ~484 Tg C of the ~4,305 Tg C (i.e., 11.3%) found in the National Forest System, with tree biomass carbon stocks on the Tongass ~12 times greater than the Chugach. This is generally consistent with estimates derived from forest inventory data that indicate tree biomass in the broader Alaskan coastal rainforest region stores 464–557 Tg C (Barrett, 2014; Smith et al., 2019; Yatskov et al., 2019; Zhu & McGuire, 2016) and that regional tree biomass carbon stocks account for ~10.7% of the ~4,330 Tg C found in forests in the National Forest System that are managed by the Forest Service (Smith et al., 2019). In these coastal rainforests, live tree biomass comprises ~31% of forest ecosystem carbon stocks, which also includes understory vegetation, snags, woody debris, litter, and especially soil organic matter (Yatskov et al., 2019). Regional forest ecosystem carbon stocks have been estimated at 1,385 based on inventory data across nine NFs in Alaska (Smith et al., 2019), while a recent query of the FIA data shows 783 Tg C for Tongass and 154 Tg C for Chugach, 937 Tg C total, which is closer to Smith et al. (2019). However, the forest ecosystem carbon stocks in the Tongass alone have been estimated at 2,679–2,800 Tg C (DellaSala et al., 2022; Leighty et al., 2006). Our analysis further underscores that Alaska's coastal rainforests, particularly the Tongass, are a carbon reservoir of national importance that should be protected to help mitigate climate change. Nevertheless, discrepancies in regional carbon stock estimates emphasize that additional efforts are needed to improve understanding of current forest ecosystem carbon stocks across the region.

Estimates of annual net C accumulation for the Tongass and Chugach National Forests are becoming available as repeated forest inventories expand in these areas. A recent report by Domke et al. (2023) estimates that the annual net change in C stocks for these two forests is about 4 $Mg\ CO_2/yr$. Converting to CO_2 density, this represents 1.3 $Mg\ CO_2/ha/yr$ or nearly twice the average for all FS national forests combined (Table 2). Several regions in the Western U.S. are losing C stocks because of increases in natural disturbances, but this is not the case for southern Alaska public forests which are protected from fire and drought by ample rainfall. The net annual accumulation of CO_2 in the two Alaska national forests is about half the average for private forest lands in the U.S. of 2.7 $Mg\ CO_2/ha/yr$, most of which occurs in Eastern regenerating forests (Domke et al., 2023). Thus, besides the value of protecting the vast accumulated C stocks in southern Alaska, these forests are also accumulating additional CO_2 each year and do not appear to be affected by increasing threats to the long-term sustainability of this accumulation rate. Some proposed policies advocate conversion of older forests with large C stocks to younger and faster growing forests rather than letting them grow, but this argument ignores the huge C debt that must be covered before there would be any net additional C accumulation because it would take many decades to centuries to re-stock the C emissions from harvesting mature and old-growth forests (Birdsey et al., 2023; Harmon et al., 1990; Law et al., 2021).

4.3. Forest Wildlife Habitat

Our analysis showed the Tongass and Chugach NFs provide important habitat for bald eagles, brown bears, and wolves. These keystone species used to occur widely in northern North America but have been extirpated from much of their historical ranges. Historically, bald eagles occurred throughout the contiguous United States and Alaska (Buehler, 2000). Brown bears were native to the western half of North America, and those in California and Mexico are extinct (Haroldson et al., 2022). The historical range of gray wolves was coast to coast and north of 20° latitude over North America—they are second only to humans in adapting to climate extremes (Laliberte & Ripple, 2004).

The Tongass and Chugach forests have relatively abundant populations of animals that have become uncommon in other parts of the U.S. Alaska has over 98% of the US brown bear population, and the largest North American breeding populations of bald eagles are in Alaska and Canada. Gray wolf distribution covers about 85% of Alaska (total 7,000–11,000 wolves), with the highest densities in the Southeast. However, brown bears, and gray wolf have been impacted by hunting and predator control programs that reduced their numbers, leading to local declines and extirpations (Crupi et al., 2017; Ripple et al., 2019).

There are three species of special concern in the coastal forests of southern Alaska: The Alexander Archipelago wolf (*Canis lupus ligoni*), the marbled murrelet (*Brachyramphus marmoratus*), and the yellow cedar (*Callitropsis nootkatensis*). The Alexander Archipelago wolf is a subspecies of the gray wolf that is found in the coastal rainforests of Alaska and British Columbia (Schoen et al., 2014). These wolves have been impacted by logging as they rely heavily on old-growth forests for their habitat, cover, den sites, and prey (Gilbert et al., 2022). The marbled murrelet is a small seabird that nests in old-growth forests along the coast of Alaska and the Pacific Northwest. These birds are particularly vulnerable to habitat loss because they rely on mature trees for nesting sites (Carter et al., 2009; Piatt & Naslund, 1995). The logging of old-growth forest in coastal Alaska has led to a decline in the marbled murrelet population. Yellow cedar in the coastal rainforests of southeast Alaska has been listed as a species of concern under the Endangered Species Act, with population declines due to logging and climate change (Hennon et al., 2018).

In the Tongass, five species of salmon with a diversity of spawning periods provide food for a high concentration of bears, eagles, and other animals over a prolonged period each year. Brown bears are the dominant predator of salmon (Levi et al., 2015). Wolves in the region obtain about 20% of their diet from actively fishing salmon, which appears to contribute to the high survival rate of pups (90% compared with 50% in Minnesota). Where other prey is low, wolves are extremely reliant on a marine diet compared to coastal bears (Szepanski et al., 1999). After spawning, the salmon carcasses provide nutrients for forests.

Extinction risk is most acute for the largest and smallest vertebrates, and the largest vertebrates, for example, bears, are most vulnerable to direct killing by humans (Ripple et al., 2019). Thus, stronger protections and reduction of harvest of both trees and animals will give them a better chance of survival and resilience to the dual crises of climate change and biodiversity loss.

4.4. Climate and Wildfire Risk

We found the Tongass and Chugach historically had the highest annual precipitation and lowest maximum temperature of all NFs, as well as the largest projected increases in annual precipitation and among the lowest projected increases in maximum temperature over the coming century. The cool, wet conditions contribute to there being little wildfire activity in the region, with future increases in wildfires likely mitigated by increases in annual precipitation.

While much attention has been paid to climate change in northern Alaska, southern Alaska is expected to experience changes that are moderate by comparison. For example, temperature extremes in southeast Alaska are expected to be small compared to the rest of Alaska (Gray et al., 2018; Lader et al., 2022), and the length of warm and dry spells is not expected to change much. Nevertheless, climate risks for forests in southern Alaska include increased frequency and severity of forest disturbances and changes in hydrology. Such risks can affect forest sustainability and resilience both inside and outside protected areas and lead to shifts in suitable habitat boundaries for vegetation and wildlife communities (Shanley et al., 2015). For example, heavy rains and flooding are expected over coastal areas, as well as warmer water temperatures and warmer springs that have impacted

Alaska yellow cedar (Hennon et al., 2018). Yet projected warmer and wetter climate in southern Alaska probably will not destabilize forest carbon and biodiversity as much as in other NFs that are expected to become hotter and drier (Buotte et al., 2019; Law et al., 2021).

Ecosystem model simulations with climate projections indicated that this cool region with low forest fire risk is expected to remain a stable carbon sink or even increase in the future due to climate change (McGuire et al., 2018; Zhu & McGuire, 2016). Simulations under scenarios of climate change for southeast and south-central regions show that if these forests are allowed to grow without harvest, forest carbon could increase by 27% by 2100 (Zhu & McGuire, 2016). Furthermore, climate change could increase the importance of protection in this region since species may disproportionately favor protected areas as their ranges shift poleward and appropriate management could slow climate-related declines (Thomas & Gillingham, 2015).

4.5. Forest Protection in Southern Alaska

We found that about 35.5% of the Tongass and 57.6% of the Chugach are preserved at GAP 1 or 2 levels of protection that meet IUCN standards for conservation. Much of the Chugach has been inventoried as roadless, but is still classified as GAP 3 status, meaning that multiple use management that may involve logging is still the priority in this forest. An initial step has been taken to limit timber harvest on a portion of the Tongass through reinstating the roadless rule. The Biden administration finalized the Alaska roadless rule in 2023 that restores roadless protection to more than 36,422 km^2 of the Tongass, keeping it free from road-building and extraction. However, other uses may still be allowed. Our results demonstrate that the priority areas for conservation of landscape-integrity over large areas include the Tongass and Chugach NFs.

4.6. Limitations

Forest inventory plot density is lower in southern Alaska than in the other NFs. Forest Service wilderness areas and interior Alaska have not been inventoried by FIA, but are in progress for inclusion in future inventories (USDA Forest Service, 2023). Observation-based forest carbon mapping combining satellite and field data could be improved and spatially derived using methods such as those of the Landscape Ecology Modeling Mapping and Analysis program (https://lemma.forestry.oregonstate.edu/data). Due to limitations with available spatial data sets, we did not assess carbon stocks in dead standing trees (i.e., snags), woody debris, trees smaller than 10 cm diameter, understory vegetation, or soil.

The analysis of habitat extent that can support apex species under future climate is limited by data availability (Gotthardt et al., 2014). Habitat and species distribution modeling based on the reference data needs improvement. Yet, these are the only consistent spatial data available. Although habitat extent in southern Alaska is likely underestimated, it is by far the largest among NFs. The results provide estimates of areas with the potential for protection of forest carbon and key species, and closer landscape analysis will refine estimates of candidate areas to protect for carbon, plant and animal species and ecological resilience under climate change.

Similarly, the ability to map human modification in Alaska is limited by data and accuracy issues, as well as pressures that are often unmapped because they differ from those experienced in lower latitudes (Reynolds et al., 2018). These unmapped pressures mean that forest integrity could be overestimated for some of these forests. Yet, these forests are experiencing tremendous pressures that demand additional protection (Trammell et al., 2022).

4.7. Policy and Management Implications

A recent United Nations proposal calls for national parks, marine sanctuaries and other protected areas to cover nearly one-third or more of the planet by 2030 as part of an effort to stop a sixth mass extinction and slow global warming (IUCN, 2021). Climate change and biodiversity loss are closely interconnected by human actions such that policies should simultaneously address synergies between mitigating climate change and biodiversity loss to maximize co-benefits (Pandit et al., 2021). NbCSs can be most effective when planning for longevity of carbon storage rather than rapid carbon sequestration. Avoiding and reversing the loss and degradation of carbon- and species-rich ecosystems of land and waters is of highest importance for combined biodiversity protection and climate change mitigation actions with large adaptation co-benefits.

Key strategies emerging for mitigating climate change and preventing biodiversity losses include:

1. Establish national strategic reserves that protect existing mature and old forests from resource extraction, and expand wilderness areas. Forests with medium to high carbon density also tend to have high critical habitat and genetic diversity (Buotte et al., 2020; Dinerstein et al., 2020; Law et al., 2021).
2. Resilience-building strategies that address elements of biodiversity (preventing extinctions, ecoregion diversity) and facilitate animal movement by connectivity of protected areas, and new and expanded protected areas.
3. Implement measurement, reporting and verification from local to national levels that are consistent and meet international standards for tracking progress in protecting forest carbon and biodiversity.

Governments must establish and achieve NbCS targets in the Nationally Determined Contributions to meet Paris Agreement goals (Dinerstein et al., 2020; Griscom et al., 2017). Currently, there is a large gap between pledges and desired outcomes (UNEP, 2022). In the U.S., more public lands have been opened up for resource extraction since 2020 compared to the previous years while at the same time pledges were made to protect 30% of lands and waters by 2030. President Biden's Executive Order 14008 is a call to action to work together with stakeholders to conserve, connect and restore 30% of U.S. lands and waters by 2030 (White House, 2021). The Tongass is the ancestral homeland of the Tlingit and Haida Peoples, who developed a climate adaptation plan with stakeholders that identifies potential impacts on tree and vertebrate species and actions to increase resilience. Collaboration and consistency with national and international climate and conservation goals will be essential.

Area-based preservation must contribute more effectively to meeting international goals that aim to protect elements of biodiversity, including preventing the accelerating extinctions and protecting the remaining intact forests as well as mature and old forests from extractions.

An integrated climate-biodiversity agenda is gaining momentum at multiple levels. We propose Strategic Forest Reserves for permanent protection of forest carbon and biodiversity at the highest levels (GAP 1 and 2, IUCN categories I–VI) to support targets that protect 30% of the area by 2030 and 50% by 2050. We found that southern Alaska's forests have high landscape integrity, carbon stocks and habitat availability for key species, and should be protected on federal lands before irreversible losses of these forests continue (Goldstein et al., 2020). The Tongass and Chugach have 30% of the forest area protected at GAP 1 or 2. Although the Chugach has no area protected at the GAP 1 level, this could be improved by transitioning current areas with less protection to GAP 1. It is possible to elevate the preservation status of GAP 3 areas on federal lands by phasing out grazing, mining, and logging and strengthening protection by administrative rule. Inventoried Roadless Areas are key GAP 3 areas that have already been identified and are available for permanent protection. Making good on our national and international pledges will determine whether resilience and climate stability can provide life support for future generations on Earth.

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.

Data Availability Statement

All custom scripts written for the analysis are publicly available through GitHub (https://github.com/ecospatial-services/seak_preservation). Furthermore, all datasets used in this study are publicly available through online repositories. The National Forest Systems Land Unit dataset is available from https://data.fs.usda.gov/geodata/edw/datasets.php. The tree canopy cover dataset is available from https://glad.umd.edu/dataset/global-2010-tree-cover-30-m. The forest landscape integrity dataset is available from https://www.forestintegrity.com/. The forest carbon stock dataset is available from https://daac.ornl.gov/VEGETATION/guides/Global_Maps_C_Density_2010.html. The MODIS burned area data are available through Google Earth Engine https://code.earthengine.google.com/. The Protected Area Database of the US (version 3.0) is available from https://www.usgs.gov/programs/gap-analysis-project/science/pad-us-data-download. The species habitat datasets are available for the Continental US from https://gapanalysis.usgs.gov/apps/species-data-download and for Alaska http://akgap.uaa.alaska.edu/species-data. The CHELSA-BIOCLIM + climate dataset is available from https://www.envidat.ch/#/metadata/bioclim_plus.

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Land use strategies to mitigate climate change in carbon dense temperate forests

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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 CO_2, disturbance from fire, and management actions at regional scales are extremely limited. Here, we examine the relative merits of afforestation, reforestation, management changes, and harvest residue bioenergy use in the Pacific Northwest. This region represents some of the highest carbon density forests in the world, which can store carbon in trees for 800 y or more. Oregon's net ecosystem carbon balance (NECB) was equivalent to 72% of total emissions in 2011–2015. By 2100, simulations show increased net carbon uptake with little change in wildfires. Reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increase NECB 56% by 2100, with the latter two actions contributing the most. Resultant cobenefits included water availability and biodiversity, primarily from increased forest area, age, and species diversity. Converting 127,000 ha of irrigated grass crops to native forests could decrease irrigation demand by 233 billion $m^3 \cdot y^{-1}$. Utilizing harvest residues for bioenergy production instead of leaving them in forests to decompose increased emissions in the short-term (50 y), reducing mitigation effectiveness. Increasing forest carbon on public lands reduced emissions compared with storage in wood products because the residence time is more than twice that of wood products. Hence, temperate forests with high carbon densities and lower vulnerability to mortality have substantial potential for reducing forest sector emissions. Our analysis framework provides a template for assessments in other temperate regions.

forests | carbon balance | greenhouse gas emissions | climate mitigation

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but regional assessments to determine feasibility, timeliness, and effectiveness are limited and rarely account for the interactive effects of future climate, atmospheric CO_2 enrichment, nitrogen deposition, disturbance from wildfires, and management actions on forest processes. We examine the net effect of all of these factors and a suite of mitigation strategies at fine resolution (4-km grid). Proven strategies immediately available to mitigate carbon emissions from forest activities include the following: (*i*) reforestation (growing forests where they recently existed), (*ii*) afforestation (growing forests where they did not recently exist), (*iii*) increasing carbon density of existing forests, and (*iv*) reducing emissions from deforestation and degradation (1). Other proposed strategies include wood bioenergy production (2–4), bioenergy combined with carbon capture and storage (BECCS), and increasing wood product use in buildings. However, examples of commercial-scale BECCS are still scarce, and sustainability of wood sources remains controversial because of forgone ecosystem carbon storage and low environmental cobenefits (5, 6). Carbon stored in buildings generally outlives its usefulness or is replaced within decades (7) rather than the centuries possible in forests, and the factors influencing product substitution have yet to be fully explored (8). Our analysis of mitigation strategies focuses on the first four strategies, as well as bioenergy production, utilizing harvest residues only and without carbon capture and storage.

The appropriateness and effectiveness of mitigation strategies within regions vary depending on the current forest sink, competition with land-use and watershed protection, and environmental conditions affecting forest sustainability and resilience. Few process-based regional studies have quantified strategies that could actually be implemented, are low-risk, and do not depend on developing technologies. Our previous studies focused on regional modeling of the effects of forest thinning on net ecosystem carbon balance (NECB) and net emissions, as well as improving modeled drought sensitivity (9, 10), while this study focuses mainly on strategies to enhance forest carbon.

Our study region is Oregon in the Pacific Northwest, where coastal and montane forests have high biomass and carbon sequestration potential. They represent coastal forests from northern California to southeast Alaska, where trees live 800 y or more and biomass can exceed that of tropical forests (11) (Fig. S1). The semiarid ecoregions consist of woodlands that experience frequent fires (12). Land-use history is a major determinant of forest carbon balance. Harvest was the dominant cause of tree mortality (2003–2012) and accounted for fivefold as much mortality as that from fire and beetles combined (13). Forest land ownership is predominantly public (64%), and 76% of the biomass harvested is on private lands.

ENVIRONMENTAL SCIENCES

SUSTAINABILITY SCIENCE

Significance

Regional quantification of feasibility and effectiveness of forest strategies to mitigate climate change should integrate observations and mechanistic ecosystem process models with future climate, CO_2, disturbances from fire, and management. Here, we demonstrate this approach in a high biomass region, and found that reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increased net ecosystem carbon balance by 56% by 2100, with the latter two actions contributing the most. Forest sector emissions tracked with our life cycle assessment model decreased by 17%, partially meeting emissions reduction goals. Harvest residue bioenergy use did not reduce short-term emissions. Cobenefits include increased water availability and biodiversity of forest species. Our improved analysis framework can be used in other temperate regions.

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Data deposition: The CLM4.5 model data are available at Oregon State University (terraweb.forestry.oregonstate.edu/FMEC). Data from the >200 intensive plots on forest carbon are available at Oak Ridge National Laboratory (https://daac.ornl.gov/NACP/guides/NACP_TERRA-PNW.html), and FIA data are available at the USDA Forest Service (https://www.fia.fs.fed.us/tools-data/).

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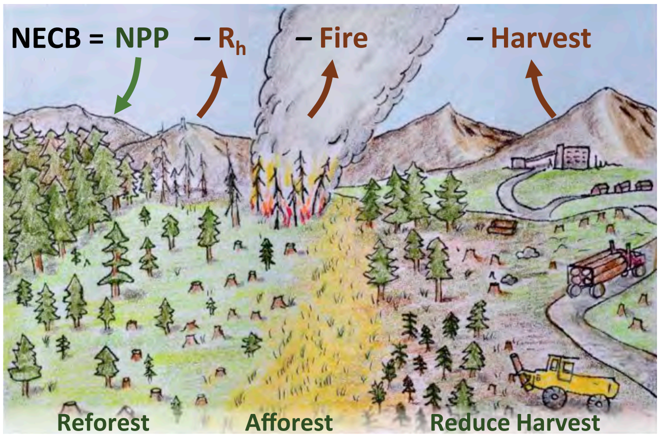

Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus Rh and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

Many US states, including Oregon (14), plan to reduce their greenhouse gas (GHG) emissions in accordance with the Paris Agreement. We evaluated strategies to address this question: How much carbon can the region's forests realistically remove from the atmosphere in the future, and which forest carbon strategies can reduce regional emissions by 2025, 2050, and 2100? We propose an integrated approach that combines observations with models and a life cycle assessment (LCA) to evaluate current and future effects of mitigation actions on forest carbon and forest sector emissions in temperate regions (Fig. 1). We estimated the recent carbon budget of Oregon's forests, and simulated the potential to increase the forest sink and decrease forest sector emissions under current and future climate conditions. We provide recommendations for regional assessments of mitigation strategies.

Results

Carbon stocks and fluxes are summarized for the observation cycles of 2001–2005, 2006–2010, and 2011–2015 (Table 1 and Tables S1 and S2). In 2011–2015, state-level forest carbon stocks totaled 3,036 Tg C (3 billion metric tons), with the coastal and montane ecoregions accounting for 57% of the live tree carbon (Tables S1 and S2). Net ecosystem production [NEP; net primary production (NPP) minus heterotrophic respiration (Rh)] averaged 28 teragrams carbon per year (Tg C y^{-1}) over all three periods. Fire emissions were unusually high at 8.69 million metric tons carbon dioxide equivalent (tCO_2e y^{-1}, i.e., 2.37 Tg C y^{-1}) in 2001–2005 due to the historic Biscuit Fire, but decreased to 3.56 million tCO_2e y^{-1} (0.97 Tg C y^{-1}) in 2011–2015 (Table S4). Note that 1 million tCO_2e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO_2e (Table S3), and 3.7-fold wildfire emissions in the period that included the record fire year (15) (Fig. 2). In 2011–2015, net wood product emissions were 34.45 million tCO_2e and almost 10-fold fire emissions, mostly due to lower fire emissions. The net wood product emissions are higher than fire emissions despite carbon benefits of storage in wood products and substitution for more fossil fuel-intensive products. Hence, combining fire and net wood product emissions, the forest sector emissions averaged 40 million tCO_2e y^{-1} and accounted for about 39% of total emissions across all sectors (Fig. 2 and Table S4). NECB was calculated from NEP minus losses from fire emissions and harvest (Fig. 1). State NECB was equivalent to 60% and 70% of total emissions for 2001–2005 and 2011–2015, respectively (Fig. 2, Table 1, and Table S4). Fire emissions were only between 4% and 8% of total emissions from all sources (2011–2015 and 2001–2004, respectively). Oregon's forests play a larger role in meeting its GHG targets than US forests have in meeting the nation's targets (16, 17).

Historical disturbance regimes were simulated using stand age and disturbance history from remote sensing products. Comparisons of Community Land Model (CLM4.5) output with Forest Inventory and Analysis (FIA) aboveground tree biomass (>6,000 plots) were within 1 SD of the ecoregion means (Fig. S2). CLM4.5 estimates of cumulative burn area and emissions from 1990 to 2014 were 14% and 25% less than observed, respectively. The discrepancy was mostly due to the model missing an anomalously large fire in 2002 (Fig. S3*A*). When excluded, modeled versus observed fire emissions were in good agreement ($r^2 = 0.62$; Fig. S3*B*). A sensitivity test of a 14% underestimate of burn area did not affect our final results because predicted emissions would increase almost equally for business as usual (BAU) management and our scenarios, resulting in no proportional change in NECB. However, the ratio of harvest to fire emissions would be lower.

Projections show that under future climate, atmospheric carbon dioxide, and BAU management, an increase in net carbon uptake due to CO_2 fertilization and climate in the mesic ecoregions far outweighs losses from fire and drought in the semiarid ecoregions. There was not an increasing trend in fire. Carbon stocks increased by 2% and 7% and NEP increased by 12% and 40% by 2050 and 2100, respectively.

We evaluated emission reduction strategies in the forest sector: protecting existing forest carbon, lengthening harvest cycles, reforestation, afforestation, and bioenergy production with product substitution. The largest potential increase in forest carbon is in the mesic Coast Range and West Cascade ecoregions. These forests are buffered by the ocean, have high soil water-holding capacity, low risk of wildfire [fire intervals average 260–400 y (18)], long carbon residence time, and potential for high carbon density. They can attain biomass up to 520 Mg C ha^{-1} (12). Although Oregon has several protected areas, they account for only 9–15% of the total forest area, so we expect it may be feasible to add carbon-protected lands with cobenefits of water protection and biodiversity.

Reforestation of recently forested areas include those areas impacted by fire and beetles. Our simulations to 2100 assume regrowth of the same species and incorporate future fire responses to climate and cyclical beetle outbreaks [70–80 y (13)]. Reforestation has the potential to increase stocks by 315 Tg C by 2100, reducing forest sector net emissions by 5% by 2100 relative to BAU management (Fig. 3). The East and West Cascades ecoregions had the highest reforestation potential, accounting for 90% of the increase (Table S5).

Afforestation of old fields within forest boundaries and nonfood/nonforage grass crops, hereafter referred to as "grass crops," had to meet minimum conditions for tree growth, and crop grid cells had to be partially forested (*SI Methods* and Table S6). These crops are not grazed or used for animal feed. Competing land uses may decrease the actual amount of area that can be afforested. We calculated the amount of irrigated grass crops (127,000 ha) that could be converted to forest, assuming success of carbon offset programs (19). By 2100, afforestation increased stocks by

Table 1. **Forest carbon budget components used to compute NECB**

Flux, Tg C·y^{-1}	2001–2005		2006–2010		2011–2015		2001–2015
NPP	73.64	7.59	73.57	7.58	73.57	7.58	73.60
Rh	45.67	5.11	45.38	5.07	45.19	5.05	45.41
NEP	27.97	9.15	28.19	9.12	28.39	9.11	28.18
Harvest removals	8.58	0.60	7.77	0.54	8.61	0.6	8.32
Fire emissions	2.37	0.27	1.79	0.2	0.97	0.11	1.71
NECB	17.02	9.17	18.63	9.14	18.81	9.13	18.15

Average annual values for each period, including uncertainty (95% confidence interval) in Tg C y^{-1} (multiply by 3.667 to get million tCO_2e).

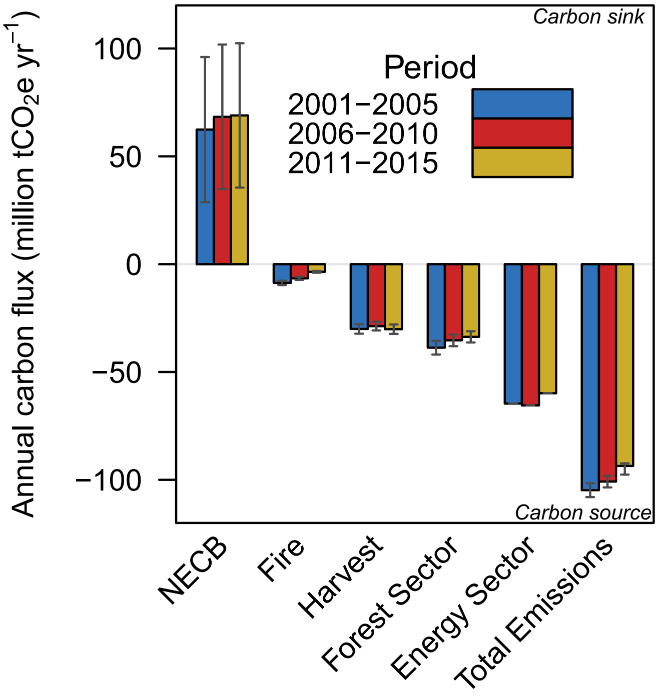

Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 95% confidence intervals (Monte Carlo analysis).

94 Tg C and cumulative NECB by 14 Tg C, and afforestation reduced forest sector GHG emissions by 1.3–1.4% in 2025, 2050, and 2100 (Fig. 3).

We quantified cobenefits of afforestation of irrigated grass crops on water availability based on data from hydrology and agricultural simulations of future grass crop area and related irrigation demand (20). Afforestation of 127,000 ha of grass cropland with Douglas fir could decrease irrigation demand by 222 and 233 billion $m^3 \cdot y^{-1}$ by 2050 and 2100, respectively. An independent estimate from measured precipitation and evapotranspiration (ET) at our mature Douglas fir and grass crop flux sites in the Willamette Valley shows the ET/precipitation fraction averaged 33% and 52%, respectively, and water balance (precipitation minus ET) averaged 910 $mm \cdot y^{-1}$ and 516 $mm \cdot y^{-1}$. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion $m^3 \cdot y^{-1}$ if 127,000 ha of the irrigated grass crops were converted to forest.

Harvest cycles in the mesic and montane forests have declined from over 120 y to 45 y despite the fact that these trees can live 500–1,000 y and net primary productivity peaks at 80–125 y (21). If harvest cycles were lengthened to 80 y on private lands and harvested area was reduced 50% on public lands, state-level stocks would increase by 17% to a total of ∼3,600 Tg C and NECB would increase 2–3 Tg C y^{-1} by 2100. The lengthened harvest cycles reduced harvest by 2 Tg C y^{-1}, which contributed to higher NECB. Leakage (more harvest elsewhere) is difficult to quantify and could counter these carbon gains. However, because harvest on federal lands was reduced significantly since 1992 (NW Forest Plan), leakage has probably already occurred.

The four strategies together increased NECB by 64%, 82%, and 56% by 2025, 2050, and 2100, respectively. This reduced forest sector net emissions by 11%, 10%, and 17% over the same periods (Fig. 3). By 2050, potential increases in NECB were largest in the Coast Range (Table S5), East Cascades, and Klamath Mountains, accounting for 19%, 25%, and 42% of the total increase, whereas by 2100, they were most evident in the West Cascades, East Cascades, and Klamath Mountains.

We examined the potential for using existing harvest residue for electricity generation, where burning the harvest residue for energy emits carbon immediately (3) versus the BAU practice of leaving residues in forests to slowly decompose. Assuming half of forest residues from harvest practices could be used to replace natural gas or coal in distributed facilities across the state, they would provide an average supply of 0.75–1 Tg C y^{-1} to the year 2100 in the reduced harvest and BAU scenarios, respectively. Compared with BAU harvest practices, where residues are left to decompose, proposed bioenergy production would increase cumulative net emissions by up to 45 Tg C by 2100. Even at 50% use, residue collection and transport are not likely to be economically viable, given the distances (>200 km) to Oregon's facilities.

Discussion

Earth system models have the potential to bring terrestrial observations related to climate, vulnerability, impacts, adaptation,

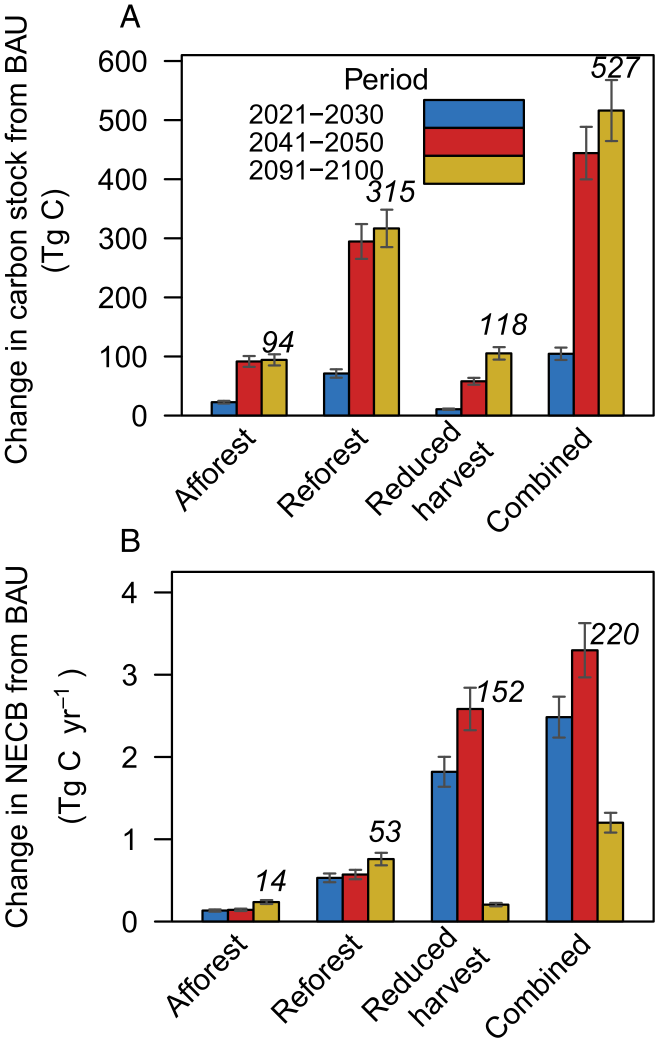

Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change in NECB for 2015–2100 (*B*). Error bars are ±10%.

and mitigation into a common framework, melding biophysical with social components (22). We developed a framework to examine a suite of mitigation actions to increase forest carbon sequestration and reduce forest sector emissions under current and future environmental conditions.

Harvest-related emissions had a large impact on recent forest NECB, reducing it by an average of 34% from 2001 to 2015. By comparison, fire emissions were relatively small and reduced NECB by 12% in the Biscuit Fire year, but only reduced NECB 5–9% from 2006 to 2015. Thus, altered forest management has the potential to enhance the forest carbon balance and reduce emissions.

Future NEP increased because enhancement from atmospheric carbon dioxide outweighed the losses from fire. Lengthened harvest cycles on private lands to 80 y and restricting harvest to 50% of current rates on public lands increased NECB the most by 2100, accounting for 90% of total emissions reduction (Fig. 3 and Tables S5 and S6). Reduced harvest led to NECB increasing earlier than the other strategies (by 2050), suggesting this could be a priority for implementation.

Our afforestation estimates may be too conservative by limiting them to nonforest areas within current forest boundaries and 127,000 ha of irrigated grass cropland. There was a net loss of 367,000 ha of forest area in Oregon and Washington combined from 2001 to 2006 (23), and less than 1% of native habitat remains in the Willamette Valley due to urbanization and agriculture (24). Perhaps more of this area could be afforested.

The spatial variation in the potential for each mitigation option to improve carbon stocks and fluxes shows that the reforestation potential is highest in the Cascade Mountains, where fire and insects occur (Fig. 4). The potential to reduce harvest on public land is highest in the Cascade Mountains, and that to lengthen harvest cycles on private lands is highest in the Coast Range.

Although western Oregon is mesic with little expected change in precipitation, the afforestation cobenefits of increased water availability will be important. Urban demand for water is projected to increase, but agricultural irrigation will continue to consume much more water than urban use (25). Converting 127,000 ha of irrigated grass crops to native forests appears to be a win–win strategy, returning some of the area to forest land, providing habitat and connectivity for forest species, and easing irrigation demand. Because the afforested grass crop represents only 11% of the available grass cropland (1.18 million ha), it is not likely to result in leakage or indirect land use change. The two forest strategies combined are likely to be important contributors to water security.

Cobenefits with biodiversity were not assessed in our study. However, a recent study showed that in the mesic forests, cobenefits with biodiversity of forest species are largest on lands with harvest cycles longer than 80 y, and thus would be most pronounced on private lands (26). We selected 80 y for the harvest cycle mitigation strategy because productivity peaks at 80–125 y in this region, which coincides with the point at which cobenefits with wildlife habitat are substantial.

Habitat loss and climate change are the two greatest threats to biodiversity. Afforestation of areas that are currently grass crops would likely improve the habitat of forest species (27), as about 90% of the forests in these areas were replaced by agriculture. About 45 mammal species are at risk because of range contraction (28). Forests are more efficient at dissipating heat than grass and crop lands, and forest cover gains lead to net surface cooling in all regions south of about 45° latitude in North American and Europe (29). The cooler conditions can buffer climate-sensitive bird populations from approaching their thermal limits and provide more food and nest sites (30). Thus, the mitigation strategies of afforestation, protecting forests on public lands and lengthening harvest cycles to 80–125 y, would likely benefit forest-dependent species.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of the total emissions reduction to ensure that regulated entities substantially reduce their own emissions, similar to California's program (19). An offset becomes a net emissions reduction by increasing the forest carbon sink (NECB). If only 8% of the GHG reduction is allowed for forest offsets, the limits for forest offsets would be 2.1 and 8.4 million metric tCO_2e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO_2e emissions reductions, and any one of the strategies or a portion of each could be applied. Thus, additionality beyond what would happen without the program is possible.

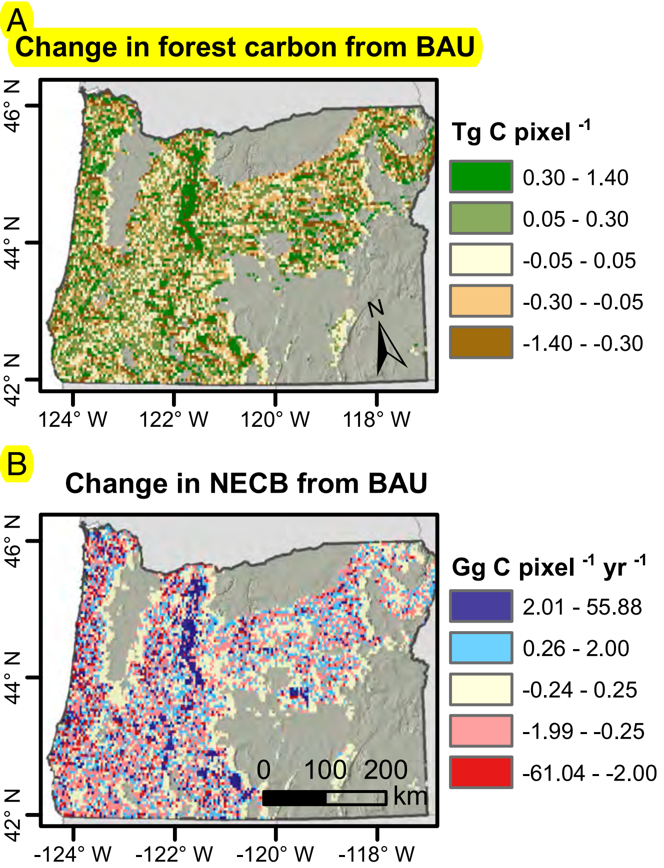

Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (*A*) and NECB (*B*) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

State-level reporting of GHG emissions includes the agriculture sector, but does not appear to include forest sector emissions, except for industrial fuel (i.e., utility fuel in Table S3) and, potentially, fire emissions. Harvest-related emissions should be quantified, as they are much larger than fire emissions in the western United States. Full accounting of forest sector emissions is necessary to meet climate mitigation goals.

Increased long-term storage in buildings and via product substitution has been suggested as a potential climate mitigation option. Pacific temperate forests can store carbon for many hundreds of years, which is much longer than is expected for buildings that are generally assumed to outlive their usefulness or be replaced within several decades (7). By 2035, about 75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends (31, 32). Recent analysis suggests substitution benefits of using wood versus more fossil fuel-intensive materials have been overestimated by at least an order of magnitude (33). Our LCA accounts for losses in product substitution stores (PSSs) associated with building life span, and thus are considerably lower than when no losses are assumed (4, 34). While product substitution reduces the overall forest sector emissions, it cannot offset the losses incurred by frequent harvest and losses associated with product transportation, manufacturing, use, disposal, and decay. Methods for calculating substitution benefits should be improved in other regional assessments.

Wood bioenergy production is interpreted as being carbon-neutral by assuming that trees regrow to replace those that burned. However, this does not account for reduced forest carbon stocks that took decades to centuries to sequester, degraded productive capacity, emissions from transportation and the production process, and biogenic/direct emissions at the facility (35). Increased harvest through proposed thinning practices in the region has been shown to elevate emissions for decades to centuries regardless of product end use (36). It is therefore unlikely that increased wood bioenergy production in this region would decrease overall forest sector emissions.

Conclusions

GHG reduction must happen quickly to avoid surpassing a 2 °C increase in temperature since preindustrial times. Alterations in forest management can contribute to increasing the land sink and decreasing emissions by keeping carbon in high biomass forests, extending harvest cycles, reforestation, and afforestation. Forests are carbon-ready and do not require new technologies or infrastructure for immediate mitigation of climate change. Growing forests for bioenergy production competes with forest carbon sequestration and does not reduce emissions in the next decades (10). BECCS requires new technology, and few locations have sufficient geological storage for CO_2 at power facilities with high-productivity forests nearby. Accurate accounting of forest carbon in trees and soils, NECB, and historic harvest rates, combined with transparent quantification of emissions from the wood product process, can ensure realistic reductions in forest sector emissions.

As states and regions take a larger role in implementing climate mitigation steps, robust forest sector assessments are urgently needed. Our integrated approach of combining observations, an LCA, and high-resolution process modeling (4-km grid vs. typical 200-km grid) of a suite of potential mitigation actions and their effects on forest carbon sequestration and emissions under changing climate and CO_2 provides an analysis framework that can be applied in other temperate regions.

Materials and Methods

Current Stocks and Fluxes. We quantified recent forest carbon stocks and fluxes using a combination of observations from FIA; Landsat products on forest type, land cover, and fire risk; 200 intensive plots in Oregon (37); and a wood decomposition database. Tree biomass was calculated from species-specific allometric equations and ecoregion-specific wood density. We estimated ecosystem carbon stocks, NEP (photosynthesis minus respiration), and NECB (NEP minus losses due to fire or harvest) using a mass-balance approach (36, 38) (Table 1 and *SI Materials and Methods*). Fire emissions were computed from the Monitoring Trends in Burn Severity database, biomass data, and region-specific combustion factors (15, 39) (*SI Materials and Methods*).

Future Projections and Model Description. Carbon stocks and NEP were quantified to the years 2025, 2050, and 2100 using CLM4.5 with physiological parameters for 10 major forest species, initial forest biomass (36), and future climate and atmospheric carbon dioxide as input (Institut Pierre Simon Laplace climate system model downscaled to 4 km × 4 km, representative concentration pathway 8.5). CLM4.5 uses 3-h climate data, ecophysiological characteristics, site physical characteristics, and site history to estimate the daily fluxes of carbon, nitrogen, and water between the atmosphere, plant state variables, and litter and soil state variables. Model components are biogeophysics, hydrological cycle, and biogeochemistry. This model version does not include a dynamic vegetation model to simulate resilience and establishment following disturbance. However, the effect of regeneration lags on forest carbon is not particularly strong for the long disturbance intervals in this study (40). Our plant functional type (PFT) parameterization for 10 major forest species rather than one significantly improves carbon modeling in the region (41).

Forest Management and Land Use Change Scenarios. Harvest cycles, reforestation, and afforestation were simulated to the year 2100. Carbon stocks and NEP were predicted for the current harvest cycle of 45 y compared with simulations extending it to 80 y. Reforestation potential was simulated over areas that recently suffered mortality from harvest, fire, and 12 species of beetles (13). We assumed the same vegetation regrew to the maximum potential, which is expected with the combination of natural regeneration and planting that commonly occurs after these events. Future BAU harvest files were constructed using current harvest rates, where county-specific average harvest and the actual amounts per ownership were used to guide grid cell selection. This resulted in the majority of harvest occurring on private land (70%) and in the mesic ecoregions. Beetle outbreaks were implemented using a modified mortality rate of the lodgepole pine PFT with 0.1% y^{-1} biomass mortality by 2100.

For afforestation potential, we identified areas that are within forest boundaries that are not currently forest and areas that are currently grass crops. We assumed no competition with conversion of irrigated grass crops to urban growth, given Oregon's land use laws for developing within urban growth boundaries. A separate study suggested that, on average, about 17% of all irrigated agricultural crops in the Willamette Valley could be converted to urban area under future climate; however, because 20% of total cropland is grass seed, it suggests little competition with urban growth (25).

Landsat observations (12,500 scenes) were processed to map changes in land cover from 1984 to 2012. Land cover types were separated with an unsupervised K-means clustering approach. Land cover classes were assigned to an existing forest type map (42). The CropScape Cropland Data Layer (CDL 2015, https://nassgeodata.gmu.edu/CropScape/) was used to distinguish nonforage grass crops from other grasses. For afforestation, we selected grass cropland with a minimum soil water-holding capacity of 150 mm and minimum precipitation of 500 mm that can support trees (43).

Afforestation Cobenefits. Modeled irrigation demand of grass seed crops under future climate conditions was previously conducted with hydrology and agricultural models, where ET is a function of climate, crop type, crop growth state, and soil-holding capacity (20) (Table S7). The simulations produced total land area, ET, and irrigation demand for each cover type. Current grass seed crop irrigation in the Willamette Valley is 413 billion $m^3 \cdot y^{-1}$ for 238,679 ha and is projected to be 412 and 405 billion m^3 in 2050 and 2100 (20) (Table S7). We used annual output from the simulations to estimate irrigation demand per unit area of grass seed crops (1.73, 1.75, and 1.84 million $m^3 \cdot ha^{-1}$ in 2015, 2050, and 2100, respectively), and applied it to the mapped irrigated crop area that met conditions necessary to support forests (Table S7).

LCA. Decomposition of wood through the product cycle was computed using an LCA (8, 10). Carbon emissions to the atmosphere from harvest were calculated annually over the time frame of the analysis (2001–2015). The net carbon emissions equal NECB plus total harvest minus wood lost during manufacturing and wood decomposed over time from product use. Wood industry fossil fuel emissions were computed for harvest, transportation, and manufacturing processes. Carbon credit was calculated for wood product storage, substitution, and internal mill recycling of wood losses for bioenergy.

Products were divided into sawtimber, pulpwood, and wood and paper products using published coefficients (44). Long-term and short-term products were assumed to decay at 2% and 10% per year, respectively (45). For product substitution, we focused on manufacturing for long-term structures (building life span >30 y). Because it is not clear when product substitution started in the Pacific Northwest, we evaluated it starting in 1970 since use of concrete and steel for housing was uncommon before 1965. The displacement value for product substitution was assumed to be 2.1 Mg fossil C/Mg C wood use in long-term structures (46), and although it likely fluctuates over time, we assumed it was constant. We accounted for losses in product substitution associated with building replacement (33) using a loss rate of 2% per year (33), but ignored leakage related to fossil C use by other sectors, which may result in more substitution benefit than will actually occur.

The general assumption for modern buildings, including cross-laminate timber, is they will outlive their usefulness and be replaced in about 30 y (7). By 2035, ~75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends, resulting in threefold as many buildings as there are now [2005 baseline (31, 32)]. The loss of the PSS is therefore PSS multiplied by the proportion of buildings lost per year (2% per year).

To compare the NECB equivalence to emissions, we calculated forest sector and energy sector emissions separately. Energy sector emissions ["in-boundary" state-quantified emissions by the Oregon Global Warming Commission (14)] include those from transportation, residential and commercial buildings, industry, and agriculture. The forest sector emissions are cradle-to-grave annual carbon emissions from harvest and product emissions, transportation, and utility fuels (Table S3). Forest sector utility fuels were subtracted from energy sector emissions to avoid double counting.

Uncertainty Estimates. For the observation-based analysis, Monte Carlo simulations were used to conduct an uncertainty analysis with the mean and SDs for NPP and Rh calculated using several approaches (36) (*SI Materials and Methods*). Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest emissions (7%), and land cover estimates (10%) using the propagation of error approach. Uncertainty in CLM4.5 model simulations and LCA were quantified by combining the uncertainty in the observations used to evaluate the model, the uncertainty in input datasets (e.g., remote sensing), and the uncertainty in the LCA coefficients (41).

Model input data for physiological parameters and model evaluation data on stocks and fluxes are available online (37).

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Management and Conservation Article

Succession of Bird Communities in Young Temperate Rainforests Following Thinning

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ABSTRACT We repeated bird and vegetation surveys in 1991–1992 and 2005–2006 among young managed stands and old-growth forests in southeast Alaska to evaluate whether pre-commercial thinning of managed stands influenced the bird community. We compared decadal changes in bird densities and forest vegetation among 3 stand types: managed stands originating from clearcuts 35 years ago that were left untreated (unthinned), managed stands thinned at uniform spacing (thinned), and old growth with no prior timber harvest. We did not detect differences in decadal trends in avian densities between thinned and unthinned stands for 15 of 16 common bird species using a repeated-measures design. Thinning did not result in greater recruitment of overstory-nesting species as predicted. This was likely because of 1) similar increases in tree heights ($\bar{x} = 9\text{–}10$ m) and canopy cover ($\bar{x} = 30\text{–}42\%$) between unthinned and thinned stands across decades and 2) the relatively young successional stage of these stands, which had only begun to recruit medium and large size conifers (dbh ≥ 36 cm). Decadal trends in densities of most (88%) understory-nesting bird species did not differ between thinned and unthinned stands. Shrub cover decreased by 22% and 31% across decades in thinned and unthinned stands, respectively. Bird community composition in managed stands reflected the general decadal changes in forest vegetation with a shift in dominance from understory species in the early 1990s (80–85% of total bird density) to an equal abundance of understory (45–54%) and overstory species in the mid-2000s. The latter was more similar to old-growth stands, which were dominated by overstory species (67–71%). Overstory-nesting birds in old growth increased in density by 49% across decades. Densities of cavity-nesting species remained unchanged in managed stands and less than densities in old growth across decades, possibly because of a lack of large trees and snags for nest sites. Overall, thinning of clearcut stands, the primary silvicultural system in the region, had few measurable benefits to birds nearly 20 years after treatment. Monitoring over the 70–100-year harvest rotation may be necessary to fully test whether thinning accelerates succession of bird communities in clearcut stands. However, partial harvests that retain large trees and snags should also be explored as alternatives to better maintain late-succession avifauna throughout the harvest rotation in southeast Alaska. © 2012 The Wildlife Society.

KEY WORDS bird density, forest birds, forest succession, silviculture, southeast Alaska, temperate rainforest, thinning.

Sustaining old-growth temperate rainforests and their characteristic fauna have been major challenges to forest managers (Szaro and Boyce 2005, DellaSala and Williams 2006, Schoen and Albert 2007). In southeast Alaska, this is because of disparities between the effects of natural disturbances and timber harvests on forests communities (Alaback 1982, Hanley 2005, Hanley et al. 2005, Carstensen 2007). The natural disturbance regime of these forests rarely includes large-scale, stand replacing disturbance events caused by fires (Noste 1969). Rather, the natural disturbance regime is characterized by gap-phase disturbances caused by diseases, insect outbreaks, and wind storms that topple individual or small groups of trees (Nowacki and Kramer 1998, Hennon and McClellan 2003, Carstensen 2007). Gap-phase disturbances result in large areas of uneven-aged forests with multi-layered canopies and well-developed shrub understories (Alaback 1982, Alaback and Juday 1989). Contrary to forests resulting from natural dynamics, clearcutting—the dominant harvest strategy in the region since the early 1950s—is a large-scale, stand-replacing disturbance that removes all vertical vegetation structure, except along non-harvest riparian buffers (Everest 2005, Kissling and Garton 2008), and thereby results in young even-aged stands (managed stands) that are atypical of the natural landscape mosaic. Wildlife species that rely on old-growth resources may therefore be reduced in abundance or even excluded from managed stands in the region (Schoen and Kirchhoff 1985, 1990; DeGange 1996; DellaSala et al. 1996; Iverson et al. 1996).

Post-harvest areas in the region typically receive no site preparation (McClellan 2005) and after 20–30 years are

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often characterized by high densities of small, closely spaced, naturally regenerating trees; single-layered and closed forest canopies; and sparsely vegetated understories (Alaback 1982, Hanley 2005). Harvested stands may take longer than the rotation age of 70–100 years to exhibit characteristics of old-growth forests (old growth; Alaback 1982).

To help ameliorate the negative effects of clearcut logging on late-successional fauna, forest managers in southeast Alaska have applied pre-commercial thinning to managed stands 20–30 years following harvest (Barbour et al. 2005, Hanley 2005). The goal of thinning is to reduce the number of regenerating trees competing for light and nutrients, increase the growth of the retained trees and understory vegetation, and ultimately accelerate succession of forest plant and animal communities (DellaSala et al. 1996, Hayes et al. 2003, Barbour et al. 2005, Hanley 2005). Since 1950, over 86,000 ha of managed stands (32%) have been thinned in southeast Alaska; most thinning was pre-commercial, took place after 1970, and did not involve post-treatment applications of herbicides to control shrub growth (Barbour et al. 2005, McClellan 2005). Despite the considerable attention to thinning in forest wildlife management in southeast Alaska, few studies have assessed whether thinning accelerates the succession of forest vegetation or wildlife communities in the region.

The only published assessment of the effects of managed-stand treatments on birds in the region was by DellaSala et al. (1996) on Prince of Wales Island, 1991–1992. They examined the abundance of breeding birds in relation to stand age (20 years vs. >150 years) and managed-stand treatments conducted 3–4 years prior to their study. Densities of breeding birds varied more between managed stands and old growth than between managed stands that were thinned or left untreated. Understory-nesting birds associated with shrub-dominated or open-forest habitats in Alaska (Kessel 1979), such as Pacific wren (*Troglodytes pacificus*), Swainson's thrush (*Catharus ustulatus*), orange-crowned warbler (*Oreothlypis celata*), Wilson's warbler (*Cardellina pusilla*), and fox sparrow (*Passerella iliaca*), were more abundant in managed stands than in old growth. Tree-nesting birds, such as red-breasted sapsucker (*Sphyrapicus ruber*), Pacific-slope flycatcher (*Empidonax difficilis*), brown creeper (*Certhia americana*), and golden-crowned kinglet (*Regulus satrapa*) were found primarily in old growth. Thinning conducted 3–4 years prior did not result in appreciable changes in bird communities in 20-year-old managed stands (DellaSala et al. 1996).

The benefits of thinning in accelerating succession of bird communities may require more time than the 3–4 years evaluated by DellaSala et al. (1996). For example, mean tree heights in managed stands were similar between unthinned (7.1 m) and thinned stands (8.0 m) and were lower than tree heights in old growth (29.1 m). Also, shrub cover (48%) was high in unthinned stands because the forest canopy (62%) had not yet closed and shaded out understory plants (DellaSala et al. 1996). Evaluations of thinning effects on accelerating succession in bird communities likely should be conducted over longer time periods to detect changes in avian densities and community structure. Such studies on birds are lacking for temperate rainforest stands >10 years following treatment (Hayes et al. 2003).

We repeated the surveys of breeding birds and forest vegetation conducted by DellaSala et al. (1996) to assess whether pre-commercial thinning that occurred 17–19 years ago resulted in a detectable change in forest structure and associated bird communities. We estimated changes in breeding bird densities and tree and understory characteristics between the time periods 1991–1992 (early 1990s) and 2005–2006 (mid-2000s) among managed stands (35 years since harvest) that remained untreated (unthinnned), managed stands that were thinned (thinned), and old growth that was never harvested. We included old growth to represent late-succession conditions for vegetation and bird communities. We predicted:

1. Breeding densities of overstory-nesting birds would increase more from the early 1990s to mid-2000s in thinned than unthinned stands because thinning would accelerate recruitment of live conifers into medium- and large-diameter classes most appropriate for nesting.
2. Breeding densities of understory-nesting birds would decline more in unthinned than thinned stands because thinning would reduce shading of understory plants.
3. Breeding densities of cavity-nesting birds would remain unchanged and at low densities in both thinned and unthinned stands because the large decay trees and snags most suitable for nesting would not yet be recruited in managed stands.

STUDY AREA

We conducted field research from 2005 to 2006 on northern Prince of Wales Island, southeast Alaska. The study area was dominated by coniferous forests that varied in structure and composition with elevation (0–305 m), slope (10–40%), age, and silviculture history. In 2001, forests in southeast Alaska were comprised of young growth (7% of forests), productive old growth with large trees (5%), old growth with small-and medium-sized trees (47%), and muskeg and subalpine forest (41%; Barbour et al. 2005, Caouette and DeGayner 2005, McClellan 2005, Albert and Schoen 2007).

Dominant trees were Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Subdominant trees were Alaska cedar (*Callitropsis nootkatensis*); lodgepole pine (*Pinus contorta*) and mountain hemlock (*Tsuga mertensiana*), which were found only in muskegs; and red alder (*Alnus rubra*), which occurred on scarified soils along roads and streams. Dominant understory shrubs were blueberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), rusty menziesia (*Menziesia ferruginea*), and devilsclub (*Oplopanax horridus*). Subshrubs (prostrate woody plants <20 cm in height) and forbs were dominated by bunchberry dogwood (*Cornus canadensis*), strawberryleaf raspberry (*Rubus pedatus*), deercabbage (*Nephrophyllidium crista-galli*), and American skunkcabbage (*Lysichiton americanus*; DellaSala et al. 1996; nomenclature following U.S.

Department of Agriculture Natural Resources Conservation Service, 2012).

We relied on the experimental design used by DellaSala et al. (1996) that divided the study area into 5 geographic blocks each with 4 treatment types ($n = 20$ stands). Within blocks, stands (35–106 ha) that were within 1 km of each other were selected based on similar topography and elevations. Our sample represented managed stands regenerating from harvests in 1969–1971 that were 1) left untreated (unthinned), 2) uniformly thinned from 1987 to 1988 at 3.7-m or 4.3-m spacing with the thinning residue left on site as slash (thinned), and 3) treated with canopy gaps in 1988–1989 by felling trees in 0.05-ha openings. Some of these managed stands contained small clusters of unharvested residual trees (0.05–1.3 ha) along riparian areas or in locations that were difficult to access for harvest (DellaSala et al. 1996). Old growth >150 years with no prior harvest (old growth) represented the fourth treatment type. Within each stand, DellaSala et al. (1996) located 5 bird and vegetation sampling points spaced 150–300 m apart and ≥50 m from the nearest forest edge. In this study, we resurveyed birds and vegetation communities at these same points consistent with a repeated measures design. The only exceptions were that 1) we moved 2 sampling points in 1 unthinned stand that had a small portion thinned since the original study, and 2) we did not resample gapped stands as most had been subsequently thinned because they did not differ significantly in forest structure and composition from unthinned stands (DellaSala et al. 1996).

METHODS

The methods we used to survey breeding birds and vegetation were previously described by DellaSala et al. (1996). At each sampling point, we remeasured vegetation in July 2005 within 4 randomly located subplots ($n = 20$ subplots/stand). We measured 8 overstory characteristics within 5-m and 10-m radius subplots in managed stands and old growth, respectively. Within each subplot we counted by species the number of stems >2 m in height for small (6–35 cm dbh), medium (36–55 cm dbh), and large (>55 cm dbh) trees. We also counted the number of snags (≥6 cm dbh). We transformed the counts of trees and snags to densities (stems/ha) for our analysis. We measured the heights (m) of 2 dominant trees that were closest to the subplot center and measured canopy cover using an ocular tube (James and Shugart 1970) to record the presence and absence of canopy vegetation (>3 m in height) at 5 points within each subplot. For the forest understory, we estimated percent cover and height (m) of shrubs within 5-m radius subplots in both managed stands and old growth. Within the 5-m subplot, we randomly located 2 microplots, 1-m radius in managed stands and 2-m radius in old growth, within which we estimated percent cover of forbs and subshrubs combined (forbs) and percent cover of woody debris (slash) in 2 height categories, <50 cm and ≥50 cm.

We used the point-transect method (Reynolds et al. 1980, Buckland et al. 2001) to estimate breeding densities of birds. In 1991, 1992, and 2005 we surveyed each stand 1 time during each of 4 consecutive 6-day intervals between 1 and 23 June; in 2006 we surveyed each stand once during each of 3 consecutive 6-day intervals between 7 and 23 June. At each point in each stand, an observer recorded the number of individual birds detected by species over an 8-min period and within a 100-m radius area centered on the sampling point. The horizontal distance to each individual bird detected was estimated to the nearest meter in 1991–1992 and within 10-m intervals in 2005–2006. We did not conduct surveys during periods of high winds or heavy rain.

Statistical Analyses

We used distance sampling (Buckland et al. 2001) to correct bird survey counts for detectability and thereby minimize bias in our estimates of bird densities. Conventional distance models without covariates can often provide density estimates that are robust to heterogeneity in the detection function (Buckland et al. 2001); however, bias in detectability of birds due to habitats, weather, observers, or time (Alldredge et al. 2007) has the potential to confound comparisons of density among strata, such as forest treatments. We therefore used distance sampling models with covariates (Marques et al. 2007) to control for such heterogeneity and strengthen our tests for treatment effects on decadal trends in avian density. We note that distance sampling only estimates the probability of detecting that proportion of birds that are available for detection by observers (i.e., singing or giving a visual cue)—it does not account for the proportion of birds that are missed during surveys because they are not vocalizing or otherwise unavailable for detection (Nichols et al. 2009). Thus our resulting estimates of density were likely biased low, particularly for those resident species whose peak display period occurred before our June surveys were conducted (Handel et al. 2009).

We restricted all statistical analyses of the bird data to those species with >100 observations resulting in sufficient sample sizes to estimate detection functions (Buckland et al. 2001:240–241). For these species, we excluded from analysis any observations that were of nestlings, juveniles, or birds flying overhead and not associated with the habitat at the survey point. We included the survey data from the gapped stands in our models of avian detectability, but we only applied the resulting detection functions to the survey data from unthinned, thinned, and old-growth stands, as these were the treatments sampled in each decade. For this analysis, we grouped into 10-m intervals the detection distances that were originally collected to the nearest meter by DellaSala et al. (1996) in 1991–1992.

For each species, we first developed a preliminary model of abundance and then truncated observations at large distances when detection probabilities were <0.1 to improve model fit near distance zero (Buckland et al. 2001:151). For each species, we then assessed the relative fit of different parametric key detection functions (half normal and hazard rate) and 1–2 adjustment terms (cosine or Hermite polynomial) to determine the combination that was most appropriate for estimating breeding density (Matsuoka and Johnson 2008). We evaluated the fit of each model using a chi-square test and considered models with significant ($P < 0.05$) chi-square values to have poor fit. We compared the relative support of models with reasonable fit using Akaike's information criterion adjusted for small sample sizes (AIC_c) and rescaled by subtracting the AIC_c value of the model in the candidate set with smallest AIC_c (Δ_i; Burnham and Anderson 2002). We further evaluated model support by examining Akaike weights (w_i).

For each species, we then applied the combination of the key detection function and adjustment terms with the smallest AIC_c to a candidate set of models that included the model with no effects and models with the univariate effects of treatment, year, decade (early 1990s vs. mid-2000s), visit within year (visit), wind, sky condition (sky), and observer ability (observer). We treated all covariates as categorical variables except wind, sky, and observer ability, which we treated as continuous variables. We calculated observer ability among the 4 species with >1,000 observations (Pacific wren, Swainson's thrush, orange-crowned warbler, and Townsend's warbler [*Setophaga townsendi*]), by 1) fitting a detection model to each species that included a factor effect for each of 7 observers with the eighth observer withheld as a reference category, 2) ranking detectability among observers separately for each of the 4 species, and 3) averaging these ranks across the 4 species. We then treated these average ranks as a continuous variable to evaluate observer effects on detectability for all species. For each species, we used AIC_c to assess the relative support for the detection models. We then used the model with the smallest AIC_c value, corrected the counts for detection probabilities (Buckland et al. 2001, Marques et al. 2007), and calculated the average breeding density (birds/ha) for each species in each stand for each decade. We also assigned each species to either an overstory-nesting or understory-nesting guild based on whether it had been found to nest primarily in trees or in the forest understory (<2 m height) in southeast Alaska (Willson and Gende 2000, Sperry 2006, Sperry et al. 2008). We then estimated the average breeding density for each guild by summing the densities of the constituent species.

In all analyses of decadal changes in vegetation and breeding bird communities, we treated the stand as the sampling unit ($n = 5$ stands for each treatment). For vegetation variables, we averaged stem counts, plant heights, and plant cover among the 20 subplots from each stand for each year (1991 and 2005) and then treated these as the values of our response variables in our analyses of decadal trends in vegetation. For each of the common species of breeding birds, we pooled points and visits within a stand for each decade, corrected the raw counts for detectability (see above), and then estimated the average breeding density by species, stand, and decade. We treated these as the values of our response variables in our analyses of decadal trends in bird densities. For each vegetation variable, bird species, and nesting guild, we then used repeated-measures analysis of variance (ANOVA) with a randomized block design (SAS Institute 1996) to test for mean differences in each response variable by treatment, decade, and the treatment × decade interaction. We used a mixed-model with compound symmetry for the covariance structure, which assumes that variance was equal among decades (SAS Institute 1996). We interpreted significant factor effects as follows:

1. Treatment × decade ($P \leq 0.05$): Decadal trends are different among treatments. When the interaction was significant, we calculated the change in the response variable across decades for each stand, used these values in an ANOVA with a randomized block design and a treatment effect, and then conducted multiple comparisons with a Tukey adjustment to identify specific mean differences in the decadal trends among treatments (Neter et al. 1990).
2. Decade ($P \leq 0.05$), treatment ($P > 0.05$), treatment × decade ($P > 0.05$): Decadal trends were similar across all treatments; no differences among treatment means in either decade.
3. Decade ($P > 0.05$), treatment ($P \leq 0.05$), treatment × decade ($P > 0.05$): No decadal trends, but means differ among treatments.
4. Decade ($P \leq 0.05$), treatment ($P \leq 0.05$), treatment × decade ($P > 0.05$): Decadal trends similar among treatments; treatment means differ by similar magnitudes in each decade.

When we found significant factor effects, we conducted multiple comparisons with a Tukey adjustment to identify specific mean differences among treatments and/or years.

We used SAS 8.0 (SAS Institute, Cary, NC) statistical package to conduct repeated measures and multiple comparison tests and program DISTANCE 5.0, release 2 (Thomas et al. 2010) to model the detection function and estimate breeding densities of birds. We considered models of detectability with $\Delta_i < 2.0$ to be best supported by the data (Burnham and Anderson 2002) and present all mean ± SE. We considered significant those mean comparisons where $P \leq 0.05$.

RESULTS

Changes in Forest Vegetation

Overstory vegetation.—We found evidence for a treatment × decade interaction from 1991 to 2005 ($F_{2,12} \geq 13.1$, $P \leq 0.001$) for 5 of the 9 overstory variables including canopy cover, tree height, small conifer densities, total conifer densities, and snag densities (Fig. 1). Canopy cover increased from 1991–2005 in unthinned ($\bar{x}_{\mathrm{change}} = 29 \pm 5\%$) and thinned stands ($\bar{x}_{\mathrm{change}} = 43 \pm 6\%$; $|t_{12}| \geq 6.4$, $P \leq 0.001$), but did not change significantly in old growth ($\bar{x}_{\mathrm{change}} = -6 \pm 2\%$; $|t_{12}| = 1.4$, $P = 0.72$). Similarly, the heights of dominant trees doubled in unthinned ($\bar{x}_{\mathrm{change}} = 10 \pm 1$ m) and thinned stands ($\bar{x}_{\mathrm{change}} = 9 \pm 1$ m; $|t_{12}| = 10.2$, $P \leq 0.001$), but did not change significantly in old growth ($\bar{x}_{\mathrm{change}} = -1 \pm 1$ m; $|t_{12}| = 0.7$, $P = 0.98$). Decadal increases in canopy cover and tree heights did not differ between unthinned and thinned stands ($|t_8| \leq 2.1$, $P = 0.15$ and $P = 0.45$), but were greater in managed stand treatments compared to old growth ($|t_8| \geq 5.4$, $P = 0.002$ and $P \leq 0.001$). In 1991, average canopy cover and tree heights in managed stands were respectively 45–72% and 23–25% of the

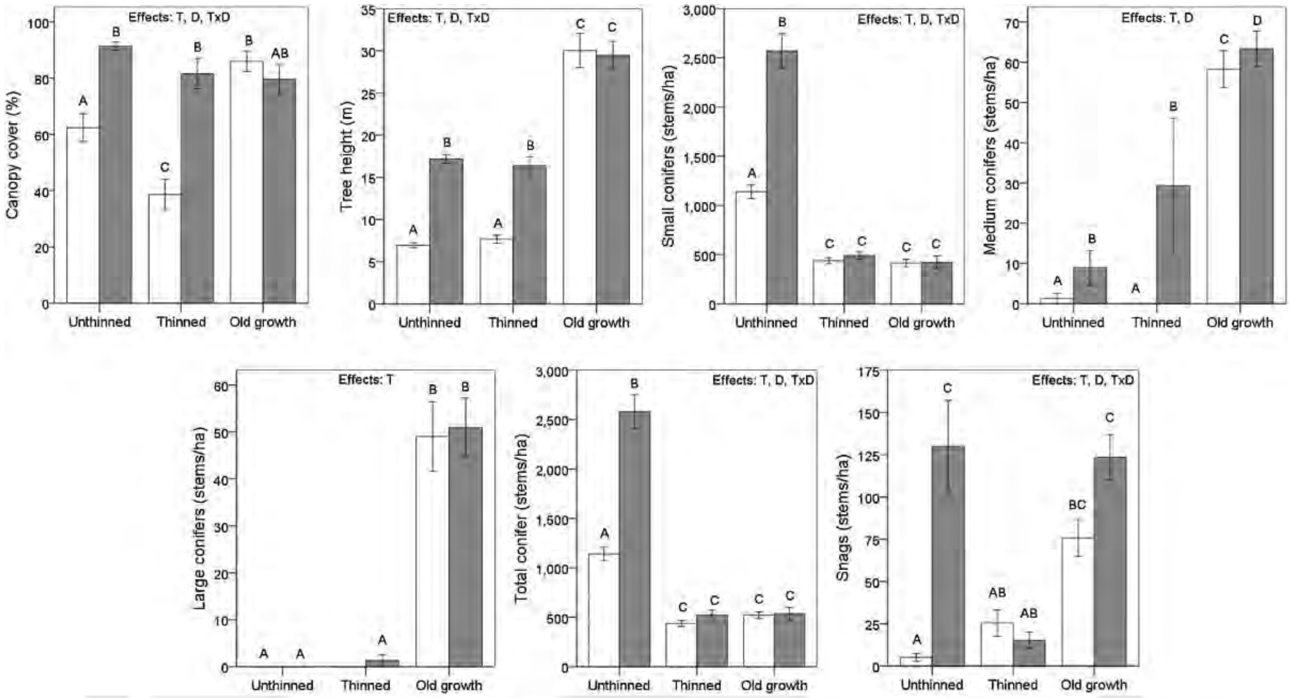

Figure 1. Average measurements of overstory vegetation ± SE by decade (white = 1991, grey = 2005) among unthinned and pre-commercially thinned stands harvested in 1971–1972 and old-growth stands ($n = 5$ stands/treatment), Prince of Wales Island, Alaska, USA. Significant ($P \leq 0.05$) effects of treatment (T), decade (D), and the treatment by decade interaction (T × D) are based on repeated measures analysis of variance. T × D indicates that the decadal trends varied among treatments. Means sharing a letter do not differ significantly between treatments or decades.

average values in old growth ($|t_{12}| \geq 4.3$, $P = 0.01$ and $P \leq 0.001$). In 2005, all treatments had similar closed canopies with ≥80% cover ($|t_{12}| \leq 2.2$; $P = 0.32$, $P = 0.50$, and $P = 1.0$); trees in managed stands remained only 53–57% the height of dominant old-growth trees ($|t_{12}| \geq 8.9$, $P \leq 0.001$; Fig. 1).

From 1991 to 2005, small conifer densities doubled ($\bar{x}_{\text{change}} = 1{,}431 \pm 106$ stems/ha) and snag densities increased 25-times ($\bar{x}_{\text{change}} = 125 \pm 29$ stems/ha; $|t_{12}| \geq 6.7$, $P \leq 0.001$) in unthinned stands, but neither changed in thinned stands or old growth ($|t_{12}| \leq 2.6$; $P = 0.18$, $P = 0.98$, $P \geq 0.99$). Thus, decadal increases in small conifer and snag densities were greater in unthinned stands than in thinned stands or old growth ($|t_8| \geq 3.1$; $P = 0.04$, $P = 0.002$, and $P \leq 0.001$). The high mortality of trees in unthinned stands increased snag densities to levels comparable to old growth in 2005 ($|t_{12}| = 0.33$, $P = 1.0$). However, total densities of conifers in unthinned stands still averaged ≥4.8 times the densities found in thinned and old growth stands in 2005 ($|t_{12}| \geq 19.6$, $P \leq 0.001$; Fig. 1). In 2005, nearly all snags (97%) in controls and 73% in old growth were small in diameter (≤35 cm dbh).

All treatments showed small increases in medium conifer densities ($\bar{x}_{\text{change}} = 5\text{–}29$ stems/ha; decade effect, $F_{1,12} = 5.2$, $P = 0.04$) that were not distinguishable among the 3 treatments (treatment × decade effect, $F_{2,12} = 1.6$, $P = 0.25$). Large conifers were absent from unthinned stands from 1991 to 2005 and were recruited into only 1 of 5 thinned stands by 2005 (Fig. 1). Thus, densities of medium and large conifers remained greater in old growth compared to managed stands in both 1991 and 2005 ($|t_8| \geq 6.1$, $P \leq 0.001$; Fig. 1). We did not detect differences in the number of tree species or densities of red alders among treatments ($F_{2,8} \leq 1.5$, $P = 0.28$ and $P = 0.33$) or between decades ($F_{1,12} \leq 0.9$, $P = 0.37$ and $P = 0.56$).

Understory vegetation.—We found a treatment × decade interaction ($F_{2,12} \geq 7.0$; $P = 0.01$, $P = 0.007$, and $P = 0.002$) for 3 understory variables: shrub cover, shrub height, and slash cover ≥50 cm in height (Fig. 2). From 1991 to 2005, shrub cover declined in unthinned ($\bar{x}_{\text{change}} = -31 \pm 6\%$) and thinned stands ($\bar{x}_{\text{change}} = -22 \pm 5\%$; $|t_{12}| \geq 4.7$, $P = 0.005$ and $P \leq 0.001$), but did not change significantly in old growth ($\bar{x}_{\text{change}} = -5 \pm 2\%$; $|t_{12}| = 1.0$, $P = 0.90$). Decadal declines in shrub cover were greater in unthinned stands compared to old growth ($|t_8| = 4.1$, $P = 0.008$), but did not vary significantly between thinned stands and unthinned stands or old growth ($|t_8| \leq 2.8$, $P = 0.06$ and $P = 0.41$). In 2005, shrub cover in thinned stands declined to levels comparable to old growth ($|t_{12}| = 0.5$, $P \geq 0.99$) but was 2.7 times the average value in unthinned stands ($|t_{12}| = 3.5$, $P = 0.04$; Fig. 2).

From 1991 to 2005, shrub height increased ($\bar{x}_{\text{change}} = 0.4 \pm 0.1$ m) and slash cover ≥50 cm in height decreased ($\bar{x}_{\text{change}} = -13 \pm 3\%$; $|t_{12}| \geq 4.9$, $P = 0.004$ and $P \leq 0.001$) in thinned stands but did not change significantly in unthinned stands and old growth ($|t_{12}| \leq 1.3$; $P = 0.77$, $P = 0.78$, $P = 0.89$, and $P = 1.0$). The decadal change in shrub height was greater in thinned stands compared to unthinned stands; the decrease in slash cover was greater in thinned stands compared to unthinned stands and old growth ($|t_8| \geq 3.5$; $P = 0.02$, $P = 0.009$, and $P = 0.007$). In 2005, slash levels in thinned stands had

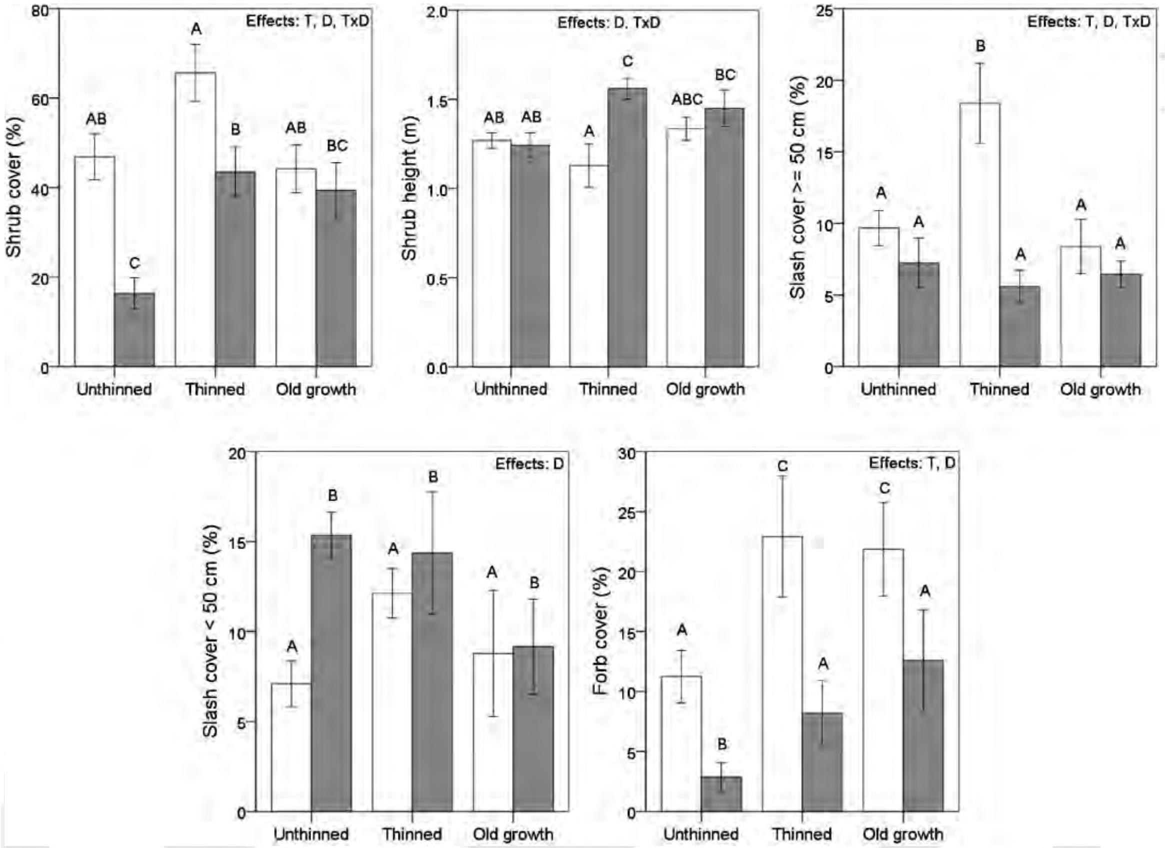

Figure 2. Average measurements of understory vegetation ± SE by decade (white = 1991, grey = 2005) among unthinned and pre-commercially thinned stands harvested in 1971–1972 and old-growth stands ($n = 5$ stands/treatment), Prince of Wales Island, Alaska, USA. Significant ($P \leq 0.05$) effects of treatment (T), decade (D), and the treatment by decade interaction (T × D) are based on repeated measures analysis of variance. T × D indicates that the decadal trends varied among treatments. Means sharing a letter do not differ significantly between treatments or decades.

declined to levels comparable to other treatments ($|t_{12}| \leq 0.8$, $P = 0.97$, and $P = 1.0$), whereas shrub heights were greater in thinned compared to unthinned stands ($|t_{12}| = 3.6$, $P = 0.03$; Fig. 2).

Slash cover <50 cm in height did not vary among treatments (treatment effect, $F_{2,8} = 1.0$, $P = 0.40$) but increased by 0.4–8% across treatments from 1991 to 2005 (decade effect, $F_{1,12} = 6.5$, $P = 0.03$). Forb cover declined by 8–15% across treatments from 1991 to 2005 (decade effect, $F_{1,12} = 45.9$, $P \leq 0.001$) and varied by treatment (treatment effect, $F_{2,8} = 7.0$, $P = 0.02$) with cover in unthinned stands less than in other treatments ($|t_{12}| \geq 2.9$, $P = 0.05$ and $P = 0.02$).

Changes in Bird Communities

We analyzed detectability among 16 common species of breeding birds (>100 detections across years and treatments); these species made up 78% of the 12,070 total detections among the 48 species encountered during the 4 years of survey. For chestnut-backed chickadee (*Poecile rufescens*), Wilson's warbler, and dark-eyed junco, the model of detectability with an intercept only was not improved by adding any of the covariate effects (Table S1, available online at www.onlinelibrary.wiley.com). We therefore did not include covariate effects on detectability when we estimated breeding densities for these species. We found support ($w_i \geq 0.95$, unless otherwise noted) for 1) observer effects on detectability for 7 bird species (Pacific-slope flycatcher [$w_i = 0.53$], Steller's jay [*Cyanocitta stelleri*; $w_i = 0.47$], Pacific wren, Swainson's thrush, hermit thrush [*Catharus guttatus*], Townsend's warbler, and fox sparrow), 2) year effects for 4 bird species (golden-crowned kinglet, American robin [*Turdus migratorius*], varied thrush [*Ixoreus naevius*], and orange-crowned warbler), and 3) a treatment effect for 2 species (red-breasted sapsucker [$w_i = 0.44$] and song sparrow [*Melospiza melodia*]; Table S1). We therefore included the appropriate covariates in the detection function when estimating breeding densities for these species. All of the detection models used to estimate densities had reasonable goodness-of-fit based on the chi-square test ($\chi^2 \leq 8.3$, $P \geq 0.07$; df varying from 2 to 7 based on number of parameters in the detection function).

From the early 1990s to mid-2000s, the composition of breeding bird communities shifted in young-growth treatments but not in old-growth stands. In the early 1990s, understory-nesting species comprised 80 ± 1%, 85 ± 2%, and 33 ± 3% of the combined densities for 16 common bird species in unthinned, thinned, and old-growth treatments, respectively. In the mid-2000s, understory-nesting species comprised 45 ± 1%, 54 ± 2%, and 29 ± 1% of the combined densities in unthinned, thinned, and old-growth treatments, respectively.

Overstory-nesting birds.—We did not find a treatment × decade interaction ($F_{2,12} = 2.7$, $P = 0.11$) in the combined densities of overstory-nesting birds and therefore did not find support for our hypothesis that thinning accelerated succession among overstory-nesting birds. From the early 1990s to the mid-2000s, densities of overstory-nesting birds increased 1.8 times in unthinned stands ($\bar{x}_{\text{change}} = 4.0 \pm 0.3$ birds/ha), 2.2 times in thinned stands ($\bar{x}_{\text{change}} = 4.2 \pm 0.5$ birds/ha), and 0.49 times in old-growth stands ($\bar{x}_{\text{change}} = 2.8 \pm 0.6$ birds/ha; decade effect, $F_{1,12} = 195.2$, $P \leq 0.001$). By the mid-2000s, densities of overstory-nesting birds in managed stands had increased to levels comparable to densities found in old growth in the early 1990s (Fig. 3). However, densities of overstory-nesting birds in managed stands remained 71–73% of densities found in old growth in the mid-2000s ($|t_8| \geq 6.3$, $P \leq 0.001$, Fig. 3).

We found a treatment × decade interaction for 3 of 8 constituent species: Pacific-slope flycatcher, golden-crowned kinglet, and Townsend's warbler ($F_{2,12} \geq 5.0$; $P = 0.03$, $P = 0.02$, and $P = 0.008$; Fig. 3). Absolute changes in density for each of these species were not different between unthinned and thinned stands ($|t_8| \leq 2.0$; $P = 0.18$, $P = 0.43$, and $P = 0.94$) and did not support the hypothesis that thinning would benefit overstory-nesting birds. Trends in bird density, however, often varied between managed stands and old growth. Pacific-slope flycatcher densities in the mid-2000s were 3 times greater than densities in the 1990s in thinned stands ($\bar{x}_{\text{change}} = 0.7 \pm 0.1$ birds/ha) and 0.7 times greater in old growth ($\bar{x}_{\text{change}} = 1.1 \pm 0.2$ birds/ha; $|t_{12}| \geq 4.5$, $P = 0.007$ and $P \leq 0.001$), but were not significantly different in unthinned stands ($\bar{x}_{\text{change}} = 0.4 \pm 0.2$ birds/ha; $|t_{12}| = 2.9$, $P = 0.11$). This was the only species that had larger decadal increases in density in old growth compared to unthinned and thinned stands ($|t_8| \geq 3.5$, $P = 0.02$ and $P = 0.002$; Fig. 3). Golden-crowned kinglet densities increased 4.5-fold in unthinned stands ($\bar{x}_{\text{change}} = 1.8 \pm 0.4$ birds/ha) and 4.9-fold in thinned stands ($\bar{x}_{\text{change}} = 1.4 \pm 0.3$ birds/ha; $|t_{12}| \geq 4.5$, $P = 0.007$ and $P = 0.001$), but did not change significantly in old growth ($\bar{x}_{\text{change}} = 0.4 \pm 0.3$ birds/ha; $|t_{12}| = 1.3$, $P = 0.76$; Fig. 3). However, decadal changes in kinglet densities did not differ significantly among treatments after the Tukey adjustment for the number of comparisons ($|t_8| \leq 2.4$; $P = 0.09$, $P = 0.15$, and $P = 0.94$). Townsend's warbler densities increased 2.5-fold in unthinned stands ($\bar{x}_{\text{change}} = 1.6 \pm 0.2$ birds/ha), 4.8-fold in thinned stands ($\bar{x}_{\text{change}} = 1.8 \pm 0.2$ birds/ha), and 1.2-fold in old growth ($\bar{x}_{\text{change}} = 1.01 \pm 0.04$ birds/ha; $|t_{12}| \geq 6.7$, $P \leq 0.001$; Fig. 3). The absolute change in density was greater in thinned compared to old-growth stands ($|t_8| = 3.9$, $P = 0.01$).

We did not detect significant differences in golden-crowned kinglet densities among treatments in the mid-2000s ($|t_{12}| \leq 1.3$, $P = 0.79$, $P = 0.91$, and $P \geq 0.99$). Thus, their decadal increases in managed stands made up

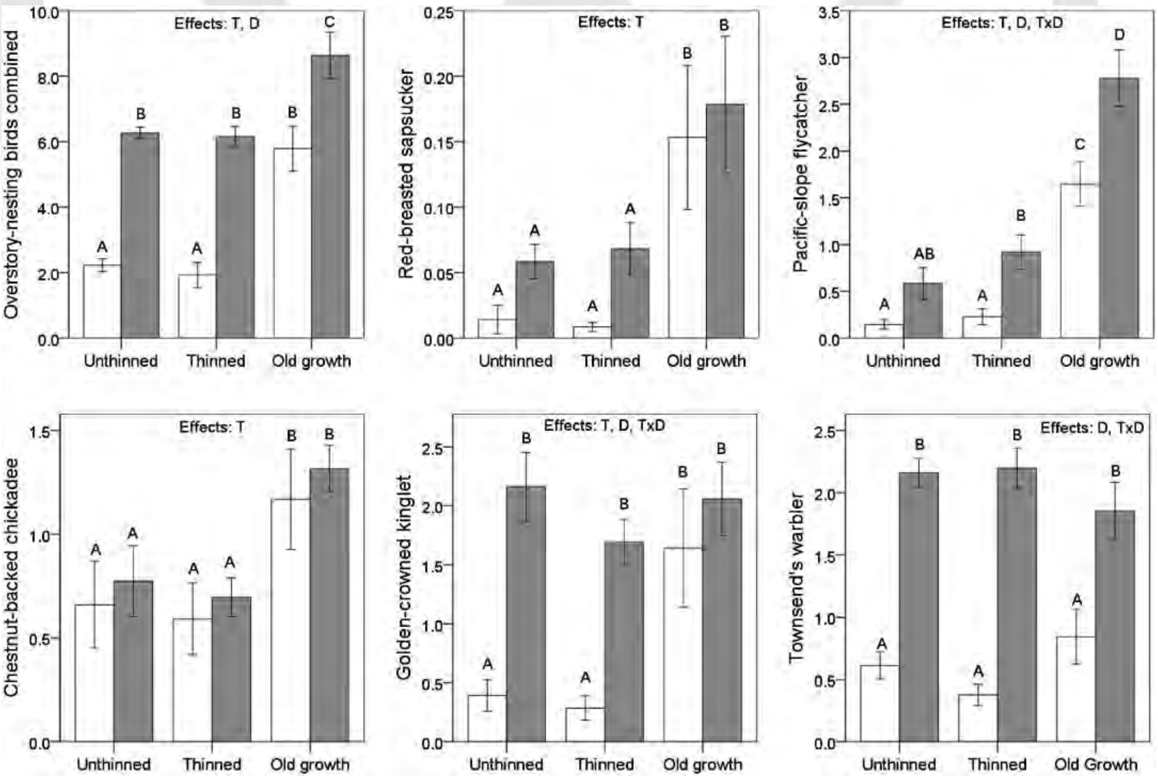

Figure 3. Average breeding densities of overstory-nesting birds ± SE (birds/ha) by decade among unthinned and pre-commercially thinned stands harvested in 1971–1972 and old growth stands ($n = 5$ stands/treatment), Prince of Wales Island, Alaska, USA. Breeding densities were corrected for detectability and were calculated from surveys conducted in 1991–1992 (white bars) and 2005–2006 (grey bars). Significant ($P \leq 0.05$) effects of treatment (T), decade (D), and the treatment by decade interaction (T × D) are based on repeated measures analysis of variance. T × D indicates that the decadal trends varied among treatments. Means sharing a letter do not differ significantly between treatments or decades.

for the large disparity in densities between old growth and managed stands in the early 1990s ($|t_{12}| \geq 3.4$, $P = 0.05$ and $P = 0.03$; Fig. 3). Pacific-slope flycatchers remained at greater densities in old growth compared to managed stands in both decades ($|t_{12}| \geq 6.7$, $P \leq 0.001$; Fig. 3). Densities of Townsend's warblers did not vary significantly among treatments in either the early 1990s or mid-2000s (treatment effect, $F_{2,8} = 0.2$, $P = 0.85$). Densities of American robins, varied thrushes, and Steller's jays did not vary significantly by treatment ($F_{2,8} \leq 4.3$; $P = 0.06$, $P = 0.09$, and $P = 0.27$) or decade ($F_{1,12} \leq 2.5$; $P = 0.14$, $P = 0.21$, and $P = 0.23$).

We found support for the hypothesis that cavity-nesting birds would not respond to thinning and that their densities would remain substantially lower in managed stands compared to old growth in the mid-2000s. Densities of the 2 cavity-nesting species, red-breasted sapsucker, and chestnut-backed chickadee, did not vary by decade ($F_{1,12} \leq 3.4$, $P = 0.09$ and $P = 0.37$), but did by treatment ($F_{2,8} \geq 7.0$, $P = 0.02$ and $P = 0.007$; Fig. 3). Across decades, densities in old growth of sapsuckers were 2.6–15 times ($|t_8| = 3.9$, $P = 0.01$) and chickadees were 1.7–2.0 times their densities in managed stands ($|t_8| \geq 3.0$, $P = 0.04$ and $P = 0.02$; Fig. 3). Although numbers of detections of brown creepers were not sufficient to estimate detection functions, all observations of this species during the early 1990s ($n = 12$ birds; DellaSala et al. 1996) and mid-2000s ($n = 4$ birds) were in old growth.

Understory-nesting birds.—We found a treatment × decade interaction for the combined densities of understory-nesting birds and for 5 of 8 constituent species ($F_{2,12} \geq 5.2$; $P \leq 0.02$, $P = 0.01$, $P = 0.007$, $P = 0.006$, and $P \leq 0.001$; Fig. 4). The combined densities of understory-nesting birds decreased by 43% in unthinned stands ($\bar{x}_{\text{change}} = -3.8 \pm 0.3$ birds/ha) and 32% in thinned stands ($\bar{x}_{\text{change}} = -3.4 \pm 0.7$ birds/ha; $|t_{12}| \geq 6.7$, $P \leq 0.001$), but remained relatively stable in old growth ($\bar{x}_{\text{change}} = 0.7 \pm 0.4$ birds/ha; $|t_{12}| = 1.5$, $P = 0.68$; Fig. 4). These decadal changes in density were different between managed stands and old growth ($|t_8| \geq 8.9$, $P \leq 0.001$), but were similar between unthinned and thinned stands ($|t_8| = 0.9$, $P = 0.66$). We therefore did not find support for the hypothesis that declines in understory-nesting bird densities would be greater in unthinned than in thinned stands. In the early 1990s, densities of understory-nesting birds in unthinned and thinned stands averaged ≥3.2 times those found in old growth ($|t_{12}| \geq 10.2$, $P \leq 0.001$). In the mid-2000s, densities of understory nesting birds in unthinned stands had declined to levels comparable to densities in old growth ($|t_{12}| = 2.7$, $P = 0.15$); densities in thinned stands averaged 1.4 and 2.1 times those in unthinned and old growth, respectively ($|t_{12}| \geq 3.7$, $P \leq 0.03$ and $P \leq 0.001$; Fig. 4).

Among the 5 species with a treatment × decade interaction, Swainson's thrush was the only species that exhibited different decadal trends in density between unthinned ($\bar{x}_{\text{change}} = -0.4 \pm 0.3$ birds/ha) and thinned stands ($\bar{x}_{\text{change}} = 0.7 \pm 0.3$ birds/ha; $|t_8| = 3.4$, $P = 0.02$). None of the other 4 understory species with a treatment × decade effect had different decadal trends in unthinned compared to thinned stands ($|t_8| \leq 2.6$; $P = 0.08$, $P = 0.12$, $P = 0.41$, and $P = 0.78$). Thus, we found limited support for our hypothesis for how thinning would benefit understory-nesting birds. Four of these species had different trends ($|t_8| \geq 2.9$; $P = 0.05$, $P = 0.02$, $P = 0.01$, and $P = 0.007$) in 1 or both managed stand treatments compared to old growth. In each instance the species declined in the managed stand treatment ($|t_{12}| \geq 4.0$; $P = 0.02$, $P = 0.009$, $P = 0.003$, and $P = 0.002$) but did not change significantly in old growth ($|t_{12}| \leq 0.4$, $P = 1.0$). Fox sparrow densities declined 96% in unthinned ($\bar{x}_{\text{change}} = -0.8 \pm 0.2$ birds/ha) and thinned stands ($\bar{x}_{\text{change}} = -0.9 \pm 0.2$ birds/ha), but remained absent from old growth (Fig. 4). Wilson's warblers declined by 94% in unthinned stands ($\bar{x}_{\text{change}} = -0.5 \pm 0.2$ birds/ha) but changed little in old growth ($\bar{x}_{\text{change}} = 0.02 \pm 0.01$ birds/ha). Orange-crowned warbler densities declined by 59% in unthinned stands ($\bar{x}_{\text{change}} = -1.1 \pm 0.3$ birds/ha) but did not change significantly in old growth ($\bar{x}_{\text{change}} = -0.09 \pm 0.05$ birds/ha). Dark-eyed junco densities declined by 75% in thinned stands ($\bar{x}_{\text{change}} = -2.6 \pm 0.8$ birds/ha) and did not change in old growth ($\bar{x}_{\text{change}} = 0.1 \pm 0.2$ birds/ha). In each of these cases, the decline in density in managed stands resulted in breeding densities comparable to densities observed in old growth in the early 1990s and mid-2000s ($|t_{12}| \leq 2.7$; $P = 0.16$, $P = 0.30$, and $P \geq 0.99$; Fig. 4).

In the early 1990s, 6 of the 8 understory nesting species had greater breeding densities in 1 or both managed stand treatments compared to old growth ($|t_{8 \text{ or } 12}| \geq 3.3$; $P = 0.03$, $P = 0.008$, $P = 0.006$, $P = 0.004$, $P = 0.002$, and $P \leq 0.001$; Fig. 4). In the mid-2000s, only 3 of these species still showed this pattern; Pacific wren and Swainson's thrush densities in managed stands and orange-crowned warbler densities in thinned stands remained 1.2–5.4 times the densities found in old growth ($|t_{8 \text{ or } 12}| \geq 3.3$, $P = 0.03$, $P = 0.002$, and $P \leq 0.001$; Fig. 4). Contrary to these patterns, hermit thrush was the only understory-nesting species that increased across treatments from the early 1990s to the mid-2000s (decade effect, $F_{1,12} = 68.3$, $P \leq 0.001$; Fig. 4). Densities of understory-nesting song sparrows did not vary significantly across treatments ($F_{2,8} = 1.1$, $P = 0.38$) or decades ($F_{1,12} = 1.7$, $P = 0.21$).

DISCUSSION

Pre-commercial thinning of young managed stands in the late-1980s was effective in meeting management goals of maintaining conifer densities and levels of shrub cover equivalent to old-growth temperate rainforests on Prince of Wales Island, Alaska. Thinning had prevented 35-year old clearcuts from entering the stem-exclusion phase, a successional stage with dense conifer growth and little understory vegetation that may last ≥150 years (Alaback 1982). Despite these benefits of thinning to young managed stands, we failed to detect differences in decadal trends (early 1990s to mid-2000s) in avian breeding densities between managed stands that were thinned versus left untreated (unthinned) for 15 of 16 bird species. We therefore found little support

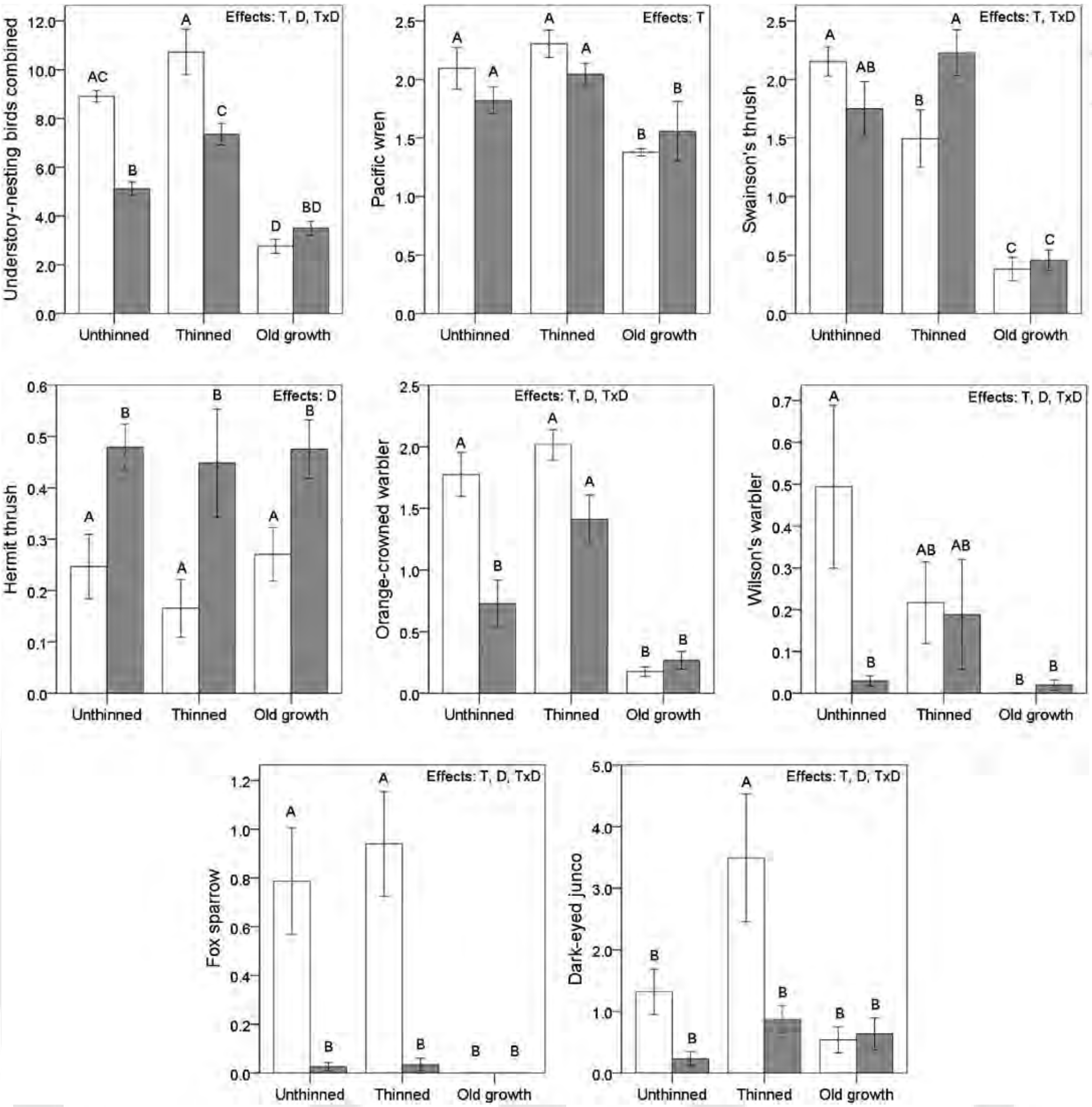

Figure 4. Average breeding densities of understory-nesting birds ± SE (birds/ha) by decade among unthinned and pre-commercially thinned stands harvested in 1971–1972 and old-growth stands ($n = 5$ stands/treatment), Prince of Wales Island, Alaska, USA. Breeding densities were corrected for detectability and calculated from surveys conducted in 1991–1992 (white bars) and 2005–2006 (grey bars). Significant ($P \leq 0.05$) effects of treatment (T), decade (D), and the treatment by decade interaction (T × D) are based on repeated measures analysis of variance. T × D indicates that the decadal trends varied among treatments. Means sharing a letter do not differ significantly between treatments or decades.

for our hypotheses that thinning would 1) increase recruitment of overstory-nesting birds and 2) minimize losses of understory-nesting birds in clearcut harvested stands. Managed stands in our study were just beginning to recruit medium- and large-diameter conifers and thinning may not benefit birds until mid-successional periods. Longer-term monitoring (70–150-yr rotation; Barbour et al. 2005) is likely needed to fully evaluate whether the ecological benefits of thinning, in terms of improving wildlife habitats and hastening the rotation age, can justify the monetary investment of applying this treatment.

Although thinning did not clearly benefit birds in the short-term, we did observe a general shift in avian community composition in young temperate rainforests from dominance by understory-nesting birds in the early 1990s (80–85% of total bird density) to equal proportions of overstory and understory-nesting birds in the mid-2000s. Approximately 35 years following clearcutting, bird communities in managed stands were beginning to more closely resemble those in old growth, which were numerically dominated by overstory-nesting birds (67–71% of total bird density) and had only 1 abundant understory-nesting species, the Pacific wren ($\bar{x} = 1.4$–1.6 birds/ha).

Overstory-Nesting Birds

We found no evidence that pre-commercial thinning increased the densities of overstory-nesting birds in 35-year-old managed stands. The combined densities of 8 common overstory-nesting species doubled in thinned stands from the early 1990s to mid-2000s; however, we also observed equivalent increases in unthinned stands. In both thinned and unthinned stands, we observed particularly large increases in the densities of overstory-nesting Pacific-slope flycatchers, golden-crowned kinglets, and Townsend's warblers. The increase in density of golden-crowned kinglets in young-growth stands across decades was noteworthy in that it eclipsed the previous 4-fold disparity in the species' density between managed and old-growth stands in the early 1990s (DellaSala et al. 1996). These species are associated with mature or old-growth forests throughout their breeding ranges (Ingold and Galati 1997, Wright et al. 1998, Lowther 2000), so we were somewhat surprised by the magnitude of their increases in managed stands during this relatively early stage of forest succession. Prince of Wales Island lacks red squirrels (*Tamiasciurus hudsonicus*), a major nest predator that is common throughout most of southeast Alaska (MacDonald and Cook 1996, Willson et al. 2003). This may have facilitated the ability of overstory-nesting birds to increase their densities with forest succession.

We suspect that overstory-nesting birds did not increase more in thinned compared to unthinned stands because thinning may not have yet accelerated conifer growth. The decadal increases in tree heights (9–10 m) and canopy cover (29–43%) that we observed were similar in thinned and unthinned stands and both stand types had only just begun to recruit medium-size conifers (>36 cm dbh) by 2005. Thus, in terms of breeding densities, these stands apparently provided comparable habitats for overstory-nesting birds. We recognize that breeding density is not necessarily a good indicator of habitat quality (Van Horne 1983; but see Bock and Jones 2004, Perot and Villard 2009), particularly following forest disturbance (Easton and Martin 2002, Matsuoka and Handel 2007). Thus, the patterns in avian densities we observed may not reflect the suitability of forests in terms of fitness measures.

Old-growth stands changed little in vegetation structure between decades, so we were surprised to find that the combined densities of overstory-nesting birds increased 49% between decades in these stands. Pacific-slope flycatchers and Townsend's warblers in particular showed decadal increases in breeding densities in old-growth and both species are sensitive to forest fragmentation (George and Brand 2002, Manuwal and Manuwal 2002, Kissling and Garton 2008). Old-growth forests in our study were remnant stands surrounded by managed stands within watersheds that were heavily harvested in the 1970s. Densities of overstory-nesting birds in these old-growth remnants may have been suppressed by harvests of surrounding stands in the 1970s. Subsequently, as the clearcuts reforested into the 2000s, the effects of fragmentation on overstory nesting birds may have abated. We note that all overstory-nesting species with decadal increases in density are migratory and factors occurring outside of our study area may have also influenced their population trends. Contrary to our findings, data from the North America Breeding Bird Survey showed that populations of Pacific-slope flycatchers and golden-crowned kinglets have been declining and Townsend's warblers have been stable in the Northern Pacific Rainforest Bird Conservation Region from 1980 to 2007 (Sauer et al. 2008).

Understory-Nesting Birds

We found little evidence that declines among understory-nesting birds were greater in unthinned compared to thinned stands. Decadal trends were similar between thinned and unthinned stands for both the combined densities of understory nesting birds and for 7 of the 8 constituent species.

Swainson's thrush was the only species that had different decadal trends in breeding density in managed stand treatments, increasing in thinned stands, and remaining relatively stable in unthinned stands. Four species of understory nesting birds experienced substantial declines in density in 1 or both managed stand treatments—orange-crowned warbler (59% decline), Wilson's warbler (94%), fox sparrow (96%), and dark-eyed junco (75%)—but their densities did not change between decades in old growth. These population trends were consistent with observed changes in shrub cover, which declined by 31% and 22% in unthinned and thinned stands, respectively, but remained unchanged in old growth. Orange-crowned warbler, Wilson's warbler, fox sparrow, and dark-eyed junco primarily nest in understory vegetation (Sogge et al. 1994, Ammon and Gilbert 1999, Nolan et al. 2002, Weckstein et al. 2002), particularly in southeast Alaska (Willson and Gende 2000), and appeared to be sensitive to reductions in shrub cover. With the exception of fox sparrow, these species avoid nesting in the subcanopy. Fox sparrows will sometimes place their nests up to 6-m high in trees (Weckstein et al. 2002), but subcanopy nests have lower survival rates compared to understory nests, which are more typical in southeast Alaska (Willson and Gende 2000). Thus, orange-crowned warbler, Wilson's warbler, fox sparrow, and dark-eyed junco appear better adapted to exploit early succession forests in southeast Alaska (Kessler and Kogut 1985, DellaSala et al. 1996, Kissling and Garton 2008). Combined densities of the 8 understory-nesting species in thinned stands were 1.4 times greater in unthinned stands in the mid-2000s, a pattern consistent with the difference in shrub cover between these treatments. However, the declining trends in both shrub cover and understory-nesting bird densities indicate that the benefits of thinning on understory communities were being lost as the forest reached a stem exclusion phase where shade limits understory development (Alaback 1982).

Other species of understory-nesting birds did not consistently decline in managed treatments in our study and some of these species appeared better adapted to use old-growth stands. Pacific wren, Swainson's thrush, and hermit thrush were among the 4 most abundant understory-nesting birds in old growth across decades and their densities tended to be either stable or increasing over time in young-growth stands. Elsewhere in southeast Alaska, nest survival of Pacific wrens and Swainson's thrushes was higher for nests placed in the subcanopy compared to nests in the forest understory (Willson and Gende 2000). Thus, the use of alternative nests sites may allow these species to use a range of successional stages (Matsuoka and Handel 2007).

Cavity-Nesting Birds

We found support for our hypothesis that densities of cavity-nesting birds would remain low in thinned and unthinned stands compared to old-growth. Numerous studies across North America have found cavity-nesting birds to be particularly vulnerable to timber harvests that remove large-diameter snags and decaying live trees (see review by Sallabanks et al. 2001). These habitat characteristics in our study occurred primarily in old growth where densities of cavity-nesting red-breasted sapsuckers and chestnut-backed chickadees were double the densities found in managed stands. Brown-creepers, which nest under slumping bark on decaying trees and snags (Hejl et al. 2002), were only detected in old-growth stands in both the early 1990s and mid-2000s. Thus, 35 years after harvest, young-growth stands had recruited limited numbers of cavity-nesting birds.

Young-growth stands will likely require several decades before trees grow to large sizes, decay, and then die in sufficient numbers to support the densities of cavity-nesting species we observed in old-growth stands. For example, in western Oregon, densities of chestnut-backed chickadees, and brown creepers breeding in 110-year-old Douglas-fir (*Pseudotsuga menziesii*) forests were 50% less than densities in old-growth stands that were >200 years old (Mannan et al. 1980). The managed stands we examined just started recruiting live conifers that were 36–55 cm in diameter-at-breast height. These are smaller than the large snags and decaying trees (>55 cm dbh) typically used as nest sites by red-breasted sapsuckers (Mannan 1977), chestnut-backed chickadees (Mannan et al. 1980), and brown creepers (Hejl et al. 2002). It is likely too early in the successional phase of these young-growth stands to realize thinning benefits. Partial-harvest techniques that retain some of the large trees and snags are known to help maintain overstory-nesting and cavity-nesting birds in managed temperate rainforests elsewhere in western North America (Chambers et al. 1997, 1999; Beese and Bryant 1999; Mazurek and Zielinski 2004; Preston and Harestad 2007). However, few to no residual trees or snags were retained during the harvest of the managed stands we examined. Thus cavity-nesting species may never be abundant in clearcut harvested stands that are managed under short rotation harvest or where dead or dying trees are consistently salvaged (Kotliar et al. 2002).

Managed stands, however, will provide foraging opportunities to some of these birds such as chestnut-backed chickadees that glean forest insects from canopy foliage (Dahlsten et al. 2002) and red-breasted sapsuckers that feed on sap from western hemlock and red alder (Walters et al. 2002). We suspect that some of our observations of these bird species in young growth may have been of individuals foraging but not necessarily nesting. Brown creepers, however, glean insects and spiders from the bark of large trees and snags (Weikel and Hayes 1999, Hejl et al. 2002) and such specialized habitat requirements for both foraging and nesting may have restricted creepers to old-growth stands in our study.

MANAGEMENT IMPLICATIONS

Pre-commercial thinning of young temperate rainforests in the late 1980s did not accelerate the recruitment of birds characteristic of old-growth forests into clearcut harvested stands in southeast Alaska. Thus, the retention of legacy trees and snags may be useful in carrying over some of the functions of old growth forests into harvested stands, and should be considered as an alternative harvest strategy in southeast Alaska (DellaSala et al. 1996, Hanley et al. 2005) where clearcutting is still the preferred harvest method.

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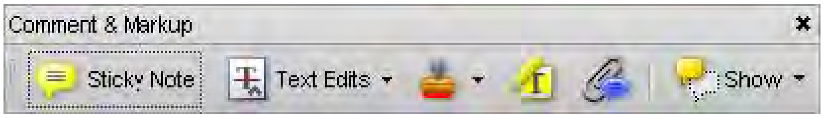

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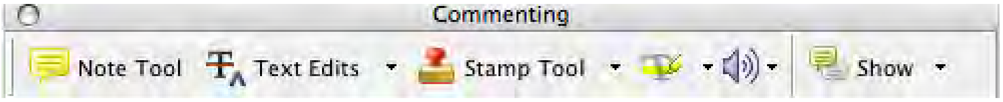

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Intact Forests in the United States: Proforestation Mitigates Climate Change and Serves the Greatest Good

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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 (CO_2), 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 CO_2 to reduce national annual *net* emissions by 11%. U.S. forests have the potential for much more rapid atmospheric CO_2 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

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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 km^2, 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 km^2–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 (10^9 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 CO_2 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

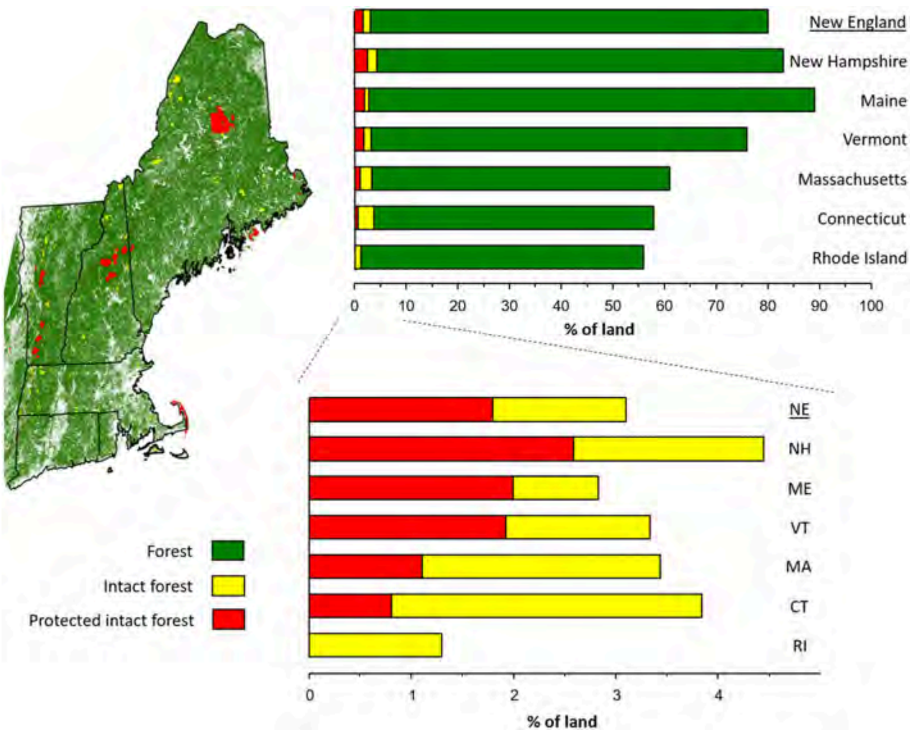

FIGURE 1 | Distribution of forest cover and intact "wildland" forest across six New England states. At left, map of overall forest cover (green) vs. forest protected legally (red) or managed currently (yellow) as intact in New England. At right, regional and state specific % forest cover (green), % managed as intact Gap 1 (limited intervention other than trails and hazard removals) but not protected legally (yellow), and % legally protected as intact forest (red, designated U.S Geological Survey (USGS) Gap 1 or Gap 2 and primarily federal and state wilderness areas, and certain national parks). Adapted and compiled from National Conservation Easement Database (2014); United States Geological Survey (2019a,b), and the University of Montana (2019). USGS Gap level 1 or 2 lands receive the highest level of protection from logging and other resource extraction and generally correspond with IUCN protected categories 1a, 1b, and II (https://gapanalysis.usgs.gov/blog/iucn-definitions/).

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 $\geq$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 classifed 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 Environmntal 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 CO_2 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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WM, SM, and EF contributed equally to conceiving, writing and editing this manuscript and all agree to its publication.

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Southeastern Alaska Conservation Strategy: A Conceptual Approach

John Schoen and David Albert

FIG 1. Gilbert Bay on the mainland south of Juneau. Additional protection for large intact watersheds is the key to an effective conservation strategy in southeastern Alaska. (John Schoen photo)

Coastal temperate rainforests are rare throughout the world. The largest temperate rainforest (representing about half of this ecosystem worldwide) occurs along the Pacific Coast from northern California through south coastal Alaska. Although the southern half of the Pacific rainforest has largely been developed, northern British Columbia and southeastern Alaska (Southeast) still retain large areas of intact forest. In fact, Southeast represents a significant portion (~30%) of the earth's remaining old-growth temperate rainforest.

Today, conservationists and resource managers have an extraordinary opportunity to conserve biological diversity and maintain ecosystem integrity throughout Southeast while balancing the diverse resource needs of local communities. We use the term biological diversity to encompass genes, species, populations, communities, ecosystems, and landscapes as well as their composition, structure, and function (Noss 1990). The term "ecological integrity" is defined by Poiani et al. (2000) as the ability to maintain component species and processes over long time frames. The time frame considered in this assessment is greater than 100 years.

To capitalize on this unique conservation opportunity, it is necessary to assess and refine the conservation strategy for Southeast and the Tongass National Forest (Tongass) before conservation options are foreclosed by substantial new development in roadless areas, forest fragmentation, and loss of rare, at risk habitats. The focus of this resource synthesis and conservation strategy was to assess original and current representation of focal resources (e.g., salmon habitat, deer habitat, large-tree old growth, etc.) across the region and identify areas of high ecological values (Chapters 2 & 3). This assessment also evaluated the cumulative ecological risks for focal species and ecological systems by biogeographic province throughout Southeast (Chapter 3). The goal of this strategy is to assist resource managers and conservationists in setting conservation priorities, minimizing environmental impacts of forest management activities, and maintaining the biodiversity and ecological integrity of Southeast's rainforest cosystem.

FOREST MANAGEMENT PRINCIPLES

The Ecological Society of America has developed a set of principles for managing national forests in the United States (Aber et al. 2000). Principles that are relevant to land management and conservation in Southeast and the Tongass include:

- Conservation of forest biodiversity requires reducing forest fragmentation by clearcuts and roads, avoiding harvest in vulnerable areas such as old-growth stands and riparian zones, and restoring natural structural complexity to cutover sites;
- Planning at the landscape level is needed to address ecological concerns such as biodiversity, water flows, and forest fragmentation;
- Despite natural disturbance and successional change, forest reserves are much more likely to sustain the full biological diversity of forests than lands managed primarily for timber production;
- Protection of water quality and yield and prevention of flooding and landslides require greater attention to the impacts of logging roads and recognition of the value of undisturbed buffer zones along streams and rivers;
- Traditional beliefs that timber harvesting can duplicate and fully substitute for the ecological effects of natural disturbance are incorrect, although newer techniques such as retaining trees and large woody debris on harvest sites can more closely mimic natural processes; and
- There is no scientific basis for asserting that silvicultural practices can create forests that are ecologically equivalent to natural old-growth forests, although our understanding of forest ecology can help restore managed forests to more natural conditions.

Additional land use principles from the Ecological Society of America (Dale et al. 2000) that are relevant to Southeast and the Tongass include:

- Examine the impacts of local decisions in a regional context;
- Preserve rare landscape elements, critical habitats, and associated species; and
- Retain large contiguous or connected areas that contain critical habitats.

TONGASS CONSERVATION STRATEGY

The conservation strategy underlying the 1997 Tongass Land Management Plan (TLMP) (USFS 1997a, b) was a significant improvement over the original plan. The fundamental conservation strategy of TLMP is based on identifying and protecting various sized habitat patches and habitat complexes (e.g., old growth reserves, riparian buffers, beach fringe buffers, and large, medium, and small habitat conservation areas [HCAs]) as well as establishing forest-wide standards and guidelines for the protection of various resources. Protection of riparian buffers and HCAs, in particular, add substantial value to the Tongass conservation strategy.

In addition, the Alaska National Interest Lands Conservation Act (ANILCA) of 1980 and the Tongass Timber Reform Act (TTRA) of 1990 permanently protected 6,479, 963 acres (2,622,405 ha) of land in Southeast. This watershed-scale protection provides an important foundation for the Tongass Conservation Strategy. Except for Admiralty Island, however, forest diversity and biological values are relatively low in most of the congressionally designated wilderness and national park and preserve areas (Chapter 3, Fig 1). For example, 65% of intact watersheds occur on the rugged mainland coast and Glacier Bay (Chapter 2). Clearly, some important habitat types (e.g., large-tree karst and flood plain spruce) are not adequately represented in conservation areas across Southeast and the Tongass (Chapter 2, Table 6). In fact, 57% of the original distribution of the most productive timber land (medium- and large-tree old growth) in Southeast exists in development land use designations (LUDs) or sub-watershed reserves (Chapter 2). This is a common problem throughout the world as the most productive lands have generally been developed first and are usually significantly under-represented in conservation areas (Scott et al. 2001a, b, Lindenmayer and Franklin 2002).

Past forest management in Southeast has significantly altered the landscape (Chapter 2, Table 5). For example, based on a Forest Service landscape analysis of southeast Chichagof (Shephard 1999), timber harvest over the last 50 years has reduced the area of old-growth forest, decreased average old-growth block size, increased the distance between blocks, decreased the amount of core to edge old growth, and removed about 44% of the rare flood plain spruce stands (over 80% of flood plain spruce have been harvested in some watersheds). Similar landscape scale changes have also occurred on northern Prince of Wales, Mitkof, Kupreanof, and Zarembo islands, as well as some of the outer islands west of Prince of Wales (refer to chapters 2 and 4 for details).

The 1997 TLMP conservation strategy incorporates the protection of old-growth forest habitat through land use designations and HCAs, buffer areas, and standards and guidelines for the matrix between reserves. These tools were designed to maintain viable populations throughout the forest. In forest development areas, this approach is largely focused on protecting habitat patches within watersheds. Additional harvest of old growth under this approach will result in:

- Loss of additional old-growth forest habitat,
- Reduced forest and habitat diversity,
- Increased habitat and watershed fragmentation, and
- Cumulative ecological impacts from additional road construction.

This within-watershed approach to habitat protection assumes a complete knowledge of the habitat relationships of many species. Without such knowledge, it is impossible to know whether all the essential habitats have been adequately protected. At the scale of individual watersheds, protecting patches of forest habitat while logging adjacent areas and constructing roads will reduce ecosystem integrity of the watershed by removing important habitat types, risking increased sedimentation and changes to hydrology, and facilitating human access thus increasing pressure on sensitive populations. In addition, there is little long-term assurance that all the protected pieces will remain administratively protected or will not unravel from trees blowing down along the edges of old-growth reserves. Many of these concerns are minimized by protecting intact watersheds.

Although past harvest targeted the most accessible and highest quality timber types (e.g., flood plain spruce and karst old growth) (refer to tables 3-6 in Chapter 2), it is likely that economic factors will continue to focus harvest on the best, most accessible timber stands remaining. This pressure will further reduce habitat diversity within affected watersheds. The cumulative effects of past and future timber harvest of large- and medium-tree old growth—in combination with the extensive harvest on adjacent private lands—will likely reduce ecosystem integrity at the watershed scale. Biological diversity and ecosystem integrity may also be compromised on a multiple watershed or regional scale within some entire biogeographic provinces with a history of intensive timber harvest (e.g., northern Prince of Wales Island, Dall Island Complex, Kupreanof-Mitkof islands) (refer to Chapter 2, Table 6; Chapter 3, Fig 2, and Chapter 4). Loss of rare habitat types (e.g., large-tree old growth) will affect the fish and wildlife populations which selectively use those habitats.

In addition to habitat loss and reduced diversity, numerous scientific studies have also implicated forest roads as having negative effects on terrestrial and aquatic ecosystems (Trombulak and Frissell 1999, US Forest Service 2001). According to the US Forest Service (2001), “Undersirable consequences (of roads) include adverse effects on hydrology and geomorphic features (such as debris slides and sedimentation), habitat fragmentation, predation, road kill, invasion by exotic species, dispersal of pathogens, degraded water quality and chemical contamination, degraded aquatic habitat, use conflicts, destructive human actions (for example, trash dumping, illegal hunting, fires), lost solitude, depressed local economies, loss of soil productivity, and decline in biodiversity.” Specifically regarding the Tongass, the panel of fish experts that evaluated the 1997 TLMP stated that “A reduction of road development in any alternative reduces risks to fish habitat.” (Dunlap 1997). Because roads have potential for introducing varied impacts to both terrestrial and aquatic ecosystems, roadless areas provide a significant foundation for developing comprehensive regional conservation strategies (Strittholt and Dellasala 2001).

REFINING THE TONGASS CONSERVATION STRATEGY

Watershed-scale Conservation

Numerous ecological studies suggest that conservation action and management should take place at the scale of entire watersheds (Stanford and Ward 1992; Naiman et al. 1997, 2000; Pringle 2001; Baron et al. 2002). For example, many of the species and trophic systems of Southeast (e.g., salmon spawning and rearing and the interactions between wildlife species and salmon) tend to be strongly linked to key ecological processes at a watershed-scale (e.g., sedimentation, stream flow, and nutrient cycling). In fact, the productivity of coastal ecosystems is strongly linked to salmon populations which are considered “keystone” species (Willson and Halupka 1999). In addition, field studies suggest that watersheds are the appropriate scale to measure and manage cumulative human impacts. Measurable indicators tend to correlate with human activity data when measured at watershed scales (Karr 1991; Roth 1996; Muhar and Jungwirth 1998; Thorton 2000; Carignan et al. 2002; Pess et al. 2002). Thus, because watersheds define an appropriate ecological unit where human impacts tend to accumulate and can be measured and because of their value for key ecological processes and the global rarity of intact watersheds, identifying and representing a range of intact watersheds should be included as a part of any credible, systematic, science-based conservation analysis. In fact, the panel of fish experts evaluating the 1997 TLMP recommended that the most effective protection of fish habitat on the Tongass would be reserves that included entire watersheds rather than only parts of watersheds (Dunlap 1997). Bryant and Everest (1998) also emphasized the importance of watershed-scale conservation: “The presence, number and distribution of intact watersheds across the landscape of the TNF (Tongass National Forest) are critical elements for sustainable salmon populations in the face of habitat loss elsewhere in southeast Alaska and the Pacific Northwest.”

The Tongass is naturally fragmented by islands and coastal ice fields and many of the islands have distinct climatic, floral, and faunal differences. This presents a challenge for conservation of biodiversity because insular populations have historically exhibited high risk of local extinction (Cook et al. 2001, also refer to Chapter 6.7). In this assessment, we used a geographic stratification based on biogeographic provinces (US Forest Service 2003) to insure that conservation areas are sufficiently distributed to maintain viable populations throughout Southeast (Chapter 2, Fig.2). An effective conservation strategy for Southeast and the Tongass should include a representative set of protected watersheds with high ecological values within each of the region’s biogeographic provinces.

In recognition of the strengths and weaknesses of the 1997 TLMP conservation strategy, we recommend adding a complementary strategy of protecting additional intact watersheds. Protecting intact watersheds with high ecological values will:

- Maintain the natural range of variation of forest types (i.e., habitat diversity);
- Minimize habitat fragmentation within protected watersheds;
- Reduce road impacts; and
- Maintain ecosystem integrity within protected areas at the watershed and province scales.

Instead of cutting timber and building roads evenly distributed throughout a forested landscape, Franklin (1989) suggested aggregating impacts to minimize habitat fragmentation. Within the Tongass Forest’s operable timber base (LUDs 3 & 4), aggregating timber harvest in fewer watersheds would enable the protection of an additional sample of intact watersheds with high ecological values. Aggregating timber harvest may also enhance efficiency of some timber operations. This landscape-scale approach (i.e., protecting more intact watersheds) would strengthen the 1997 TLMP conservation strategy and maintain conservation options over time. Protecting intact watersheds would essentially hedge our bets by maintaining conservation options in recognition of the high degree of uncertainty associated with ecological systems. Scientists and managers have incomplete knowledge of many of Southeast’s ecological processes and species habitat requirements. We assume that by protecting intact watersheds—from ridge top to ridge top and headwaters to estuary—and their natural range of variability, ecological integrity within the watershed will be maintained. This landscape-scale strategy would also increase the probability of protecting wide-ranging species like brown bears and wolves that are placed at risk by expanding road systems and increased human access.

These recommendations are consistent with the 1994 TLMP peer reviewers’ comments (Kiester and Eckhardt 1994) to keep landscape options open and not further fragment large blocks of high-volume (large-tree) old growth or eliminate rare, potentially important, habitat types. This complementary conservation strategy—protecting an additional sample of intact watersheds within each biogeographic province—also parallels the September 1997 joint statement of the peer review committee (Powell et al. 1997) which stated: “Perhaps of greatest concern is the failure to protect the Forest’s remaining pristine watersheds.”

Assessing Ecological Values of Watersheds

In the watershed strategy described in this report, we selected a suite of focal species and ecological systems to estimate ecological values at the watershed level. We used habitat capability models from the Tongass Land Management Plan (as modified by an interagency review group of wildlife experts) to assess the winter habitat value of deer and the summer habitat value for brown bear. We used the brown bear model to also represent black bear habitat. An interagency and university team of experts developed a nesting habitat model for marbled murrelets based on data from Alaska and British Columbia. Salmon spawning and rearing habitat was assessed by combining the ADF&G Fish Distribution Database (FDD) with the USFS Stream Inventory. An inventory of upland and riparian large-tree forests was assembled from USFS forest and soils inventory data. Estuary occurrence data were derived from the intertidal emergent vegetation class (E2EM) from the USF&WS National Wetlands Inventory (NWI) data and interpreted from Landsat ETM imagery for areas where NWI was not available.

To assess the relative ecological value of watersheds, watershed comparisons were made within biogeographic provinces (22 distributed throughout Southeast). Watershed value comparisons were conducted using the Marxan spatial optimization tool (Possingham et al. 2000, also refer to Chapter 2). Marxan is a spatially-explicit tool for developing and evaluating reserve networks based on specific conservation goals. The utility of Marxan is to identify a set of areas that meet user-specified goals for representation of all focal species and ecological systems while minimizing total area and maximizing within-area connectivity. Using a simulated annealing algorithm, an "optimal solution" is identified by iterative comparison of millions of alternative designs. In this application, areas that were consistently identified as part of the optimal solution under a range of scenarios were considered to have high ecological value for the combined set of focal species and ecological systems, and therefore useful elements for the design of a regional conservation network (Pressey et al. 1994).

Marxan runs were conducted for individual variables as well as all variables combined and Southeast experts reviewed and evaluated the results.

The watershed analysis included the following variables:

Terrestrial:
- Brown & black bear summer habitat
- Black-tailed deer winter habitat
- Marbled murrelet nesting habitat
- Large-tree forest
  - Riparian
  - Upland

Freshwater:
- Salmon spawning and rearing habitat

Coastal:
- Estuaries

Marxan runs for all resources combined identified core areas of ecological values within watersheds (Chapter 2, Fig 18) as well as 4 tiers (quartiles) of ecological value (Chapter 2, Fig 20 & 21) at the watershed scale within provinces with the top 2 tiers representing 50% of ecological value within the province.

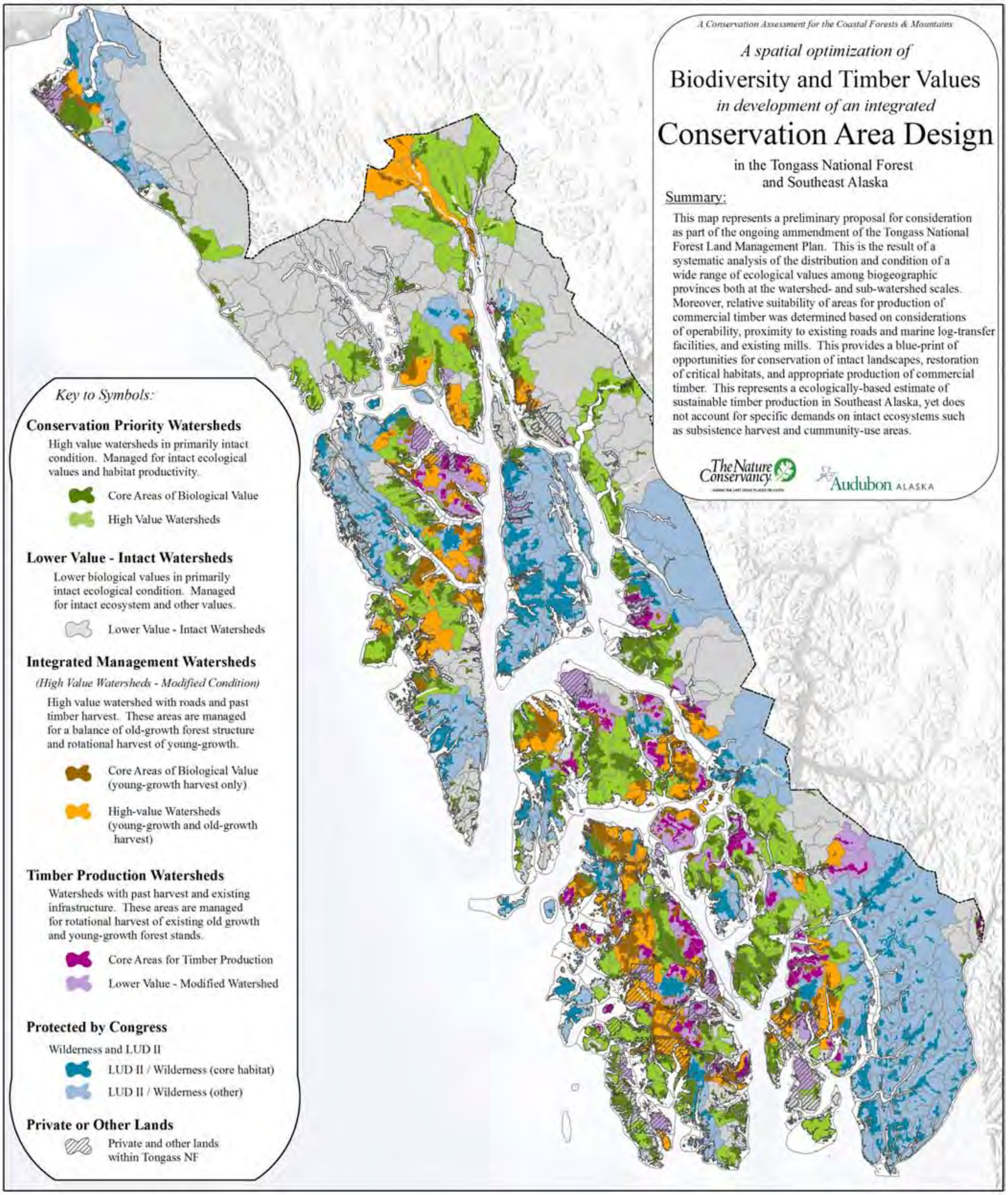
Assessing Timber Suitability of Watersheds

While Marxan was originally developed as a tool for conservation, it can also be applied to evaluate an optimal design for production of timber. We applied it to meet goals based on economic factors including operability type, proximity to existing infrastructure, and minimum overlap with core areas of biological value (Chapter 2). The optimal solutions over a range of demand scenarios were combined as an index of relative suitability for timber production under economic and biodiversity constraints.

Conservation Area Design

The ecological ranking of watershed values, core areas of biological value within watersheds, and the index of suitability for timber production were combined into a spectrum of conservation opportunities based on ecological value, habitat condition, and economic opportunity. This spatial optimization of biodiversity and timber values was used to develop an integrated conservation area design for the Tongass National Forest and southeastern Alaska (Fig 2). This map combines analyses for 1) the Marxan Core Areas of ecological values, 2) the Marxan top tier watersheds (top 50% of ecological values) for both intact (roadless) and modified (roaded) watersheds, and 3) Marxan timber suitability analysis.

The combined ranking of ecological values at the watershed- and sub-watershed scales, along with the ranking of relative suitability for timber production provides an analytical framework for development of conservation and management prescriptions across a range of ecological conditions. For example, intact watersheds with highest concentrations of ecological values (shown in green, Fig 2) represent a globally rare opportunity for conservation of coastal rain forest ecosystems and associated species and are considered as high priorities for additional landscape-scale conservation. These watersheds contain approximately 34% of existing habitat values for all focal species and ecological systems combined (Table 1).



A spatial optimization of
Biodiversity and Timber Values
in development of an integrated
Conservation Area Design
in the Tongass National Forest
and Southeast Alaska

Summary:

This map represents a preliminary proposal for consideration as part of the ongoing ammendment of the Tongass National Forest Land Management Plan. This is the result of a systematic analysis of the distribution and condition of a wide range of ecological values among biogeographic provinces both at the watershed- and sub-watershed scales. Moreover, relative suitability of areas for production of commercial timber was determined based on considerations of operability, proximity to existing roads and marine log-transfer facilities, and existing mills. This provides a blue-print of opportunities for conservation of intact landscapes, restoration of critical habitats, and appropriate production of commercial timber. This represents a ecologically-based estimate of sustainable timber production in Southeast Alaska, yet does not account for specific demands on intact ecosystems such as subsistence harvest and cummunity-use areas.

Key to Symbols:

Conservation Priority Watersheds

High value watersheds in primarily intact condition. Managed for intact ecological values and habitat productivity.

- 🟩 Core Areas of Biological Value
- 🟩 High Value Watersheds

Lower Value - Intact Watersheds

Lower biological values in primarily intact ecological condition. Managed for intact ecosystem and other values.

- ⬜ Lower Value - Intact Watersheds

Integrated Management Watersheds

(High Value Watersheds - Modified Condition)

High value watershed with roads and past timber harvest. These areas are managed for a balance of old-growth forest structure and rotational harvest of young-growth.

- 🟫 Core Areas of Biological Value (young-growth harvest only)
- 🟧 High-value Watersheds (young-growth and old-growth harvest)

Timber Production Watersheds

Watersheds with past harvest and existing infrastructure. These areas are managed for rotational harvest of existing old growth and young-growth forest stands.

- 🟪 Core Areas for Timber Production
- 🟪 Lower Value - Modified Watershed

Protected by Congress

Wilderness and LUD II

- 🟦 LUD II / Wilderness (core habitat)
- 🟦 LUD II / Wilderness (other)

Private or Other Lands

- ▨ Private and other lands within Tongass NF

FIG 2. An integrated conservation area design based on spatial optimization of biodiversity and timber values in the Tongass National Forest and Southeast Alaska.

An important set of watersheds with high concentrations of ecological values but which have also sustained substantial roading and logging activity represent areas appropriate for a balanced prescription with emphasis on young-growth for timber production and restoration of habitat values for fish and wildlife. These areas are described as zones of “Integrated Management” (shown in orange, Fig 2) to emphasize the necessity to maintain critical ecosystem functions throughout the forest matrix in the context of overall forest management objectives. Core areas of biological value within the Integrated Management Zone (shown in brown) represent the highest concentration of intact ecological values and, in this context, represent important opportunities for conservation of remaining old growth structural characteristics within the matrix and for enhancing connectivity among watersheds. Integrated Management Watersheds represent approximately 15% of existing habitat values for the combined focal species and ecological systems (Table 1).

Watersheds with lower ecological values are described as “intact” (<= 10% cut) or “modified” (>10% cut) based on the condition of original productive forest lands. “Lower Value – Intact Watersheds” (shown in gray, Fig 2) are typical of extensive areas of bedrock and glacial dominated landscapes along the mainland coast and southern and eastern Baranof Island. These areas contain lower ecological values, and represent approximately 10% of existing habitat for combined focal species and ecological systems (Table 1).

Watersheds with lower ecological values, past timber harvest activities, and the most substantial timber infrastructure (shown in light orchid, Fig 2) are described as “Timber Production Watersheds” and are generally the most appropriate areas for continued timber management. Within these watersheds, discrete areas with the highest suitability for timber production (shown in dark orchid) may provide the most appropriate sites for economic timber operations. In this way, objectives for efficient production of timber can be accomplished within a smaller land base and fewer roads, and allow greater flexibility for conservation of intact landscapes (within Conservation Priority Watersheds) and restoration (within Integrated Management Watersheds). Some of the Timber Production Watersheds also have brown core areas where old-growth conservation should be considered.

Congressionally protected lands (designated wilderness and LUD II areas) are shown as blue on the map and are unavailable for development. These watersheds contain approximately 32% of existing habitat values for all focal species and ecological systems combined (Table 1).

The primary underpinnings of this conservation strategy are to: (1) focus conservation on watersheds and sub-watershed core areas with the highest ecological values; (2) concentrate timber production within the smallest land base and with the least impact on intact habitat values; and (3) facilitate a rapid transition from old-growth to second-growth timber harvest. These management actions are recommended to optimize the opportunity for maintaining the biodiversity and ecological integrity of the Southeast rainforest ecosystem while also providing for a sustainable timber industry within the region.

Conservation Priority Watersheds (Fig 2) within the Tongass National Forest, excluding congressionally designated Wilderness and LUD II lands, are listed (in ranked order) by province in Table 2. These largely intact watersheds generally encompass the highest ecological values within each province and represent some of the highest conservation priorities on the Tongass National Forest. Again, it is important to recognize that these Conservation Priority Watersheds were ranked within biogeographic province not between provinces. A comprehensive protected areas strategy for the Tongass should consider including these high-value watersheds within each province’s conservation network. This will maintain a geographic stratification within the region’s overall protected areas strategy.

Integrated Management Watersheds (Fig 2) within the Tongass National Forest, excluding congressionally designated Wilderness and LUD II lands, are listed (in ranked order) by province in Table 3. These watersheds have had a history of intensive logging and roading but still retain substantial ecological values because they were originally some of the most productive watersheds in Southeast. Specific restoration opportunities include the North Prince of Wales, Revilla, Mitkof, Kuiu, and East Chichagof provinces.

Analytical Tools

The watershed data for focal resources used in these analyses are included in the watershed matrix (Appendix B). The matrix (an excel spreadsheet) provides much of the details behind the maps. It is organized by province and rank orders watersheds by their combined ecological values. Ecological values for individual focal species and systems are also ranked along with the percentage value that resource contributes to the overall province. Each watershed has a VCU # and watershed name, a total Marxan score (range 0-50), and its rank within the 4 tiers (quartiles) of ecological value. Additionally, total watershed area, miles (km) of road, and acres (ha) clearcut are included in the matrix.

Finally, a selected set of GIS data layers were compiled for viewing in Arc Reader, a share-ware utility for read-only access to the GIS database (available upon request and packaged separately on DVD). This tool allows individuals to use a personal computer and scroll through a map of Southeast, at any scale, and apply a set of data filters to view landscape, habitat, and focal species data as well as ecological values of core areas, watershed (VCU) rankings, and TLMP land use designations and habitat reserves.

These maps, the watershed matrix, and GIS database provide useful tools for evaluating current conservation measures, setting conservation priorities, and refining the conservation strategy for Southeast and the Tongass. This assessment and analytical tools do not represent a final conservation strategy at this time but can be used for making informed, science-based, decisions as a conservation strategy for Southeast is further updated and refined. The data presented here summarize the ecological values of watersheds within provinces based on the focal species and systems selected for this analysis. Community and subsistence values are not included in this analysis but are important attributes that must also be incorporated into a conservation strategy for Southeast and the Tongass. Special features, such as unique fish stocks, endemic species, karst caves, and ecological connectivity should also be considered in developing an effective conservation strategy and can be incorporated as they become available.

SUMMARY OF CONSERVATION RECOMMENDATIONS

The ecological integrity (i.e., long-term productivity and resilience of fish, wildlife, and their habitats) of Southeast's rainforest ecosystem will depend, in large part, on balancing industrial development with sound conservation measures, including an expanded watershed-scale reserve system for this region. An expanded system of intact watershed reserves would complement the current TLMP conservation strategy and minimize risks to ecosystem integrity, including sensitive populations of fish and wildlife and rare habitat types (e.g., large-tree old-growth forests). The establishment of additional watershed reserves also would expand the scientific benchmark for monitoring future habitat and population changes and determining the cause of such change. This may become an important tool for evaluating the effects of global climate change in Southeast. Audubon Alaska and The Nature Conservancy have identified core areas of biological value as well as Conservation Priority Watersheds and Integrated Management Watersheds. To maintain ecosystem integrity and conserve fish and wildlife populations and the natural range of variability of habitat types, we recommend consideration of the following conservation measures throughout Southeast and the Tongass.

1. Maintain and expand the existing conservation reserve network to include additional intact watersheds (Conservation Priority Watersheds) throughout Southeast and the Tongass;
2. Each of Southeast's 22 biogeographic provinces should include a representative set of intact watershed reserves of high ecological value;
3. The watershed matrix ranks watersheds on their ecological values based on focal species and ecological systems. The highest ranked watersheds should be given conservation priority. Conservation Priority Watersheds have been mapped (Fig 2) and encompass the highest ecological values (for intact watersheds) within each province. Conservation Priority Watersheds may provide a useful template for expanding the watershed reserves in provinces with under-represented reserves;
4. Establish ecological restoration priorities for selected watersheds throughout Southeast and the Tongass;
5. Some provinces (e.g., North Prince of Wales, Kupreanof / Mitkof) have undergone substantial resource development activities and may be at risk of losing their ecological integrity. Developed watersheds which still maintain relatively high ecological values (e.g., Integrated Management Watersheds) have been mapped (Fig 1) and should be given first priority for restoration activities;
6. Establish scientific benchmarks for long-term ecological research and monitoring in selected watershed reserves within representative provinces distributed across Southeast;

7. Use the Arc Reader GIS database to review and refine the TLMP old-growth reserve structure;
8. Standards and guidelines strengthen conservation measures throughout the forest matrix and should be reviewed and revised, where appropriate, in consultation with species experts from state and federal resource agencies and universities;
9. Apply best management practices (e.g., TLMP conservation strategy including HCAs, OGRs, habitat buffers, standards and guidelines, and State Forest Practices Act guidelines) to resource development projects conducted in matrix lands throughout Southeast. Particular emphasis should be placed on maintaining riparian buffers and productive salmon spawning and rearing habitat throughout Southeast and the Tongass;
10. Consider establishing additional critical habitat areas surrounding state lands and waters that include high-value and/or sensitive fish and wildlife habitats and where multiple land or water jurisdictions overlap, consider developing co-management agreements to safeguard fish and wildlife habitat values.

TABLE 1. Percent distribution of existing habitat values for focal species and ecological systems among watershed conservation priorities within the Integrated Conservation Area Design framework.

Focal Species and Ecological System	Distribution of habitat values among watershed conservation priorities (% of existing values)					
	Protected by Congress	Conservation Priority	Integrated Management	Lower Value Intact	Timber Production	Total
Large-tree Forest Types						
Riparian forest	43.4%	33.4%	16.1%	3.0%	4.2%	100.0%
Upland forest	31.5%	32.1%	25.1%	3.8%	7.5%	100.0%
Habitat Capability Models						
Brown & Black Bear	36.2%	34.1%	11.8%	11.8%	6.1%	100.0%
Sitka Black-tail deer	27.3%	36.0%	17.1%	9.8%	9.8%	100.0%
Marbled Murrelet	36.0%	31.9%	14.4%	9.4%	8.3%	100.0%
Freshwater Salmon Distribution						
King	36.9%	31.4%	19.9%	10.6%	1.1%	100.0%
Coho	23.3%	35.5%	20.9%	11.4%	8.9%	100.0%
Sockeye	32.4%	38.1%	13.0%	12.9%	3.5%	100.0%
Pink	28.0%	35.2%	20.6%	7.1%	9.0%	100.0%
Chum	29.1%	35.8%	21.0%	7.4%	6.7%	100.0%
Steelhead	30.5%	35.7%	20.7%	6.2%	6.9%	100.0%
All Focal Targets	31.7%	34.3%	15.3%	10.0%	8.7%	100.0%

TABLE 2. Conservation Priority Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on intact watersheds (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
East Chichagof Island	Chicken Cr	1960	100.0%	0.0%	21,436
	Poison Cove	2790	13.4%	85.9%	7,151
	Crab Bay	2320	14.6%	85.3%	11,017
	Goose Flats	2260	14.2%	85.8%	23,111
	Ushk Bay	2810	15.6%	80.3%	21,284
	Broad Island	2460	17.1%	82.8%	16,848
	Saltry Bay	2310	14.2%	85.8%	18,353
	Long Bay	2280	36.4%	63.6%	19,178
	Deep Bay	2800	12.8%	82.5%	18,180
	Seal Bay	2290	20.2%	79.8%	21,905
	Little Basket Bay	2400	19.0%	81.0%	10,155
	Whip Station	2210	90.7%	9.4%	4,546
	Neka Bay	2010	22.0%	78.1%	39,557
East Baranof Island	Saook Bay	2940	13.2%	86.8%	23,839
	Lake Eva	2950	99.7%	0.3%	12,395
	Deadman Reach	2890	47.4%	52.6%	8,125
	Kelp Bay - South Arm	3140	100.0%	0.0%	35,118
	Kelp Bay - Middle Arm	2980	51.7%	48.3%	27,746
West Baranof Island	Sitka Sound - Aleutkina Bay	3200	97.2%	2.8%	7,627
	Kruzof I. - Sea Lion Cove	3050	70.2%	29.9%	10,960
	Krestof Sound	3090	90.3%	9.7%	8,963
	Redoubt Lake	3500	95.3%	3.2%	28,147
	Deep Inlet	3220	100.0%	0.0%	6,954
	Salmon Lake	3230	13.6%	86.4%	7,663
	Fish Bay	2870	96.4%	3.6%	41,305
	Big Bear / Baby Bear	2880	17.6%	67.9%	7,141
	Kruzof I. - Mount Edgecumbe	3080	92.5%	7.5%	53,550
	Nakwasina Passage	3000	57.8%	42.2%	19,899
	Sukoi Inlet / N. Krestof	3030	39.6%	60.4%	18,138
	Big Bay	3490	92.9%	5.7%	9,414
Kuiu Island	Reid Bay	4160	17.6%	81.5%	16,043
	Kuiu - Salt Lagoon	4180	38.2%	61.7%	9,634
	Security Bay	4000	43.6%	54.6%	28,775
	Howard Cove	4100	99.9%	0.0%	12,752
	Kingsmill Point	4010	100.0%	0.0%	13,286
	Bay of Pillars	4030	99.8%	0.2%	29,886
	No Name Bay	4170	38.0%	61.9%	10,009

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

TABLE 2 (cont.). Conservation Priority Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on intact watersheds (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
Kupreanof and Mitkof Islands	Lower Castle River	4350	58.6%	41.4%	32,318
	Rocky Pass	4280	92.9%	7.1%	48,412
	Lake Kushneahin	4310	19.8%	80.2%	22,500
	Colp Lake	4460	18.2%	81.6%	11,290
	Totem Bay	4320	16.4%	83.6%	42,544
	Big John Bay	4270	94.4%	5.6%	25,152
	Upper Castle River	4360	15.1%	84.9%	21,248
	Duncan Bay	4380	26.1%	73.9%	27,447
	Lovelace Cr	4300	19.7%	80.3%	14,563
	Towers Arm	4400	27.4%	72.0%	26,813
	Irish Lakes	4290	16.7%	83.3%	54,647
	Woewodski Island	4480	19.0%	78.4%	24,863
	Blind Slough	4510	83.1%	16.9%	9,614
Etolin / Zarembo / Wrangell Is.	Kunk Lake	4630	99.6%	0.4%	11,141
	Burnett Bay	4680	24.8%	75.2%	23,197
	Woronkofski Island	4610	9.4%	90.6%	14,532
	Streets Lake	4660	94.2%	5.9%	17,336
	Thoms Lake	4790	49.6%	45.5%	25,061
	Southwest Cove	4710	16.8%	83.0%	8,674
	Chichagof Pass	4620	18.7%	81.4%	16,290
	Mosman Inlet	4670	16.3%	83.8%	24,798
Revilla Is. / Cleveland Pen.	Union Bay	7090	99.2%	0.8%	14,642
	Port Stewart	7190	21.8%	78.2%	22,580
	Helm Bay	7160	98.5%	1.5%	17,079
	West Gravina Island	7620	79.8%	20.2%	8,792
	Yes Bay	7240	100.0%	0.0%	42,926
	Moser Bay	7430	19.0%	81.0%	14,044
	Spaceous Bay	7220	28.2%	71.8%	31,347
	Bostwick Inlet	7630	16.0%	84.0%	19,905
	SW Cleveland Peninsula	7120	53.1%	46.9%	14,584
	Vixen Inlet	7200	29.8%	70.2%	24,859
	Granite Cr CP	7170	38.9%	61.1%	10,280
	Deer Island	5250	28.4%	71.7%	9,329
	Behm Narrows	7310	99.9%	0.1%	19,765
	SW Cleveland Peninsula	7130	96.7%	3.3%	9,498
	Smugglers Cove	7150	98.5%	1.6%	13,920
	Emerald Bay	7210	67.1%	32.9%	8,011
	Swan Lake	7450	89.8%	10.1%	23,744

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

TABLE 2 (cont.). Conservation Priority Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on intact watersheds (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
Revilla Is. / Cleveland Pen. (continued)	Bell Arm	7280	100.0%	0.0%	12,917
	Orchard Creek	7340	91.0%	8.9%	32,858
	Hickman Pt	7230	100.0%	0.0%	6,850
	Cannery Creek	7100	17.5%	82.5%	5,412
	California Cove	7580	96.5%	3.6%	11,594
	Betton Island	8641	91.8%	8.2%	5,432
	Duke Island	7670	99.7%	0.3%	39,263
	SE Thorne Arm	7600	17.4%	82.5%	11,127
	Reflection Lake	7270	100.0%	0.0%	11,117
	Upper Vixen	7180	26.2%	73.8%	11,850
	Sunny Bay	5260	20.4%	79.6%	17,659
North Prince of Wales	Cholmondeley Sound (West Arm)	6740	20.0%	80.0%	19,901
	Waterfall	6310	58.9%	41.1%	16,284
	Barns Lake	5520	48.6%	51.4%	9,695
	Sarkar Lakes	5541	100.0%	0.0%	24,949
	S. Honker Divide	5750	68.1%	31.9%	18,306
	Salt Lake Bay	5920	95.3%	4.7%	14,655
	NW Sukkwann Is	6710	55.0%	45.0%	22,844
	Whale Passage	5510	43.6%	56.4%	13,312
	Center Peak	5760	99.6%	0.4%	15,292
	McKenzie Inlet	6180	49.5%	50.5%	17,365
	S Sukkwan Is	6700	47.8%	52.2%	16,850
	Sweetwater Lake	5730	43.2%	56.8%	25,939
	Sunny Cove, Cholmondeley Sound	6750	36.5%	63.5%	6,570
	Lower Thorne River	5971	82.5%	17.5%	3,455
	Sukkwan Strait	6720	81.4%	18.6%	28,633
	Thorne River Falls	5780	49.5%	50.6%	6,411
	Tracodero Bay	6250	27.8%	72.2%	31,290
	Clover Bay	6170	76.0%	24.0%	14,207
	North Honker Divide	5740	78.7%	21.4%	26,681
	Cristoval Channel	5930	46.3%	53.7%	16,237
	Calder Bay	5311	23.0%	77.0%	15,907
	Port Estrella	6300	12.3%	87.7%	17,209
	Mt Francis	5410	65.0%	35.1%	6,059
	Davidson	5470	18.5%	81.5%	3,171
	Soda Bay	6320	9.6%	90.4%	14,470
	Nossuk Bay	5910	13.7%	86.3%	8,849
	Baird Peak	5820	13.8%	86.3%	4,124
	Trollers Cove	6150	24.0%	76.0%	10,012
	Control Lake / Upper Thorne	5960	76.3%	23.7%	12,602

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

TABLE 2 (cont.). Conservation Priority Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on intact watersheds (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
South Prince of Wales	S Arm Moira Sound	6920	20.6%	78.9%	23,699
	Nutkwa Inlet	6850	7.7%	92.0%	18,158
	Kassa Inlet	6890	48.1%	50.0%	10,636
	Mabel Bay	6880	16.0%	84.0%	8,167
	Hidden Bay	6950	100.0%	0.0%	4,844
	Nichols Bay	7040	99.3%	0.0%	17,270
	Stone Rock Bay	7020	100.0%	0.0%	9,339
	Ingraham Bay	6940	43.5%	56.5%	6,200
Outside Islands	Port Santa Cruz	6340	28.1%	71.9%	11,631
	San Fernando - S	6280	100.0%	0.0%	9,960
	Port Refugio	6350	17.8%	82.3%	9,085
Dall / Long Islands	Bobs Bay	6390	16.8%	83.2%	6,081
	Essoway Lake	6590	97.1%	2.9%	14,136
	Waterfall Bay	6480	99.1%	0.9%	7,209
	McLeod Bay	6660	85.0%	15.0%	3,440
	Devil Cove	6460	61.9%	38.1%	7,120
	Hook Arm	6410	66.6%	33.4%	4,621
	Port Bazan	6560	32.8%	67.2%	14,908
	Datzkoo Hbr	6630	88.5%	11.5%	3,616
	Sea Otter Hbr	6420	77.6%	22.4%	7,105
	Welcome Cove	6470	100.0%	0.0%	3,634
	Meares Passage	6370	18.3%	81.7%	6,035
	Driver Bay	6400	40.5%	59.6%	3,079
	Gold Hbr	6510	95.3%	4.7%	5,469
	Fisherman Cove	6440	48.2%	51.8%	3,445
Lynn Canal / Mainland	Cowee Creek	230	10.6%	89.4%	26,936
	Pt. Couverden	1170	16.4%	83.6%	11,184
	Earth Station	1150	100.0%	0.0%	8,389
	Eagle / Herbert River	260	98.2%	1.8%	38,786
	Lincoln / Shelter Island	1240	32.8%	56.6%	8,084
	St. James Bay	1110	50.3%	39.5%	23,335
	Nun Mountain	1120	88.0%	11.9%	22,228
	Echo Cove	250	12.7%	65.9%	12,821
	Katzehin River	90	100.0%	0.0%	55,631
	Gilkey River	150	99.9%	0.0%	42,279
	Antler River	140	100.0%	0.0%	28,649
	Sullivan Mountain	950	19.9%	80.1%	16,303
	Dayebas Creek	80	100.0%	0.0%	10,907
	Pt. Danger	1080	9.0%	91.0%	3,633
	William Henry Bay	1070	61.4%	38.0%	7,488
	West Sullivan	970	17.1%	82.9%	6,659

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

TABLE 2 (cont.). Conservation Priority Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on intact watersheds (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
Taku Mainland	Taku River	460	97.6%	2.4%	111,669
	Port Houghton Salt Chuck	790	27.5%	72.5%	42,519
	Port Houghton - Robert Is.	820	12.6%	86.6%	13,185
	Sandborn Canal	840	39.3%	60.7%	17,437
	Gilbert Bay	570	59.6%	40.4%	28,037
	Slocum Inlet	510	14.4%	85.6%	16,525
	Dry Bay	690	14.8%	85.2%	12,416
	Pt. Houghton - Dalgren	830	12.2%	87.8%	10,785
	Williams Cove	641	100.0%	0.0%	7,600
	Port Snettisham	550	28.8%	71.2%	22,293
	Limestone Inlet	530	100.0%	0.0%	9,960
	Taku Inlet	410	24.4%	75.6%	33,010
	Taku Harbor	520	9.4%	90.6%	6,950
	Sand Bay	680	10.3%	89.7%	8,227
	Heigs Peak	560	48.0%	52.0%	12,520
Stikine Mainland	Farugut Bay - S. Arm	900	94.6%	5.4%	27,851
	Marsha Peak	5010	9.2%	90.8%	28,180
	Madan Bay	5040	11.1%	88.9%	16,722
	Little Lake Eagle	5190	99.9%	0.1%	44,197
	Tom Creek	5100	70.6%	29.5%	27,274
	Cat Cr	870	12.1%	87.9%	14,029
	Marten Lake	5090	100.0%	0.1%	14,603
	N Arm Faragut Bay	890	14.2%	85.9%	17,299
	Virginia Lake	5020	13.0%	86.5%	30,947
	Blake Channel	5050	35.3%	64.8%	26,293
	Dry Bay-Grand Point	4830	5.3%	94.7%	10,737
	Oerns Creek	5080	100.0%	0.1%	13,590
	Aaron Creek	5030	99.9%	0.1%	45,572
Chilkat River Complex	Takhin River	Non-TNF	0.0%	100.0%	79,562
	Ferebee River	Non-TNF	0.0%	100.0%	57,711
	Davidson Glacier	Non-TNF	4.8%	95.2%	45,518
	Chilkat River	Non-TNF	32.6%	67.4%	80,645
	Upper Chilkat River	Non-TNF	11.5%	88.5%	67,752
	Garrison Glacier	Non-TNF	0.0%	100.0%	34,661
	Chilkoot River	Non-TNF	2.2%	97.8%	95,029
	Taiya River	Non-TNF	0.0%	91.9%	124,725
Yakutat Forelands	Ahrnklin River (estuary)	3710	99.8%	0.0%	7,264
	Ahrnklin River	3720	99.6%	0.4%	64,228
	Khantaak Islands	3680	25.5%	74.4%	4,015

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

TABLE 3. Integrated Management Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on developed watersheds with high values and restoration opportunities (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
East Chichagof Island	Port Frederick Portage	2020	77.8%	22.2%	17,420
	False Island	2450	10.9%	89.0%	23,863
	Sitkoh Bay	2430	12.1%	87.9%	26,614
	Game Creek	2040	3.0%	97.1%	35,470
	Corner Bay	2360	10.7%	89.2%	11,582
	False Bay	2100	38.6%	61.5%	21,076
	Kennel Creek	2170	15.5%	84.5%	10,270
	Upper Mud Bay	1930	0%	100%	20,998
East Baranof Island	Appleton Cove	2930	12.1%	87.9%	13,871
	Peschani Point	2910	18.3%	81.7%	11,311
	Catherine Island	2970	40.2%	59.8%	15,858
	Rodman Bay	2920	11.5%	88.5%	25,200
	Kelp Bay - Portage Arm	2960	26.3%	73.7%	16,332
West Baranof Island	Sitka / Indian River	3110	60.7%	39.3%	21,119
	St. John the Baptist	3020	88.1%	11.9%	21,439
	Redoubt Bay	3210	20.0%	80.0%	9,441
	Shelikof Bay	3070	13.4%	86.6%	15,128
	Nakwasina River	2990	70.4%	29.6%	23,633
	Nakwasina Sound	3010	23.8%	76.3%	5,685
	Katlian Bay – North	3130	57.8%	42.2%	32,745
	Katlian Bay – South	3120	25.6%	74.4%	11,207
	Camp Coogan	3190	100%	0%	5,006
Kuiu Island	Saginaw Bay	3990	11.8%	88.2%	25,210
	Rowan Bay	4020	12.4%	87.6%	32,556
	Kadake Creek	4210	33.1%	66.9%	34,607
	Keku Islands	3980	20.6%	79.4%	14,208
Kupreanof / Mitkof Islands	Wrangell Narrows	4470	16.6%	83.2%	60,047
	Big Creek	4500	23.5%	76.5%	20,397
	Sumner Mountains	4520	19.1%	80.9%	30,907
Etolin / Zarembo / Wrangell	N. Wrangell Islands	4550	25.2%	74.8%	8,602
	Baht	4560	14.4%	85.6%	17,957
Revilla Island / Cleveland Peninsula	Buckhorn Lake	7530	18.3%	81.7%	32,452
	Salt Lagoon – Revilla	7470	13.4%	86.1%	20,334
	Carroll Creek	7440	22.3%	77.7%	32,051
	Carroll Inlet	7460	17.0%	83.0%	29,941
	Klu Creek	7330	32.4%	67.6%	16,767
	Settlers Cove	8642	41.7%	58.3%	15,620
	Ward Cove	7500	42.6%	57.5%	16,985
North Prince of Wales Island	Harris River	6220	13.8%	86.2%	26,536
	Shimaku Cr	5940	0.2%	99.8%	18,598
	Staney Creek (estuary)	5871	25.8%	74.2%	8,514
	Trout Cr	5430	34.6%	65.4%	16,085
	Port Protection	5270	76.4%	22.5%	8,380

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

TABLE 3 (cont.). Integrated Management Watersheds for combined focal species and ecological systems based on the Marxan spatial optimization tool parameterized with emphasis on developed watersheds with high values and restoration opportunities (refer to Conservation Area Design Map, Fig 2).

Biogeographic Province	Watershed Name[a]	VCU	Administrative protection (%)	Development Lands[b] (%)	Acres
North Prince of Wales Island (continued)	Sea Otter Sound	5550	35.6%	64.4%	15,568
	Lower Staney Creek	5880	12.4%	87.6%	26,662
	Edna Bay	5460	9.5%	90.5%	14,113
	Shaheen Creek	5890	46.0%	54.0%	20,725
	Control Lake	5950	11.4%	88.6%	20,761
	Flicker Creek	5290	14.7%	85.3%	14,913
	New Tokeen	5560	34.7%	65.3%	7,134
	Salt Chuck N. Karta	5980	21.4%	78.5%	12,686
	Red Lake	5330	17.6%	82.4%	13,347
	Thorne Bay	5860	19.1%	80.9%	15,582
	Klawock Lake & Inlet	6091	2.2%	97.8%	44,533
	Logjam Creek	5770	22.9%	77.1%	29,425
	Exchange Cove	5390	19.3%	80.7%	9,045
	Naukati Bay	5710	8.6%	91.4%	19,463
	Buster Bay	5300	15.1%	84.9%	11,005
	Red Bay	5320	13.2%	86.8%	15,594
	Salmon Bay Highlands	5340	38.8%	61.0%	8,633
	Salmon Bay Rapids	5350	24.9%	75.1%	6,727
	Colpoys	5341	24.3%	75.6%	2,030
	El Capitan Lake	5360	25.2%	74.8%	9,249
	El Capitan Peak	5371	17.4%	82.6%	9,614
	Whale Pass - Big Creek	5380	8.4%	91.6%	12,542
	Squaw Creek	5400	20.5%	79.5%	5,150
	Neck Lake	5500	17.6%	82.4%	10,623
	Sarheen Cove	5492	52.2%	47.9%	7,028
	Twelve Mile Arm	6210	32.8%	67.3%	28,337
	Head Trocodero Bay	6240	27.5%	72.5%	19,508
	Hydaburg River	6210	13.9%	86.1%	28,507
	Hetta Inlet	6730	4.3%	95.7%	39,814
Lynn Canal / Mainland	Montana Creek	280	68.6%	31.4%	8,900
	Homeshore (Icy Strait)	1200	10.5%	89.5%	12,444
	Ansley Basin	1180	40.1%	60.0%	13,594
	Peterson Creek / Eagle River	270	64.6%	35.5%	12,887
	Upper St. James River	1060	79.3%	17.2%	19,752
	Humpy Creek	1190	59.5%	40.5%	30,403
Stikine River / Mainland	Point Agassiz Peninsula	4890	17.1%	82.9%	40,522
	Eagle Bay	5200	50.7%	49.2%	18,216
	N Fork Bradfield River	5140	24.4%	75.6%	29,094

[a] Watersheds with >85% designated within legislatively protected areas are not shown.

[b] Development lands include areas available for timber harvest under the 1997 TLMP as well as private or other lands lacking administrative protection or conservation buffers.

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REVIEW

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Wildlife studies on the Tongass National Forest challenge essential assumptions of its wildlife conservation strategy

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Abstract

The Tongass National Forest in southeast Alaska, USA, includes the Alexander Archipelago and narrow North American mainland, comprising one of the largest remaining, largely pristine, coastal temperate rainforest in the world. Management of the Tongass has become increasingly challenging because of expectations of a conservation framework designed to maintain viable populations of native wildlife species while decades of extensive clearcut logging of old-growth forests has continued. We used the findings of multiple published studies conducted on the Tongass from 1998 to 2017 to examine 4 assumptions of its wildlife conservation strategy (WCS): forest planning assessments of wildlife viability were realistic, forest management and conservation policies are implemented at appropriate ecological scales, old-growth reserves are effective habitat conservation areas and ensure functional connectivity, and forest-wide standards and guidelines ensure sufficient habitat for sensitive species in managed landscapes. Several ecological field studies, population and spatial analyses and modeling, and statistical analyses revealed that wildlife viability assessments to evaluate forest plan alternatives underestimated the risk of extinction by only examining individual vulnerable species rather than considering joint probabilities across multiple species; the ecological scale of management and conservation policies do not adequately consider area-sensitive vulnerabilities of island communities as evidenced by the increasing risk of extirpation of island endemics whose populations have become isolated and reduced; old-growth reserves are unlikely to maintain viable populations of endemic small mammals in isolation or as functionally connected metapopulations; and a spatially explicit analysis of individual home ranges demonstrated that forest-wide standards and guidelines provide about half the breeding habitat needed by a federally listed endemic raptor, the Queen Charlotte goshawk *(Accipiter gentilis laingi)*, of which only half of that is secure. Thus, assertions that the WCS is properly functioning as designed are dubious because a comprehensive monitoring plan has not been implemented and vital underlying assumptions are not supported by available science. We recommend 3 forest management and conservation policy adjustments: limit size and location old-growth forest harvests, restore forests through intermediate stand management of second growth, and conduct a formal review of WCS elements and assumptions.

KEYWORDS

biodiversity, clearcut logging, ecological scale, island endemics, old-growth forests, reserve network, temperate rainforest, wildlife viability

The Tongass National Forest (Figure 1) is one of the largest, relatively pristine, temperate rainforests in the world (DellaSala et al. 2011, 2022) with 6.7 million ha distributed across ≥20,000 islands and a narrow mainland in southeast Alaska, USA (Everest et al. 1997). It extends from the southern tip of Prince of Wales Island 800 km north to the Hubbard Glacier.

Southeast Alaska is globally recognized for its expansive tracts of intact rainforest that contribute to climate stabilization (DellaSala et al. 2022). Wind disturbance plays a fundamental role in shaping forest dynamics, at large and small scales, and over a continuum dependent on landscape features including exposure, landscape position, and topography. These forests support complete wildlife communities, most notably all-inclusive trophic assemblages that include primary producers to top carnivores (Vynne et al. 2021). The Alexander Archipelago has a terrestrial mammalian fauna with a nested structure that resulted primarily from differential colonization following glacial retreat (Conroy et al. 1999, Sawyer et al. 2019). Regardless of the primary mechanism, habitat loss and fragmentation are expected to reduce diversity of mammalian taxa in southeast Alaska through increasing extinction probabilities (Burkey 1995, Frankham 1998, Crooks et al. 2017, Püttker et al. 2020, Vynne et al. 2021). Furthermore, vital interspecific interactions across ecological communities are altered if a predator, prey, or symbiote is extirpated (Smith 2012*a*, Brodie et al. 2018, Kelt et al. 2019).

In 1997, Tongass planners were commissioned to manage wildlife habitats to maintain viable, widely distributed populations of existing native and desired non-native vertebrate species as directed by the 1982 viability rule of the 1976 National Forest Management Act (NFMA; U.S. Forest Service [USFS] 1982). Procedures

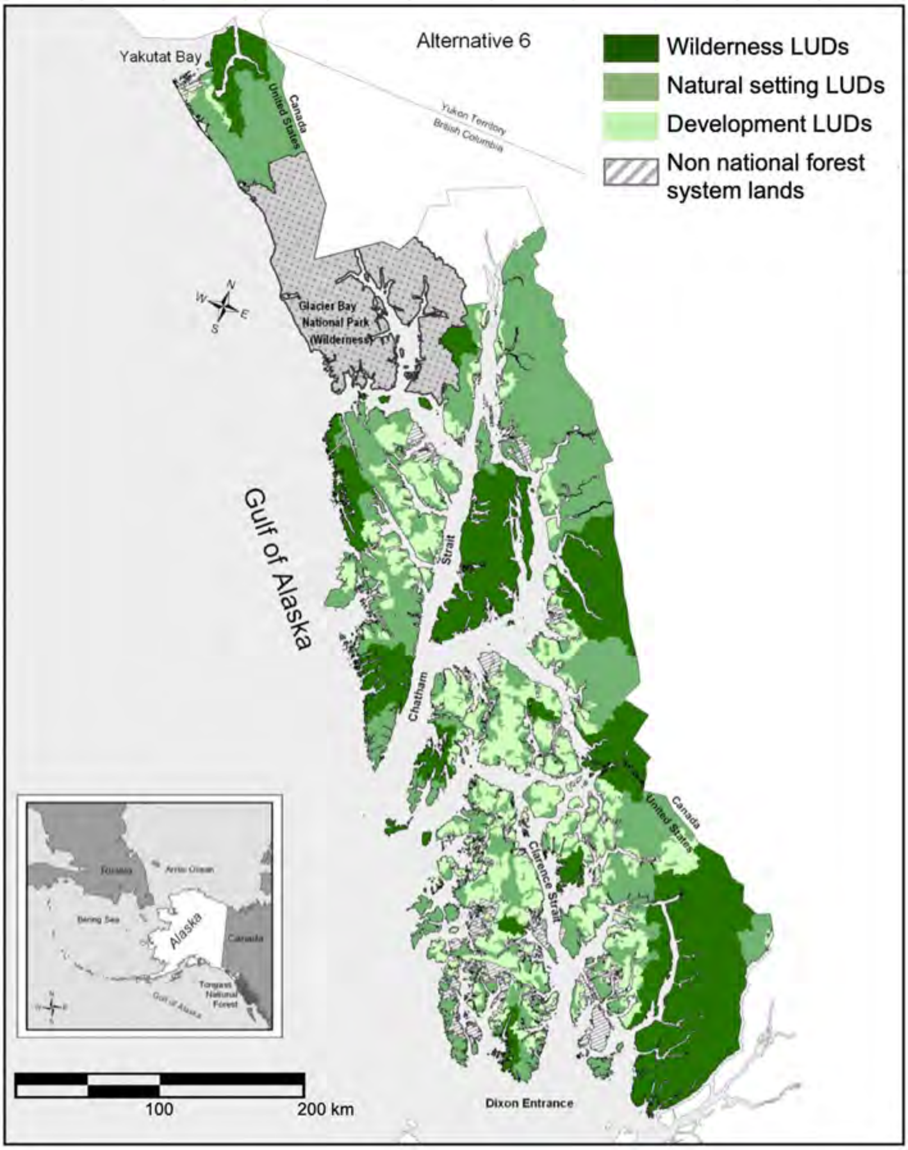

FIGURE 1 The Tongass National Forest in southeast Alaska, USA, extends from the southern tip of Prince of Wales Island 800 km north to the Hubbard Glacier and includes the Alexander Archipelago and a narrow strip of North American mainland encompassing 6.7 million ha. Single ranger districts exceed the size of many national forests in the continental United States. The Wildlife Conservation Strategy old-growth reserve network is depicted as wilderness and natural setting land use designations (LUDs) within Alternative 6 of the 2008 Forest Plan Amendment (USFS 2008). Wilderness LUDs include wilderness areas and National Monuments. Natural setting LUDs includes lands that maintain old-growth forest: congressionally designated unroaded areas; old-growth forest LUDs; remote and semi-remote recreation; municipal watersheds; special interest areas; wild, scenic, and recreational rivers; and research natural areas. Development LUDs include timber production, modified landscapes, scenic viewsheds, and experimental forests; <25% of these lands are suitable for timber harvest. Non national forest system lands represent state, Native, and private lands (USFS 2008).

for implementing NFMA viability provisions are expected to occur through the following processes: 1) describing the ecological context, 2) identifying species of viability concern, 3) collecting information on species of viability concern, 4) identifying species groups, 5) describing conservation approaches, 6) developing land and resource management plan (LRMP) alternatives, 7) evaluating the effects of LRMP alternatives on viability, and 8) conducting monitoring activities.

Historical timber management of the Tongass limited old-growth rainforest available to planners in framing a conservation strategy. A large majority of timber harvests occurred before the 1997 forest plan revision (USFS 2008), with cumulative disturbance and ecological consequences from 5 decades of high grading (i.e., exclusive harvest of the most valuable forests) across the region, including large-tree stands and expansive landscapes with contiguous productive old-growth (timber volume >46.6 m^3/ha) forests (Albert and Schoen 2012). While approximately 79% of the Tongass remains largely undisturbed and undeveloped (stream and shoreline buffers, reserves, wilderness areas), the majority of the unmanaged portion is highly fragmented, composed of ≥20,000 small (<400 ha), uninhabited islands with little opportunity for timber harvest (USFS 1997). The managed portion (~21%) has been subjected to intensive broad-scale disturbance from extensive clearcut logging that produced sharply contrasting land cover types within single landscapes (Figure 2). The highest rates of change occurred among biogeographic provinces and landform associations that originally contained the largest concentrations of highest volume, productive old growth (POG). Although only 12% of POG forests have been logged, large-tree stands were reduced by ≥28%, karst forests by 37%, and landscapes with the highest volume of contiguous old growth by 66.5% (Albert and Schoen 2012).

The USFS responded to this management challenge with a comprehensive, science-based revision of the forest plan (Swanston et al. 1996). The 1997 Tongass Land and Resource Management Plan (TLMP; USFS 1997) combined familiar, previously used elements and processes gleaned from the scientific literature with regional ecological information from journal publications, workshops, expert panels, and agency reports to design a unique, strategic conservation framework (Swanston et al. 1996, Everest et al. 1997, Smith and Person 2007, Smith et al. 2011, Smith 2013). Emulating natural disturbances offered an approach to designing management plans that maintain prevailing ecological conditions (Nowacki and Kramer 1998). Tongass planners chose a management plan alternative that departed substantially from the natural disturbance regime in which ≥95% of canopy openings produced by windstorms average <0.03 ha (Nowacki and Kramer 1998). The 1997 TLMP continued to emphasize

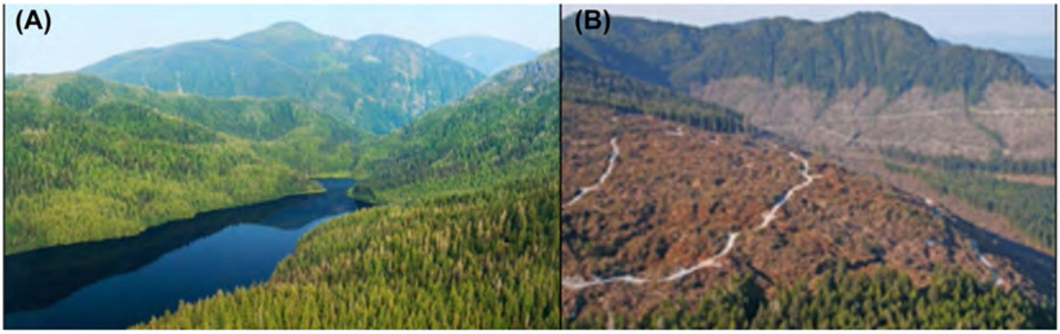

FIGURE 2 Timber management of the Tongass National Forest in southeast Alaska, USA, was dichotomous, producing sharply contrasting unmanaged and managed landscapes of A) intact old-growth temperate rainforests (photo by Alan Wu/Flickr Creative Commons) and B) extensive clearcuts (photo by John Schoen). A small proportion (12%) of the entire Tongass National Forest was logged; still, 67% of the highest volume forests were harvested (Albert and Schoen 2012). Some smaller islands experienced broad-scale disturbance across a significant proportion of the entire distribution of resident endemic mammals (Smith et al. 2011, Smith and Fox 2017).

clearcut logging, adding broad-scale disturbance to expansive landscapes of young, unmanaged, even-aged second growth (USFS 1997).

Despite its size and southeast Alaska's highly fragmented island biogeography, an important and far-reaching central hallmark of the 1997 TLMP is that the Tongass National Forest is largely managed as a single contiguous forest ecosystem. This has been evident from expectations that the Tongass would continue to persist as interconnected late-successional ecosystems across southeast Alaska (Shaw 1999), assessments and summary data would be presented as forest-wide statistics (USFS 1997, 2008, 2016), and management would disregard the variety and significance of unique biota and ecological communities (Smith 2012*a*), including the consequences of disproportionate loss and fragmentation of available habitat from cumulative effects of logging to island endemics (Smith and Person 2007, Smith et al. 2011, Albert and Schoen 2012, Smith 2013, Smith and Fox 2017).

Although amendments to TLMP have occurred since 1997 (USFS 2008, 2016), today the Tongass Wildlife Conservation Strategy (WCS) remains largely intact (USFS 2016). Unfortunately, a continuous decline in funding since 1997 has limited resources and capability to implement a proposed comprehensive long-term monitoring plan for sensitive or other vulnerable species (Smith et al. 2011, Smith 2013, Smith and Fox 2017). Consequently, there is little documentation regarding the implementation of management or conservation actions or corresponding responses and outcomes for intended forest resources.

Until recently, the most apparent alterations or amendments to the WCS have been the removal, movement, or change in composition of designated old-growth reserves (Smith et al. 2011). Small old-growth reserves have remained spatially inexplicit (USFS 2008), obscuring assessments of landscape structure and functional connectivity. In the 2016 forest plan amendment, an immeasurable number of small (many isolated) conservation areas totaling 1.3 million ha of old-growth forest were established across the Tongass, and 8,350 ha of old-growth forest was preserved among 73 watersheds to protect anadromous streams (USFS 2016: appendix D). It remains unclear if the watershed allocation was in addition to the old-growth reserve network expectation that ≥16% of the area be retained as old-growth forest (USFS 1997: appendix K). Regardless, without additional research, including spatially explicit analyses of watersheds and surrounding landscapes, contributions to functional connectivity or essential habitat of sensitive or old-growth obligate wildlife remain uncertain.

The Tongass WCS embodies a complex land and resource management framework intended to maintain biological diversity that comprises numerous elements, some of which are integrated within a hierarchical structure that is susceptible to systemic failure because each component is essential for overall functioning (Smith et al. 2011, Smith 2013). Although some elements have been successfully implemented for select species under specific circumstances elsewhere (USFS and Bureau of Land Management 1994), the Tongass WCS was implemented as an experiment with several essential underlying assumptions (Smith and Person 2007, Smith et al. 2011, Smith 2013). Yet statements asserting or accepting the 1997 Tongass WCS as a scientifically sound foundation from which to base management decisions continued to occur in forest and project planning documents (USFS 2008: D26, USFS 2016: K1–3), meetings, internal communications (W. P. Smith, USFS, personal communications), received emails, internal and cooperator meetings, oral comments during public workshops and meetings, and external communications (e.g., newspaper articles). Such assertions lack sufficient monitoring data or supporting evidence from scientific studies, potentially enabling further threats to essential old-growth ecosystems and native wildlife.

Our objective was to illustrate apparent disparities between designed expectations and documented outcomes of implementing the WCS through an investigation of published wildlife research conducted on the Tongass, including studies explicitly designed to examine inherent assumptions. Specific objectives were to use published results to examine 4 assumptions of the Tongass WCS: forest planning assessments of wildlife viability were realistic, forest management and conservation policies are implemented at appropriate ecological scales, old-growth reserves are effective habitat conservation areas and ensure functional connectivity, and standards and guidelines ensure sufficient habitat for sensitive species in managed landscapes.

STUDY AREA

Southeast Alaska is composed of mainland extending south along the western coast of Canada and >1,000 islands. The area includes fjords and glaciated mountain ranges and a cool, wet (200–600 cm annual precipitation) maritime climate, with mean monthly temperatures ranging from 13°C in July to 1°C in January (Smith and Nichols 2003, 2004). Elevation ranges from sea level to 1,643 m. The region is highly fragmented, with islands ranging in size from <1 ha to 6,670 km^2. The narrow mainland is largely isolated from other large, contiguous landmasses because of mountains, glaciers, and ice fields immediately to the east (Everest et al. 1997). Southeast Alaska is further stratified by 21 biogeographic provinces according to various configurations of physical, climatic, and biotic features. About 4 million ha (60%) is rainforest, of which 2.2 million ha is productive forests (USFS 1997). Coniferous rainforest dominates the landscape from shoreline to about 600-m elevation. The forest canopy is dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) in uplands but includes shore pine (*Pinus contorta*), mountain hemlock (*Tsuga mertensiana*), western redcedar (*Thuja plicata*), and Alaska-cedar (*Chamaecyparis nootkatensis*) in wetlands (Nowacki and Kramer 1998); remaining areas are riparian, alpine, muskeg, or sparsely vegetated mountain peaks and other rock formations (Smith and Nichols 2003, 2004). About 90% of commercial forests are upland Sitka spruce–western hemlock forests (USFS 1997).

Large trees (>75-cm diameter), downed and decaying wood, snags, and heterogeneous substrates are key components of old-growth rainforest ecosystems (Alaback 1982, Nowacki and Kramer 1998). The understory is dominated by blueberry (*Vaccinium* spp.), especially in canopy gaps (Smith and Nichols 2003, 2004; Smith 2012*a*). Unmanaged forests have a multilayered overstory of uneven-aged trees, dominant trees that generally are ≥300 years old, and structurally diverse understories (Alaback 1982; Smith and Nichols 2003, 2004). These forests vary in structure from scrub, or low-volume, communities of short (<10 m), small (<0.5-m diameter) trees with open canopies and dense, shrubby understories on poorly drained sites (peatland) to high-volume stands with a closed canopy, tall (>60 m), large (>3-m diameter) trees, and a predominantly herbaceous understory on highly productive sites (Harris and Farr 1974, Alaback 1982). The western hemlock-Sitka spruce forest type constitutes most of the closed-canopy forests in the region (Alaback 1982). It is spatially heterogeneous at a fine scale (<1 ha) and typically occurs on low-elevation, well-drained sites, often as a mosaic with fens and muskegs (Smith and Nichols 2003, 2004).

Southeast Alaska has a unique mammalian fauna that is significantly correlated with island isolation and extinction events resulting from differential colonization and island area effects (Conroy et al. 1999). Consequently, southeast Alaska is a hot spot of endemism (Cook et al. 2001), with varying and unique mammal assemblages and ecological communities (Cook and MacDonald 2001; Cook et al. 2001, 2006; Smith 2012*a*). The life history of birds is also influenced by the fragmented nature of the region, most notably northern goshawks (*Accipiter gentilis*) and other species that require large breeding ranges (Smith 2013). Prominent indigenous vertebrates include the Queen Charlotte goshawk (*A. g. laingi*), marbled murrelet (*Brachyramphus marmoratus*), Alexander Archipelago wolf (*Canis lupus ligoni*), brown bear (*Ursus arctos*), American marten (*Martes americana*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), and numerous endemic small mammals whose distributions are restricted (MacDonald and Cook 1996, Smith 2005, Cook et al. 2006), including the following island endemics: Prince of Wales Island flying squirrel (*Glaucomys sabrinus griseifrons*), Wrangell Island vole (*Myodes gapperi wrangeli*), and Suemez Island ermine (*Mustela erminea seclusa*).

METHODS

Because the purpose of this review was not a meta-analysis or systemic literature review, we first conducted literature searches focused on our published research papers and the citations within and summarized the findings of numerous studies conducted in Southeast Alaska during 1998–2017. We then used a Web of Science^{TM} word search conducted 31 May 2021 using the keywords Tongass, management, wildlife, and conservation. This search produced 57 results. We expanded our search by reviewing the publications citing relevant sources from this search and by reviewing the sources cited within all of these. We extracted publications from the search output that focused on research or management of wildlife within the Tongass that related to ≥1 of the 4 objectives for this review. We excluded studies of wildlife species that were not identified as a focal or management species within TLMP (e.g., bears, bald eagle [*Haliaeetus leucocephalus*]).

Viability assessments (objective 1)

An initial, integral step in developing a forest plan that prioritizes maintaining biological diversity is establishing a procedure in which planners can objectively evaluate the effect of LMRP alternatives on the persistence of native wildlife (Shaw 1999). The USFS convened numerous risk assessment panels during the 1997 TLMP revision (USFS 1997). Each panel comprised subject matter experts with knowledge of the natural resource under consideration. Seven panels estimated the relative risk that implementation of a range of alternative approaches to management of the Tongass would impose upon continued persistence of select wildlife species across the landscape. Ostensibly, the chosen set of species represented a broad enough range of taxa and ecological lifestyles that the breadth of possible responses to each of the 10 forest plan alternatives under consideration was captured in responses of vulnerable species but with little or no correlation among species' responses to a particular alternative (Shaw 1999).

An eighth panel evaluated old-growth ecosystems, assigning likelihood scores to outcomes that characterized the persistence of interconnected and representative late-successional ecosystems across southeast Alaska according to 3 attributes: abundance and ecological diversity, which considered if "old growth would be equal to or greater than long-term (i.e., 100 years) average and is well distributed across environmental gradients, provinces, and community types;" processes and functions, which considered whether the full range of disturbance processes are represented, and if "stand structure-dynamics and landscape structure-dynamics-age attributes occur across all provinces;" and whether connectivity would be as "effective as it was prior to large-scale timber harvest" (Shaw 1999: 11–12). Assessments from each of the panels became an integral element of the effects analyses that ultimately determined the management policies and actions incorporated in the 1997 TLMP (USFS 1997).

Risk assessment panels evaluated the likelihood of persistence of the northern goshawk, Alexander Archipelago wolf, brown bear, marbled murrelet, American marten, Sitka black-tailed deer, and other terrestrial mammals (Shaw 1999). Other terrestrial mammals included a group of more widely distributed mammals and a group of endemic small mammals whose known distribution in southeast Alaska is restricted (MacDonald and Cook 1996, Smith 2005, Cook et al. 2006). To assess the influence of varying management applications and intensities on wildlife viability, panels examined the marginal risk (individual extinction probability) of vulnerable species under each alternative and focused attention on the taxon with the highest projected risk of extinction with implementation of the alternative. This most sensitive species and its probability of extinction was used to reflect the risk to wildlife population viability for all vertebrates across the planning area for the alternative under consideration (Shaw 1999). This approach has been challenged because of untenable assumptions regarding the interpretation and application of select, individual vulnerable species from viability assessments to conservation planning (Soulé 1987, Smith and Zollner 2005, Jenkins et al. 2021).

Number of species influences the probability of any extinction

Smith and Zollner (2005) detailed an approach to assessing wildlife viability that explicitly considers the risk of any extinction among vulnerable vertebrate species in the planning area, calculated as the "likelihood of at least one success" (Snedecor and Cochran 1980: 115). Thus, the assessed probability of extinction following implementation of an alternative is the joint probability of marginal probabilities, each of which represents the risk to viability of individual species (Smith and Zollner 2005). They created a scenario with multiple hypothetical species at risk using each's corresponding independent marginal probabilities (acknowledging distinctive rather than correlated responses) for each of several management alternatives, similar to procedures used in planning TLMP (Shaw 1999). Smith and Zollner (2005) used this scenario to illustrate how the probability of any extinctions and the probability of the single most likely extinction differ as a function of the number of species examined. Recall, one panel assessed viability risks of a group of 26 terrestrial mammals (Shaw 1999) that included 14 endemic small mammal taxa and 12 additional terrestrial mammal taxa (USFS 2008: appendix D68). Moreover, endemic mammals were the most vulnerable of all wildlife species to future landscape disturbances assessed by the panel (Swanston et al. 1996: 11).

When marginal probabilities are used to calculate the joint probability of any extinction under each management alternative, the risk to wildlife viability is consistently and markedly higher than that obtained from selecting the most vulnerable species at risk (Figure 3). This occurs because the risk of local extirpation increases with the number of extinction-prone species in a region (Smith and Zollner 2005). Furthermore, the 1982 NFMA planning rule to ensure wildlife viability explicitly charges managers with the responsibility of protecting all vertebrates in a planning area, not just selecting species that appear to be the most vulnerable (Shaw 1999, Smith and Zollner 2005). Forest plan alternatives that pose the highest risk to more vulnerable species might not necessarily represent the greatest threat to wildlife communities, in part because of the variety of unique assemblages and their interspecific relationships and dependencies (Conroy et al. 1999, Smith 2012*a*, Smith and Fox 2017, Kelt et al. 2019, Jenkins et al. 2021) but also because of the varying number of sensitive species that occur among southeast Alaska's unique fragmented communities (Conroy et al. 1999, Smith 2012*a*, Colella et al. 2021).

Tongass planners in 2008 did acknowledge the influence of the number of species at risk on the probability of any extinction and compared 1997 assessment panel results among management alternatives with corresponding joint probability estimates and among proposed forest plan alternatives (USFS 2008: D85–86).

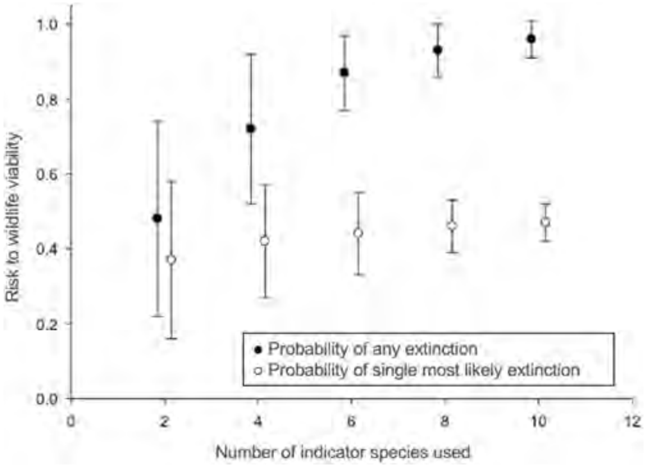

FIGURE 3 Disparity in risk to wildlife viability between estimating the probability of the most likely extinction (extinction of most sensitive species) and the probability of any extinction when assessing the relative risk that implementation of alternative approaches to management of national forest would impose upon continued persistence of indigenous wildlife across the landscape. Figure reprinted with permission from Smith and Zollner (2005).

Still, it remains unclear whether the joint probability calculations used the mean marginal probability of each wildlife assessment panel ($n = 7$) or included the marginal probabilities of each of the 14 individual endemic small-mammal taxa and 12 other terrestrial mammals. The latter seems unlikely because marginal probabilities were not assessed for each of the 26 terrestrial mammals (Shaw 1999). More importantly, the acknowledged higher extinction risks did not appear to raise concerns sufficient to generate discussion about acceptable threshold values of viability risks relative to policy or implementing future management actions or conservation measures (USFS 2008).

Implicit in the Tongass approach is an assumption that similar species are perfectly correlated in how each responds to a management alternative (Shaw 1999). Such an assumption is not ecologically tenable (Szaro 1986, Soulé 1987, Todd and Burgman 1998, Jenkins et al. 2021). Vertebrate faunas comprise diverse ecological assemblages of organisms that include herbivores, granivores, insectivores, carnivores, and omnivores, which often use the environment at different scales and in different ways (Wiens et al. 1993, Lancaster 1996, Kelt et al. 2019). Species in wildlife communities, even those with seemingly similar habitat affinities and life histories, do not respond to disturbance uniformly within habitat patches (Szaro 1986, Laurance 1991, Niemi et al. 1997) or across broader spatial scales (McGarigal and McComb 1995). Consider also the nature of forces that influence wildlife populations; anthropogenic disturbances are additive and extraneous to ecosystems (Püttker et al. 2020). Because wildlife communities evolved under unique environmental circumstances, local populations respond differently to anthropogenic disturbances compared with natural regimes (Wilson et al. 2005). Individual species likely respond differently to the same anthropogenic disturbance (Szaro 1986, Wiens et al. 1993, McGarigal and McComb 1995, Niemi et al. 1997). Within the same community, species of management concern can require strikingly different disturbance regimes and consequently respond divergently to the same management prescription (Smith 2013). Thus, it is unrealistic to expect that a select set of vulnerable species can represent the risk to viability of the entire vertebrate fauna across numerous unique, diverse communities with varying life histories and sensitivities to anthropogenic disturbance and spatial context (Wiens 1989, 1996).

Managing a large-scale island archipelago (objective 2)

Issues of ecological scale are a major concern in wildlife conservation, and many ecological patterns and processes are scale-dependent (Wiens 1989). Perceptions of how populations are spatially subdivided and impressions of extinction and dispersal dynamics depend on the scale at which the population is viewed (Wiens 1996). Conservation of biological diversity also requires maintaining evolutionary diversity (genetic and life-history attributes) of organisms indigenous to a region (Cook and MacDonald 2001, Colella et al. 2021), including the composition, structure, and functions of local ecological communities (Smith 2005, Watson et al. 2018, Grantham et al. 2020). Land management planning for the Tongass National Forest, however, has occurred at the scale of millions of hectares (USFS 1997, 2008, 2016), which is a much broader scale than the contiguous landscapes available to fragmented wildlife populations and ecological communities across an island archipelago and isolated mainland (MacDonald and Cook 1996, Conroy et al. 1999, Cook et al. 2001). Cook et al. (2001) listed 24 endemic mammals, several of which occur only on one or a few islands (MacDonald and Cook 1996, Smith 2005, Cook et al. 2006, Colella et al. 2021). The entire known distribution of the Suemez Island ermine, a small carnivore, is <160 km^2 (MacDonald and Cook 1996). Moreover, several species encompass multiple, genetically distinct lineages (some representing incipient or new species) attributable to independent colonization histories from divergent source populations (Cook et al. 2006). The insular landscapes of the Alexander Archipelago have produced highly endemic populations that should be prudently managed as hotspots of biological and evolutionary diversity. Thus, islands available for timber harvest should each initially be considered an independent biological unit (Cook et al. 2006).

Consequences of management at inappropriate ecological scales among island communities

The Wrangell Island vole is a habitat specialist that achieves its highest densities in old-growth forests (Figure 4A) and is unable to sustain breeding populations in peatland scrub (mixed-conifer) forest (Figure 4B), clearcuts (Figure 4C), or second growth (Figure 4D,E; Smith and Nichols 2004, Smith et al. 2005*a*, Smith and Fox 2017). This red-backed vole is known only from Wrangell and Etolin islands (MacDonald and Cook 1996, Runck 2001). Wrangell Island is 544 km^2 (54,400 ha) and 85% of the island is in Tongass National Forest, of which 72% is available for timber harvest. Approximately 2,700 ha of old-growth forest has been clearcut logged, with a proposed timber project to harvest an additional 16,600 ha (USFS 2019). Moreover, there are no explicit conservation directions or actions to protect this vulnerable island endemic from local extirpations (USFS 1997: 4–87).

On Wrangell Island, voles are sympatric with the Keen's mouse (*Peromyscus keeni macrorhinus*), a habitat generalist that flourishes in old-growth, managed, and scrub forests (Smith and Fox 2017). Keen's mouse can be an intense competitor of voles, with interspecific competition between the 2 species explaining more variation in vole abundance (and vice versa) among habitats than the variance associated within habitats (Smith and Fox 2017). Thus, clearcut logging of old-growth forests on Wrangell Island favors populations of the Keen's mouse by creating habitats that breeding vole populations cannot exploit and further reducing vole abundance across managed landscapes because of increased interspecific competition from increasing mice populations (Smith and Fox 2017). Furthermore, opportunities for voles to reoccupy managed landscapes are limited because broad-scale disturbance can take ≥300 years for ecological succession to achieve old-growth forest conditions (Nowacki and Kramer 1998).

Thus, when forest management is applied indiscriminately across archipeleagos (*defacto* contiguous landscapes), it is implemented at inappropriate ecological scales and thus insensitive to the variation and uniqueness of species composition, phylogeography, life-history attributes, and interspecific relationships among island communities (Cook et al. 2006). The consequences of disproportional habitat loss and fragmentation typical of island endemics results in isolation, local extirpation, and overall reduction of endemic populations, increasing risk of extinction (Burkey 1995, Frankham 1998, Crooks et al. 2017, Püttker et al. 2020, Vynne et al. 2021).

Effectiveness of old-growth reserve system (objective 3)

The WCS has 2 components, each representing sharply contrasting management and landscape conditions. The first is a forest-wide, old-growth reserve network (Figure 1; USFS 1997) in which the reserves and other protected lands are expected to provide sufficient habitat to sustain viable, well-distributed populations of old-growth-obligate wildlife (Iverson and Renè 1997, Smith and Person 2007). This network was intended to serve as a coarse filter to maintain a functional and interconnected old-growth ecosystem (USFS 2008: D6). Coarse filters use the compositional integrity and functional proficiency of landscapes or ecosystems as surrogates to predict or ensure the wellbeing of particular taxa or ecological communities (Jenkins et al. 2021). A second function of the old-growth reserve system is to facilitate functional connectivity of protected lands, which also contributes old-growth structural elements in the development land-use designations of the Tongass planning area within which timber harvest and other anthropogenic disturbances occur over time.

The old-growth reserve network included all non-development lands and a system of large, medium, and small habitat conservation areas (reserves). Islands <400 ha were included and received protection from additional logging (USFS 1997, 2016). Each major watershed is required to have at least a small reserve encompassing ≥16% of its area. The preferred biological objective of a small reserve is to contain ≥50% POG; the minimum prescription is ≥25% POG. Medium reserves were delineated as contiguous landscapes of ≥4000 ha with ≥2000 ha of POG, of which ≥50% must be in the highest volume category. Large reserves must be ≥16,000 ha of contiguous landscape, with ≥50% POG and ≥25% in the highest volume category (USFS 1997: appendix K).

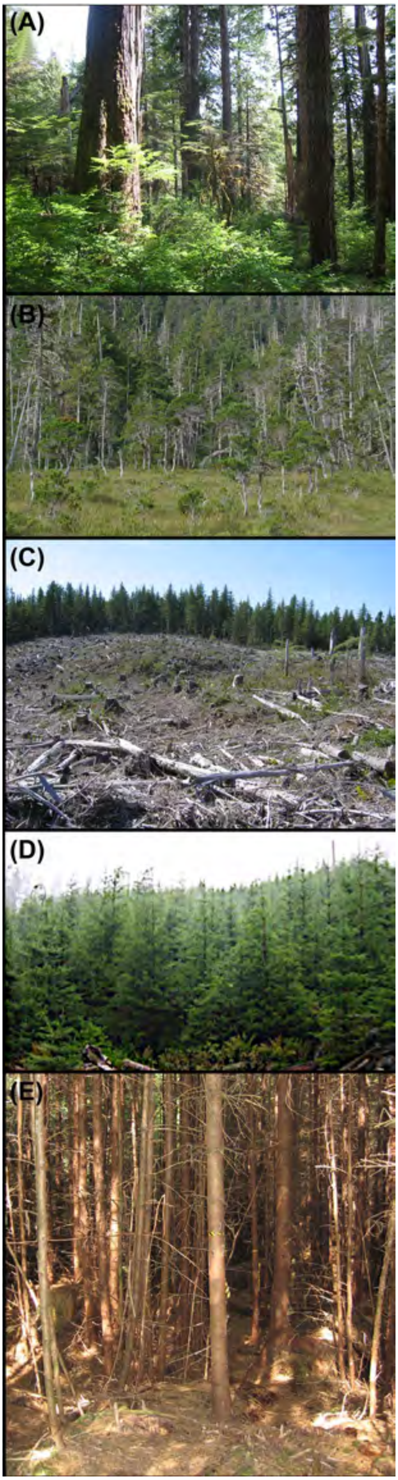

FIGURE 4 Common management stages and corresponding vegetation structure available to endemic small mammals in managed landscapes of the Tongass National Forest, southeast Alaska, USA: A) old-growth forest, B) peatland scrub forest, C) clearcut, D) young (<20 yr) second growth, and E) unthinned older (>40 yr) second growth.

The second WCS component includes active management of the matrix (commercial clearcut logging). Land managed for timber production was expected to contribute little toward maintaining biological diversity (USFS 1997: appendix N). Within the matrix, forest-wide standards and guidelines were implemented to uphold remaining components of the old-growth ecosystem. A standard is a course of action or level of achievement that must be accomplished to achieve forest goals and are mandatory. A guideline is also a course of action that must be followed, but guidelines relate to activities in which site-specific factors might require flexibility and require further analysis. Therefore, forest-wide standards and guidelines serve as fine filters to protect specific resources (e.g., old-growth forests) and functions (e.g., streamside buffers), facilitate connectivity across old-growth forests, and to ensure sufficient habitat for individual sensitive species (USFS 1997: chapter 4). Thus, for wildlife populations to persist in heterogeneous landscapes, either individual habitat patches must be large enough to provide for viable populations in isolation (Smith and Person 2007, Crooks et al. 2017) or the juxtaposition of suitable habitat within the matrix must allow for interpatch movements that facilitate meta-population dynamics (Smith 2012*b*, Fahrig et al. 2021).

Habitat conservation areas

The northern flying squirrel (*Glaucomys sabrinus*) was selected as the design (proxy) species for small old-growth reserves (≥650 ha) in the 1997 TLMP (USFS 1997) because of its assumed dependency on POG. Northern flying squirrels are k-selected, omnivorous, mature-forest obligates (Smith et al. 2004, 2005*b*; Smith 2007, 2012*b*; Holloway and Smith 2011) with specialized gliding locomotion (Scheibe et al. 2006). The underlying premise was that if the Tongass conservation strategy maintained viable and widely distributed populations of flying squirrels across the planning area, it would support other small mammals with similar life histories and habitat needs (Swanston et al. 1996, USFS 1997). Northern flying squirrels inhabit forests along southeast Alaska's mainland coast and occur on ≥15 islands of the Alexander Archipelagos (MacDonald and Cook 1996, Smith 2005, Schoen et al. 2006). The Prince of Wales Island flying squirrel (*G. s. griseifrons*) is an island endemic with reduced genetic variation (Bidlack and Cook 2001) that is considered a subspecies of ecological concern in the Tongass National Forest (Schoen et al. 2006) and is listed by the International Union for the Conservation of Nature as potentially endangered (Hafner et al. 1998).

Small old-growth reserves were expected to function as habitat conservation areas that provide sufficient habitat to facilitate occupancy by flying squirrels, and functionally connected populations interspersed throughout the matrix would behave as a metapopulation (Fahrig and Merriam 1985, Fahrig et al. 2021). Although there was no design requirement to ensure physical connectivity among old-growth reserves or with other non-development land-use designations, the assumption was that POG retained through other features of the conservation strategy (larger old-growth reserves, standards and guidelines) will establish landscape connectivity to facilitate dispersal across the matrix (USFS 2008: D8).

Persistence in habitat conservation areas

Smith and Person (2007) examined whether flying squirrels are likely to persist in isolation over a range of time periods in small habitat conservation areas with varying compositions of old-growth spruce-hemlock and mixed-conifer forests (Figure 4A) consistent with forest plan guidelines for both preferred and minimum habitat objectives (USFS 1997: appendix K). Given these guidelines, Smith and Person (2007) models revealed that the probability of persistence over a planning horizon of 100 years in small habitat conservation areas with the preferred prescription (50%) of spruce-hemlock composition was 0.73–0.77 and for the minimum prescription (25%), probabilities were 0.66–0.71. Furthermore, to sustain isolated populations over long periods (100 yr) with a high level (≥0.95) of confidence, flying squirrels require very large (244,600 ha) reserves of 100% optimum habitat. Medium (2000 ha POG) and large reserves (8000 ha POG) as currently specified (USFS 1997: appendix K) have a <0.90 probability of sustaining viable populations of flying squirrels over the 100-year planning horizon (Smith and Person 2007). These persistence estimates have been evaluated in the field. For example, on Kosciusko Island, flying squirrels were apparently extirpated from a 50-ha remnant patch of old-growth forest surrounded by <50-year-old second growth (E. A. Flaherty, Purdue University, unpublished data), and Shanley et al. (2013) observed that flying squirrels were not found in patches <29 ha and only selected the largest fragments locally and at the landscape scale with the minimum patch size for occupancy of 48 ha. Both suggest that likelihood of persistence is low in these small, isolated patches.

Functional connectivity and dispersal in managed landscapes

Given this uncertainty, Smith et al. (2011) evaluated the efficacy of small reserves as a functionally connected network that provided temporary suitable habitat for flying squirrels dispersing among large and medium reserves. They estimated the number of immigrants required to persist in small reserves for 25 and 100 years, landscape resistance to movement, and maximum effective dispersal distance via least-cost path analysis among small and larger reserves to ensure the required number of immigrants (Pyare and Smith 2005). Landscape resistance and risk of predation were higher in clearcuts (Figure 4C) than mature forests (Smith 2012*b*). Similarly, unthinned second growth (Figure 4E) obstructed visibility of suitable habitat (perceptual range) and impeded gliding (Flaherty et al. 2008, Smith 2012*b*). These dispersal barriers are a significant concern when an estimated 162 dispersers/year are needed to sustain populations for 100 years in small reserves comprising 25% primary habitat and ≥6 juvenile dispersers/year are needed to achieve a 0.95 probability that a breeding pair would reach a patch in which flying squirrels were recently extirpated (Smith et al. 2011).

Considerations of dispersal distance across managed matrix habitat is also important for maintaining persistence of flying squirrels. The maximum effective dispersal distance (Pyare and Smith 2005) for a 0.95 probability persistence over 100 years ranged from 844 m for small old-growth reserves with 25% primary habitat to 1,151 m for small old-growth reserves that comprise 100% primary habitat. Corresponding values for persistence in small old-growth reserves over 25 years were 1,172 m and 1,174 m (Smith et al. 2011). Remarkably, the maximum value of 1,174 m fell well within the distance that juveniles can move through intact landscapes (~7 km) over short time periods (Smith 2012*b*). Unfortunately, most of northern Prince of Wales Island has been clearcut logged (Figure 5), and ≥50% of small old-growth reserves prescribed in the 1997 TLMP for northern Prince of Wales (Figure 5) were isolated and not functionally connected to a source population (Smith et al. 2011).

These results underscore the vital role of immigration in rescuing sinks or facilitating metapopulation viability of northern flying squirrels among unsustainable fragmented populations, and the extent to which permeability of landscape elements can influence dispersal and functional connectivity of subpopulations in a managed matrix (With and Crist 1995, Richards et al. 2002, Pyare and Smith 2005, Smith et al. 2011, Trapp et al. 2019). The expectation that the Prince of Wales Island flying squirrel will function as a metapopulation with successful dispersal among old-growth fragments or reserves in managed landscapes is not supported by the findings of multiple studies examining this island endemic's habitat relations, population dynamics, and dispersal capability, including perceptual limitations, locomotion, energetics, and diet (Smith 2012*b*). Without large trees to facilitate gliding (Vernes 2001), flying squirrels must use quadrupedal (walking or running) locomotion, which is energetically more expensive than gliding (Scheibe et al. 2006, Flaherty et al. 2010*a*) and increases travel time (Byrnes and Spence 2011), leading to increased risk of predation (Smith 2012*b*). Additionally, flying squirrels cannot replenish energy stores by foraging as they disperse across clearcuts and second-growth stands because of the absence of preferred food resources (Flaherty et al. 2010*b*, Price et al. 2017). Finally, flying squirrels are unable to perceive old-growth forests across managed stands and are therefore unlikely to initiate movements across these more energetically expensive and risky land cover types (Flaherty et al. 2008).

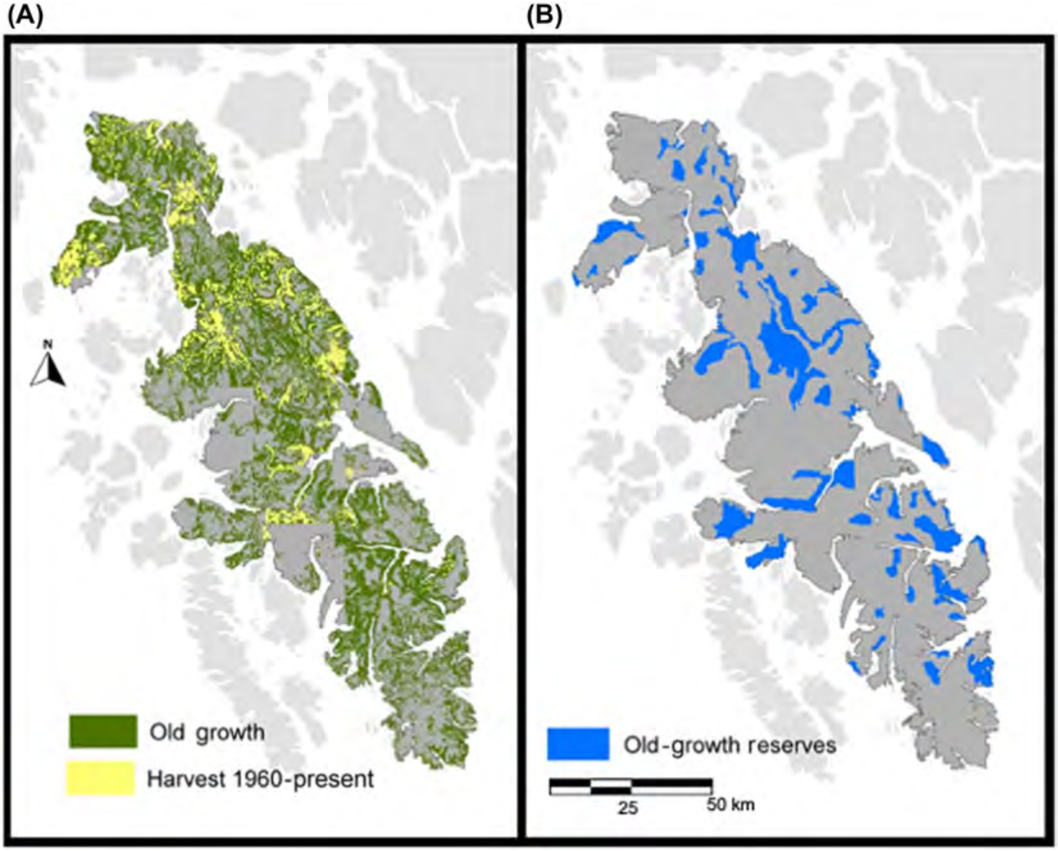

FIGURE 5 Prince of Wales Island, Alaska, USA, depicting the distribution of A) old-growth rainforest and areas logged since 1960 and B) old-growth reserves (USFS 1997).

Forest-wide standards and guidelines (objective 4)

The second component of the WCS uses forest-wide standards and guidelines, which are implemented for the protection or management of different forest resources (USFS 1997: chapter 4). Standards and guidelines apply to all or most areas of the Tongass, are organized by resource conservation status, and are used in conjunction with additional standards and guidelines included within each management prescription (USFS 1997: chapter 3). Standards and guidelines were established to manage locally important habitat for native wildlife (USFS 1997: chapter 4) and sensitive species (USFS 1997: 4–87), especially those that were not explicitly considered by viability assessment panels (Shaw 1999) or selected as ecological proxies in the design of the old-growth reserve network (Iverson and Renè 1997, USFS 1997, Smith 2013).

The northern goshawk was designated a sensitive species and underwent viability risk assessment (Shaw 1999). Goshawks received special consideration on the Tongass largely because of concerns over populations of the endemic Queen Charlotte goshawk (Iverson et al. 1996). Formally described as a metapopulation (Sonsthagen et al. 2012), the Queen Charlotte goshawk's distribution includes Prince of Wales and barrier islands and coastal British Columbia and nearby islands. The United States Fish and Wildlife Service listed all areas with known nests, except Prince of Wales Island, as threatened subpopulations in 2012 (U.S. Fish and Wildlife Service 2012), although all subpopulations are deemed essential for long-term viability (Sonsthagen et al. 2012) and ≥33% of POG on Prince of Wales Island has been converted to second growth (USFS 2008: appendix E; Albert and Schoen 2012). The most imminent threats to breeding populations are loss or fragmentation of nesting or foraging habitat from logging (Figure 2B) without ensuing intermediate stand management (Figure 4E), which eliminates nest trees and reduces prey diversity and availability (Reynolds et al. 1992, Finn et al. 2002, McGrath et al. 2003, Mahon and Doyle 2005, Northern Goshawk *Accipiter gentilis laingi* Recovery Team 2008).

In western North America, breeding home ranges of northern goshawks are spatially configured as a hierarchical sequence of 3 areas (Andersen et al. 2005), all of which need to be considered simultaneously in land use planning (Reynolds et al. 2006, Northern Goshawk *Accipiter gentilis laingi* Recovery Team 2008): nest area, post-fledging area, and foraging area. Nest areas provide alternate nest trees, roost trees, and prey plucking posts, and serve as centers of essential breeding behaviors or life-history events (Reynolds et al. 1992, 1994, 2006). Post-fledging areas surround active nest trees, average 800 ha in southeast Alaska (Iverson et al. 1996), and represent the core-use area of adult female and young goshawks after fledging but before becoming independent of adults and dispersing (Kenward 1982, Kenward et al. 1993, Kennedy et al. 1994). McClaren et al. (2005) suggested the biological role of post-fledging areas and nest areas are similar and to consider them as one functional component. Regardless, the habitat composition of post-fledging areas should be similar to nest areas (Reynolds et al. 2008). Foraging areas comprise the majority of northern goshawk breeding home ranges and are especially important for adults providing food to young and for juveniles prior to natal dispersal. Breeding home ranges in southeast Alaska average 21 km^2 (Iverson et al. 1996). The combined home range of breeding pairs can be much larger than that of individual birds (Boal et al. 2003).

The 1997 TLMP did not incorporate concepts of nest area, post-fledging area, and foraging area habitat management, which underpin conservation planning to sustain viable populations of northern goshawks across its distribution (Reynolds et al. 2006, Northern Goshawk *Accipiter gentilis laingi* Recovery Team 2008). Still, Tongass forest-wide policy is focused on protecting confirmed and probable goshawk nests (USFS 1997: chapter 4); standards and guidelines propose to accomplish this by maintaining an area of ≥40 ha of POG generally centered over the nest tree or probable nest site (Figure 6). Another stated objective is to manage foraging habitat to retain essential features of forest stand structure in areas of timber harvest (Figure 2B) because tree density of unmanaged second growth (Figure 4E) reduces prey abundance and diversity and prevents aerial pursuit of prey by goshawks (Reynolds 1983, Salafsky et al. 2007).

Despite a substantial increase in knowledge since the 1997 TLMP revision, the implications of those new insights to goshawk conservation and land-use policies in southeast Alaska had not been revised in forest plan amendments (Smith 2013). Without long-term monitoring, it has remained unclear whether a network of reserves designed explicitly for other wildlife species (USFS 1997) or protection of goshawk nest trees in landscapes intensively managed for timber, would provide sufficient habitat to sustain breeding populations of the northern goshawk across the planning area (Finn et al. 2002). What is clear from the literature is neither coarse-filter nor fine-filter components of the WCS appear relevant to northern goshawk life history or conservation planning; 40-ha nest buffers (Figure 6) and habitat conservation areas distributed across expansive landscapes of even-aged second growth have never been applied as mitigating measures elsewhere in its distribution (Smith 2013).

Smith (2013) conducted a spatially explicit analysis of contributions of the Tongass WCS to the breeding home ranges of northern goshawks across southeast Alaska. He used 136 confirmed nest-tree locations and empirically derived estimates (Iverson et al. 1996) to delineate corresponding virtual post-fledging areas and female breeding home ranges, within which they calculated the area of 4 cover types and 4 land-use categories. They derived preferred habitat from empirical studies in southeast Alaska (Iverson et al. 1996). About 30% of nests had >51% of post-fledging areas in preferred habitat but >91% of post-fledging area was in an unsecure (unprotected from development) land-use designation; 60% of post-fledging areas had >51% in an unsecure designation, whereas only 16% had >51% in the protected old-growth forest. Among cover types, preferred habitat comprised an average of 39.4% of the post-fledging area. Smith (2013) obtained similar results from an analysis of the female breeding home range but with notable differences. The percentage of the broader landscape that consisted predominantly (>75%) of lands available for development was greater than in post-fledging areas (Smith 2013). The percentage of the total

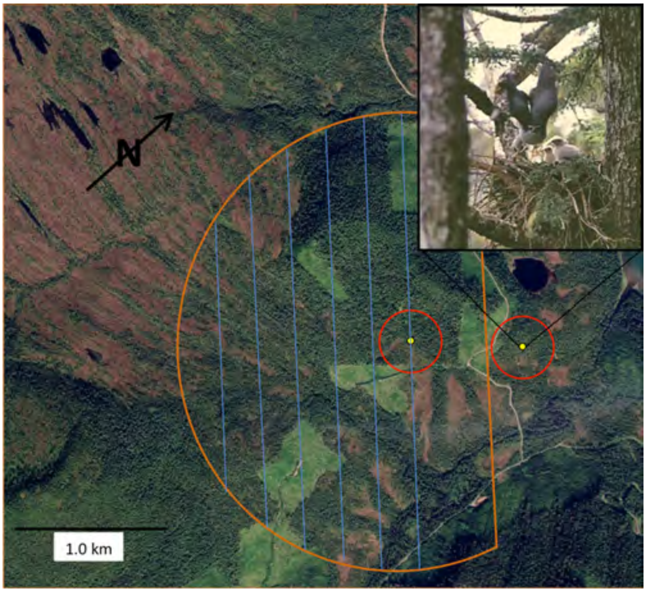

FIGURE 6 Northern goshawk nest sites (yellow spheres) during 1999 to 2001 in managed landscapes of the Tongass National Forest in southeast Alaska, USA (image courtesy of Google Earth), with an active nest (photo by Craig Flatten) in the canopy of old-growth rainforest. Red circles represent circular 40-ha old-growth buffers (360-m radius) prescribed for active goshawk nests by forest-wide standards and guidelines in the Tongass Land Management Plan (USFS 1997, 2008, 2016). Area with blue lines within the orange semi-circle depicts half the typical goshawk post-fledging area (PFA); the mean radius of goshawk PFAs is 1,600 m, whereas the radius of breeding female home ranges averages 2,600 m (Smith 2013). Light green areas along logging roads are recent clearcuts; light brown areas are muskegs.

home range with 26–50% of the total area in preferred habitat also increased compared with post-fledging areas, whereas about half as many home ranges had ≥51% of this broader landscape in preferred habitat as compared with the post-fledging area (Smith 2013). From these analyses, it is clear that the Tongass WCS is not contributing sufficient secure habitat to sustain breeding pairs of the northern goshawk across southeast Alaska.

RESULTS

Based on this review, we conclude that the Tongass Land Management Plan is not meeting expectations of ≥4 essential assumptions of the WCS. Additional empirical evidence from the literature supports a conclusion that the WCS has not met expectations of maintaining an interconnected old-growth forest ecosystem. Extensive high-grading and disproportional harvest of the most productive forest have substantially reduced old-growth forest abundance and diversity (Albert and Schoen 2012). Expansive even-aged clearcuts produced landscapes that support a fraction of the old-growth obligate species and provide little functional connectivity, isolating wildlife communities in many of the remnant old-growth patches (Smith et al. 2011).

The Tongass WCS was implemented as an experimental conservation plan composed of numerous elements, some of which are founded in sound ecological science and theory and were successfully implemented elsewhere with different wildlife species and circumstances. A systematic, comprehensive long-term monitoring scheme was proposed as a means to document implementation of management actions and conservation measures, and to record responses and outcomes of select forest resources (i.e., to evaluate if the WCS was functioning according to expectations). In the absence of monitoring data, we chose to use the results of wildlife studies on the Tongass that were designed to examine the robustness of vital underlying assumptions.

The enormity and complexity of the Tongass present unprecedented management and conservation challenges, most notably the highly fragmented and isolated nature of southeast Alaska. Empirical evidence from the literature provides examples of isolated ecological communities, varying in composition, ecological roles, and relationships among members, and the potentially irreversible consequences of cumulative broad-scale anthropogenic disturbances on old-growth obligate species, many of which are endemic. The Wrangell Island vole and Prince of Wales Island flying squirrel are examples of endemics for which a substantial part of their historical distribution has been clearcut logged, local populations have become extirpated or isolated, and total populations are reduced, all of which influence persistence. Given the proclivity for endemism, the discontinuity of landscapes further stratified among 21 biogeographic provinces, and the diversity of unique plant and animal assemblages with varied ecological functions and dependencies, it is unrealistic to expect that the Tongass can be managed as a single rainforest ecosystem or according to a conservation strategy that relies on isolated old-growth forest remnants scattered across vast landscapes of unmanaged, even-aged second growth (coarse filter) and uninformed, ineffective fine-filter mitigation measures.

The conceptual framework and procedures used by planners to assess the risk to viability of native wildlife underestimated the effects of implementing each of 10 forest plan alternatives across the planning area. Consequently, when forest management planning and implementation are considered in the context of widespread fragmentation, isolation and endemism, ecological scale, variation and complexity of ecological communities, and an incomplete monitoring plan with substantial gaps in data and analyses, serious questions arise about the effectiveness of the WCS in maintaining widely distributed, viable populations of native wildlife, especially old-growth obligate endemics.

A network of old-growth reserves functioning as habitat conservation areas across intensively managed landscapes can be effective in sustaining viable populations of sensitive, old-growth obligate species. Establishing small, medium, and large habitat conservation areas, each designed to sustain proxy species operating at appropriate ecological scales and collectively establishing functionally connected landscapes, is an empirically based coarse-filter approach. Nonetheless, demographic analysis revealed that the size of a habitat conservation area (with 100% POG) required to sustain viable northern flying squirrel populations in isolation over the planning horizon exceeds the size of medium and large old-growth reserves, the preferred prescriptions of which contain only 50% POG. Further analysis demonstrated that landscapes within the matrix were not functionally connected and incapable of facilitating demographic or genetic rescue among small-mammal endemics. Despite having comparably high densities, the viability risk of the Prince of Wales Island flying squirrel is higher today because subpopulations have become isolated, local extirpations have occurred, and the overall population is reduced. Furthermore, because the northern flying squirrel was selected as a proxy, the effects of cumulative habitat loss and functionally discontinuous landscapes have implications for other old-growth obligate small mammals, especially island endemics.

The WCS also includes forest-wide standards and guidelines as a fine-filter approach to retain, replace, or mitigate essential conditions, mostly in managed landscapes. Forest-wide standards and guidelines are essential for sensitive species such as the Queen Charlotte goshawk that require a diversity of land cover types, including mature or old-growth forest. Forest management guidelines throughout its distribution invariably prescribe rotational management of the entire planning area, which produces landscapes that are a mosaic of cover types varying in stand age, structure, and spatial extent, thereby supporting a wide range of potential avian and mammalian prey species. Landscapes across the Tongass are a sharply contrasting dichotomy of old growth and expanses of even-aged second growth, most of which were logged during a few decades with little (<20%) ensuing intermediate stand management. Unfortunately, neither the reserve network nor the prescribed standards and guidelines accomplish the objective of providing sufficient breeding habitat to sustain northern goshawks across the Tongass.

DISCUSSION

To address apparent deficiencies and meet expectations of the 1982 viability rule of the 1976 National Forest Management Act, we propose 3 revisions to forest management and conservation policies. First, further commercial harvests of old-growth forests should emulate the primary natural disturbance regime (wind) in size of canopy gaps, frequency of occurrence, and landscape conditions (e.g., forest stand composition and exposure, canopy structure) and circumstances (e.g., slope, aspect, wind severity and direction; Nowacki and Kramer 1998), which will prohibit commercial broad-scale clearcut logging. This policy will reduce further negative effects to old-growth obligate wildlife, especially island endemics (Cook et al. 2006, Smith and Person 2007, Smith et al. 2011, Smith and Fox 2017), and acknowledge the contribution of southeast Alaska's rainforest in mitigating climate change (DellaSala et al. 2022). Second, restoration of forests throughout the matrix through intermediate stand management of second growth should become a forest management priority, especially on Prince of Wales Island and other islands that support island endemics whose native distributions have been substantially reduced by clearcut logging. Priority should be given to landscapes in which old-growth forests are isolated and to second-growth forests along anadromous streams.

Intermediate stand management will reduce midstory density and expedite ecological succession toward achieving mature forest conditions (Nowacki and Kramer 1998) that will benefit the federally listed Queen Charlotte goshawk (Smith 2013) and increase functional connectivity of managed landscapes for endemic small mammals (Flaherty et al. 2008, 2010*a*, *b*; Smith et al. 2011; Howard 2022). Healthy anadromous streams support salmon populations that provide vital marine nutrients required for forest regeneration and development (Quinn et al. 2018, Schoen 2020). Restoration of riparian forests will directly contribute to the health and diversity of the old-growth forest ecosystem (Schoen 2020).

Thirdly, we recommend the Tongass National Forest undertake a formal review of WCS elements that appear incapable of achieving mandated or desirable expectations because of extensive historical timber harvests, misimplementation of proposed or established policies, or untenable assumptions. The review will require an updated assessment of forest resources to accurately inventory and map habitats (Shanley et al. 2021), and extensive research to document the diversity and life-history needs of southeast Alaska's unique ecological communities (Cook et al. 2006), with an initial focus on populations and habitat of the Queen Charlotte goshawk and island endemic mammals that have experienced substantial broad-scale disturbance (Smith et al. 2011, Smith 2013). Conservation measures need to consider the unique life-history attributes of sensitive species. Recognizing the hierarchical structure of goshawk breeding home ranges is fundamental to designing and implementing an effective conservation plan.

MANAGEMENT IMPLICATIONS

Future conservation and management policies and actions will require consideration of recent research findings (especially from the Tongass) and a comprehensive long-term monitoring plan to evaluate implementations and corresponding responses and outcomes. Clearly, an adaptive management approach that explicitly acknowledges and considers the uniqueness of southeast Alaska's varied landscapes and spatial context, geological history, fauna, and ecological communities will provide insights into the complexities and limitations of imposing established forest management policies and actions. A new paradigm that employs new knowledge with systematically scheduled assessments from monitoring programs will provide timely, meaningful evaluations of the consequences of management actions that can remedy existing deficiencies and improve WCS effectiveness.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

The work summarized in this manuscript did not analyze new data collected from studies of wildlife or humans.

DATA AVAILABILITY STATEMENT

Data sharing not applicable because we did not generate new data. All data referenced in this review are included in published articles cited in the manuscript.

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The Importance of Alaska for Climate Stabilization, Resilience, and Biodiversity Conservation

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Alaska is globally significant for its large tracts of intact habitats, which support complete wildlife assemblages and many of the world's healthiest wild fisheries, while also storing significant amounts of carbon. Alaska has 1/3 of United States federal lands, the bulk of the United States' intact and wild lands, and over half of the country's total terrestrial ecosystem carbon on federal lands. Managing Alaska's public lands for climate and biodiversity conservation purposes over the next 30–50 years would provide meaningful and irreplaceable climate benefits for the United States and globe. Doing so *via* a co-management approach with Alaska's 229 federally recognized tribes is likely not only to be more effective but also more socially just. This paper lays out the scientific case for managing Alaska's public lands for climate stabilization and resilience and addresses three primary questions: Why is Alaska globally meaningful for biodiversity and climate stabilization? Why should Alaska be considered as a key element of a climate stabilization and biodiversity conservation strategy for the United States? What do we need to know to better understand the role of Alaska given future scenarios? We summarize evidence for the role Alaska's lands play in climate stabilization, as well as what is known about the role of land management in influencing carbon storage and sequestration. Finally, we summarize priority research that is needed to improve understanding of how policy and management prescriptions are likely to influence the role Alaska plays in global climate stabilization and adaptation.

Keywords: Alaska, climate change mitigation, adaptation, biodiversity, carbon storage

INTRODUCTION

Alaska is globally significant for its large tracts of intact habitats and their role in conserving biodiversity and storing carbon while supporting traditional and cultural uses (Kofinas et al., 2010; Reynolds et al., 2018; Dinerstein et al., 2020). Alaska holds one third of United States federal lands, the bulk of the United States' intact and wild lands, and 62 percent of the country's terrestrial ecosystem carbon stocks on federal lands (Merrill et al., 2018). The Alaska Native Claims Settlement Act of 1971 (ANCSA) established twelve (later thirteen) Alaska Native regional corporations and over 200 local village corporations, representing a total of 44 million acres (17,806 km^2) of land (**Figure 1**). Alaska is home to 229 federally recognized tribes and it is the United States state with the highest proportion of American Indian and Alaska Native people[1]. Alaska has >30% of the United States coastline[2] and 63% of the nation's wetlands (Hall et al., 1994). Most of Alaska far exceeds landscape condition values of even the most protected places in the contiguous United States (Reynolds et al., 2018; **Figure 2**). The intactness of Alaska's systems as part of a national climate change mitigation strategy has been underexplored in both science and public policy.

In discussing the role of Alaska's intact systems in fostering biodiversity and storing carbon, it is important to recognize that the region is already experiencing and will continue to experience climatic changes that will influence carbon sequestration and storage capacity across landscapes. While physically Alaska's landscapes are largely undeveloped (**Figure 3**), the region is changing quickly. Presently, climate change is the biggest driver of change for Alaska's ecosystems, species, and people, and this has been well documented (Stone et al., 2002; Chapin et al., 2004; Hinzman et al., 2005; Brubaker et al., 2011). Likewise, cultural and economic climate change impacts across Alaska have been reviewed elsewhere (e.g., Hinzman et al., 2005; Wolken et al., 2011; Cochran et al., 2013; Berman and Schmidt, 2019). With reference to these previous reviews, this analysis focuses on carbon dynamics and ecosystem integrity.

Due to the geographic size and spatial extent of Alaska's landscapes, along with the relative intactness of many of its ecological systems, recent reviews suggest that Alaska could contribute over 50% of total carbon storage for the entire United States (Zhu and McGuire, 2016). Northern permafrost soils contain almost two times the amount of stored carbon as that found within the atmosphere. However, soil carbon concentrations will change with the melting of permafrost (Hugelius et al., 2014; Jones et al., 2017). The decomposition of permafrost carbon could accelerate climate warming through the loss of stored carbon, and methane releases have been widely documented from warming lakes (Jorgenson et al., 2001). The interaction of marine and terrestrial systems across seasonal variations makes predicting changes to total carbon storage challenging (Parmentier et al., 2017). Likewise, as will be discussed, the effects of climate change on the frequency and intensity of wildfires add complexity to issues of carbon balance. Here we focus on the role that Alaska's intact systems and species might play in maintaining biodiversity, storing carbon, and mitigating climate change – even as climate change continues to affect those systems.

Global climate targets have been established in order to prevent the worst effects of climate change, including disruption to weather patterns, extreme heat and flood events, water and food shortages, and loss of biodiversity and essential ecosystem services (IPCC, 2018). Naturally functioning ecosystems are critical for mitigating greenhouse gas emissions and meeting global climate targets *via* both protecting existing carbon stocks and new sequestration (Griscom et al., 2017; Teske, 2019). These natural-climate solutions (NCS) include proforestation (allowing forests to continue to grow), which is the most rapid means to accumulate additional carbon in forests and out of the atmosphere (Law et al., 2018; Moomaw et al., 2019). Other strategies—including conservation and restoration that increase carbon storage and/or reduce greenhouse gas emissions—are increasingly recognized as essential to meeting global climate targets (Griscom et al., 2017; Seddon et al., 2020). Nearly all pathways to staying below 2°C rise in average global temperature require preventing conversion of the vast majority of Earth's remaining, terrestrial habitats (Teske, 2019). Significantly, much of the land essential to achieving carbon storage objectives is also essential for protecting biodiversity (Dinerstein et al., 2019, 2020; Buotte et al., 2020).

Protection of intact and low human-impact forests is one of the most cost-effective ways to mitigate climate change. Globally, forests store 662 Gt C, or 75% of the amount currently in the atmosphere (Food and Agricultural Organization, 2020), and terrestrial ecosystems (primarily forests) annually remove 30% of excess carbon emitted by human activities. A large portion of this carbon is found in the globally important forest and wetland areas of the tropics and boreal region (Bradshaw and Warkentin, 2015). Protection of intact ecosystems from industrial land uses is particularly important since carbon storage values are diminished as natural areas are degraded or converted (Grünzweig et al., 2004; Martin and Watson, 2016).

Though the impacts to Alaska systems from climate change are well established, there has been little focus on the potential contribution of Alaska land and water management to climate stabilization (Zhu and McGuire, 2016). Though Alaska's marine areas are also extremely significant for global biodiversity and carbon budgets, we focus here on terrestrial ecosystems. We synthesize existing literature and provide expert input to answer three primary questions: Why is Alaska globally meaningful (for biodiversity and climate)? Why should Alaska be a key element of a climate stabilization and biodiversity conservation strategy for the United States? What do we need to know to better understand the role Alaska will play in climate stabilization and resilience given projected changes?

THE GLOBAL SIGNIFICANCE OF ALASKA FOR BIODIVERSITY, CLIMATE STABILIZATION, AND RESILIENCE: INTACT HABITATS AND BIODIVERSITY

Alaska is recognized for its naturally functioning ecosystems, undammed rivers, complete wildlife assemblages, and healthy populations of fish and wildlife. Much of this is attributed to its large tracts of intact or undeveloped habitat, which are important for sustaining ecological and evolutionary processes central to

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[1] https://www.bia.gov/regional-offices/alaska

[2] www.coast.noaa.gov

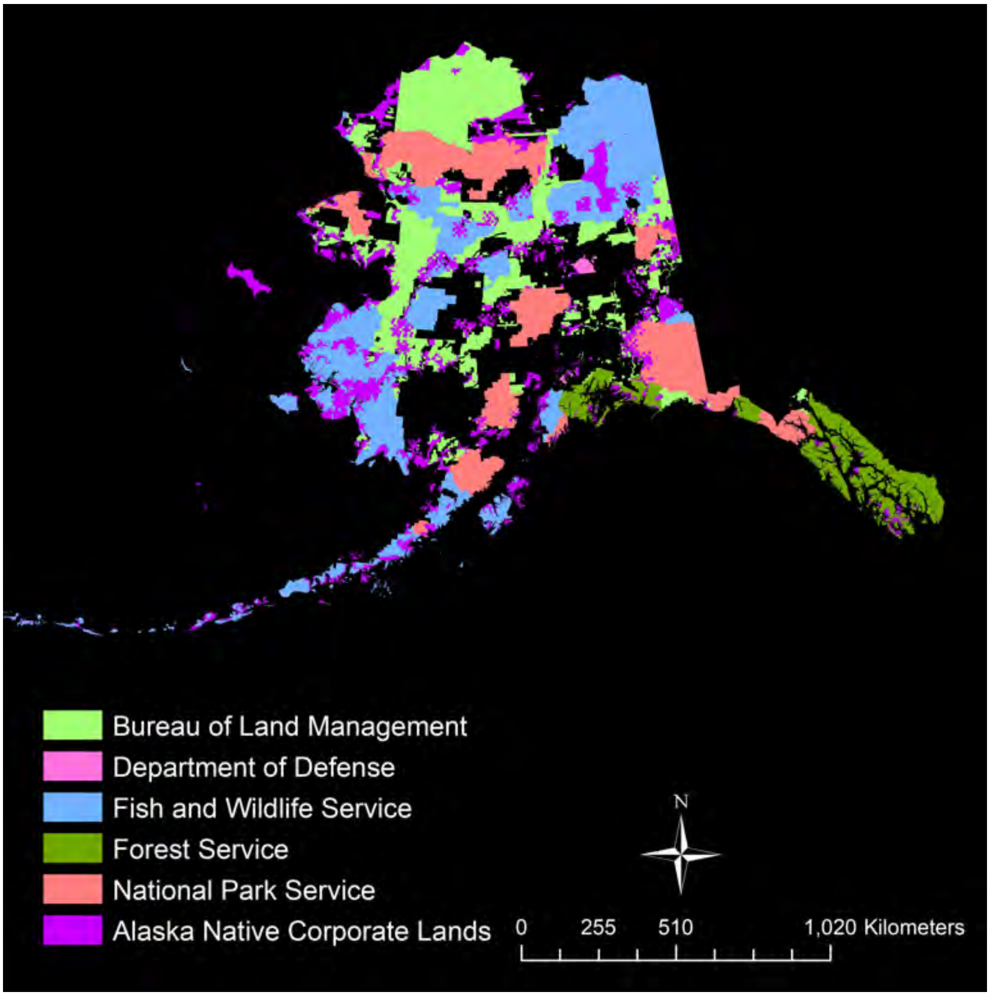

FIGURE 1 | Federal and Alaska Native corporate lands in Alaska.

the long-term persistence of biodiversity (**Figure 2**; Locke et al., 2019). The majority of the world's most significant congregations of species, remaining migrations, and sheer numbers of individuals of many species occur in the world's most intact landscapes (Betts et al., 2017). Ecologically intact ecosystems are becoming increasingly limited on the planet, making their identification and conservation an important priority (Plumptre et al., 2019). These remaining intact landscapes contain the last strongholds for many imperiled species (Watson et al., 2016). In Alaska, they also support Alaska Native peoples, who currently and historically maintain complex and vibrant traditions of subsistence hunting, fishing, and gathering. These traditions are key to not only the cultures and people themselves, but also to public policy (Wheeler and Thornton, 2005).

Large tracts of undeveloped areas also support a majority of the world's remaining intact mega-fauna assemblages, as well as species sensitive to exploitation or conflicts with humans (Morrison et al., 2007; Ripple et al., 2014, 2015). Alaska is the only location in the United States outside of the Yellowstone Ecosystem that has landscapes with their full roster of historically present (AD1500) large mammals (Morrison et al., 2007). The state as a whole is a global priority for conserving or restoring large mammal assemblages, as all of Alaska's ecoregions contain either complete or near-complete rosters of their historically present large mammals (Dinerstein et al., 2020). Alaska is also a priority for conserving the increasingly rare phenomenon of mass migration of large terrestrial mammals, with a number of significant caribou migrations occurring throughout the region (Harris et al., 2009).

Alaska hosts a number of globally significant sites for large aggregations of breeding shorebirds. The state provides breeding habitat for more shorebirds than any other state in the United States and hosts between 7 and 12 million shorebirds, or as much as 50% of all the shorebirds that occur in North America[3]. Most of the world's population of three shorebird species, entire populations of five subspecies, and large portions of North America's populations of six other species or subspecies depend on Alaska's habitats[2]. The Copper River Delta supports

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[3] www.fws.gov/alaska/pages/migratory-birds/shorebirds; accessed 1 October 2020

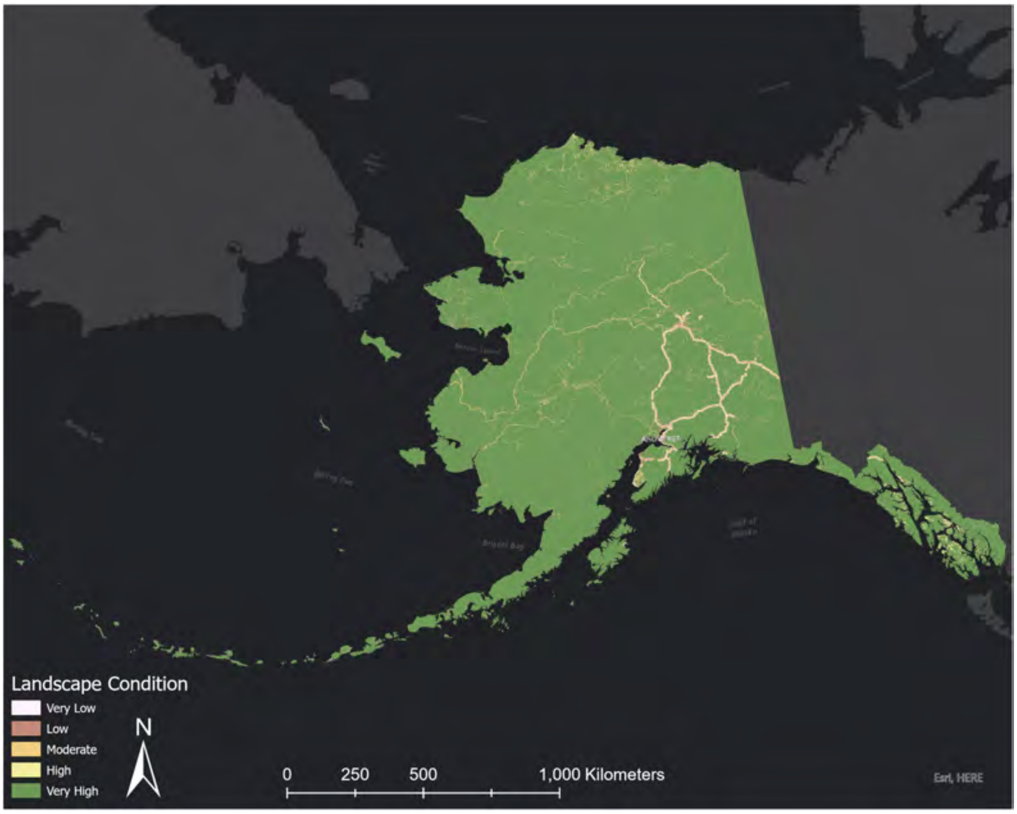

FIGURE 2 | Landscape condition of Alaska; data from Trammell and Aisu (2015). Landscape condition uses a method developed by Hak and Comer (2017) but was modified to better represent the effect of human development on systems in Alaska. Each type of human footprint (e.g., major highways or logging) is assigned a site impact score, which are a relative and scaled measure of the overall impact of a human activity on the landscape, and a decay score to represent the gradual decreasing impact as you move away from the activity (Trammell and Aisu, 2015). This is meant to represent the physical impact of human activities to the landscape, not necessarily all the ecological impacts.

what is thought to be the world's largest concentration of shorebirds, with between 5 and 8 million shorebirds visiting each spring. Concentrations of over one million birds each occur at ten key migration or stopover sites in Alaska[3]. 155 Key Biodiversity Areas, globally significant sites for species conservation, occur in the state (Birdlife International, 2019). According to the National land cover database, 24% of Alaska is forested, and 74% is vegetated (i.e., not all ice and barren land (**Figure 3**).

Salmon-producing regions of Alaska are highly diverse, ranging from rainforest, to boreal forest, to Arctic tundra lowlands.[4] Alaska's contribution to global salmon catch is profound; roughly half of the world's sockeye salmon spawn in the Bristol Bay watershed and rivers along the Gulf of Alaska alone produce one-third of the world's wild salmon (Schoen et al., 2017). Salmon are known to use approximately 36,000 km of streams in the state, which equates to nearly three trips around the globe; and cataloging of salmon occurrence in Alaska is incomplete and ongoing due, in part, to insufficient funding. No other place on Earth has as many healthy and diverse populations of wild salmon.

In Alaska, large tracts of intact habitat support multiple runs of salmon. Maintaining multiple populations with diverse responses to environmental fluctuations within a landscape provides greater ecological resilience to threats and stochastic events (Schindler et al., 2010). The Tongass and Chugach National Forests in southeastern and southcentral Alaska represent some of the largest tracts of intact rainforest in the world (Orians and Schoen, 2017) and these forests support diverse and productive Pacific salmon fisheries (Johnson et al., 2019). Intact landscapes support habitat diversity allowing, for instance, the peak migration timing of the same species in nearby streams to vary by 3 weeks or more due in part to temperature differences. This variability allows trout, bears, and various birds (e.g., gulls) to eat salmon and salmon eggs for months rather than weeks by moving progressively from colder to warmer streams (Ruff et al., 2011; Schoen et al., 2017). Diversity in the timing of migration can also extend fishing seasons and improve food security for Indigenous and other people (Nesbitt and Moore, 2016). Further, salmon provide a bridge between marine, freshwater, and terrestrial ecosystems, enriching adjacent forests through nutrient transfer that enhances tree growth (Quinn et al., 2018), and carbon sequestration.

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[4] www.alaskasalmonandpeople.org

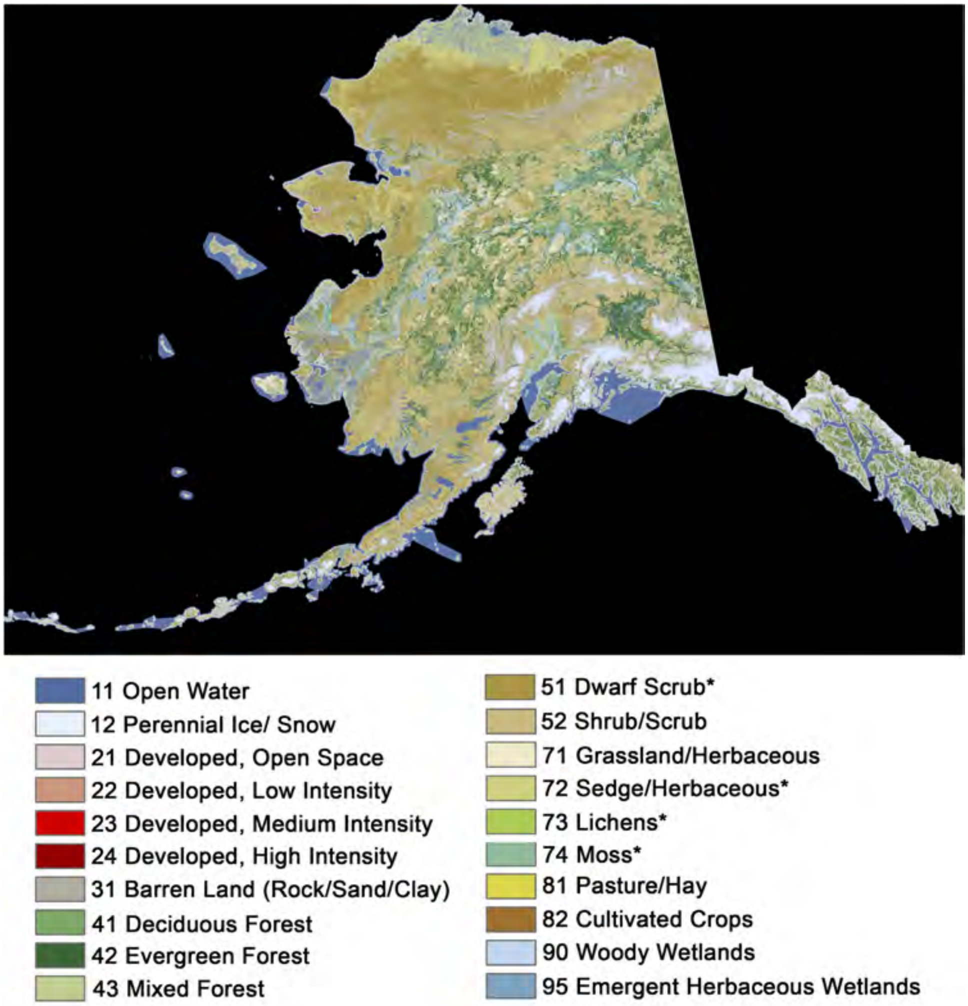

FIGURE 3 | Land Cover for Alaska according to the National Land Cover Database maintained by the United States Geological Service. * Alaska only.

The coastal temperate rainforests of coastal British Columbia and southeast Alaska exhibit a distinct aspect of "intactness" that is rarely replicated globally: river systems and their surrounding watersheds with no history of industrial exploitation or modern urban development (Lertzman and MacKinnon, 2013). These watershed ecosystems represent not just ecological communities, seral stage distributions, and carbon stores in their historic proportions and configurations on the landscape, but also are more likely to maintain the hydrological, geomorphic, and other physical processes that sustain the ecosystems over time. These undeveloped watersheds represent a globally rare and significant, process-based conservation opportunity.

INTACT ECOSYSTEMS AND CARBON STORAGE

The temperate rainforests of the Pacific Northwest, including those in the southeast of Alaska, contain the most extensive examples of undeveloped and semi-natural temperate rainforest remaining globally, and are recognized for their significance in storing large amounts of carbon (Hudiburg et al., 2009; Law et al., 2018). Trees in the Pacific Northwest often live for 800 years or more, storing carbon in boles and roots for that length of time, and they continue to accumulate carbon annually (Hudiburg et al., 2009; Stephenson et al., 2014; Lutz et al., 2018). In Oregon and Washington, forests east of the Cascade crest, large trees (greater than 21 inches in diameter) are only 3% of the trees but account for almost half of the total tree biomass (Mildrexler et al., 2020). Protecting more forest carbon on public lands, lengthening harvest cycles, and reforestation contribute the most to increase forest carbon storage and sequestration (Law et al., 2018). These findings led to the promotion of proforestation, or letting forests grow, as a high priority climate mitigation strategy globally (Moomaw et al., 2019, 2020).

The rainforests of southeast Alaska are notable for supporting large tracts of old growth forest, where tree size and biomass are higher than in younger forests. There is more old-growth than young forest area in Alaska (Pan et al., 2011), and the most effective measure to protect existing carbon stocks is to protect and maintain existing old growth stands. The total carbon stock in the forest and soils of the Tongass National Forest in southeast Alaska alone is 8% of that of the forests in the conterminous United States (Leighty et al., 2006). Protecting forests with old trees will also confer co-benefits to wildlife, biodiversity, and other ecosystem services including the provision of microclimate buffering under future extreme climate conditions and various cultural ecosystem services (Sutherland et al., 2016).

The boreal forest biome, which covers much of interior Alaska, is increasingly recognized for the important role it plays in carbon storage (Dinerstein et al., 2020; Wells et al., 2020). The forests in Alaska have relatively low carbon density in living vegetation compared with coastal forests (Domke et al., 2018), but when maps of total biomass (including soil) are included, these areas stand out as globally significant (Dinerstein et al., 2020; Soto-Navarro et al., 2020; **Figures 4**, **5**). Half the carbon in Alaska and Canada's boreal zone is stored in coniferous forests (Schuur et al., 2018). The boreal forests of Alaska show growth increases in productivity at the boreal-tundra ecotones where it is colder and sparsely forested, and drought-induced declines in productivity throughout interior Alaska, indicating a biome shift is underway (Beck et al., 2011). These forests also lose a substantial amount of carbon in wildfires, primarily from the burning of soils and duff (Goetz et al., 2012; Kasischke and Hoy, 2012).

Disturbances reduce the net carbon sink, yet have been challenging to quantify in this region. Satellite and field observations showed that the Alaska Boreal Interior ecoregion's above ground biomass carbon averaged 29.3 MgC ha^{-1} from 1984 to 2014, and 36.8 MgC ha^{-1} in the Boreal Cordillera ecoregion (Wang et al., 2021). The total biomass stocks in the Alaska Boreal Interior averaged 1,410 TgC for the same period. The net change in above ground biomass carbon was +60 and +143 TgC for the ecoregions, respectively, though most of the Boreal Cordillera ecoregion is in Canada. This indicates that the above ground carbon of these forests was still a net carbon sink after accounting for disturbance losses from primarily wildfires and harvest. On an area basis, harvest impacts on above ground carbon were nearly two times larger than from wildfire (Wang et al., 2021).

While the forests of Alaska are globally significant carbon storehouses, the vast majority of carbon in Alaska is stored in undisturbed soils. Globally, peatlands-wetlands whose soils consist almost entirely of organic matter-cover just 3% of the Earth's surface but store more carbon than any other types of ecosystems and for longer periods of time. Due to rising temperatures, permafrost is thawing rapidly and is thus altering carbon storage dynamics with potentially dire consequences. But as new unfrozen peatlands form, more carbon may be taken from the atmosphere due to increased plant growth. The carbon balance of these peatlands is changing rapidly with as yet unknown consequences for carbon storage and hence the global climate (McGuire et al., 2012; Graven et al., 2013; Commane et al., 2017). While long-term warming will likely restructure Arctic tundra, there are multiple lines of evidence of Arctic greening and increasing productivity (Berner et al., 2020).

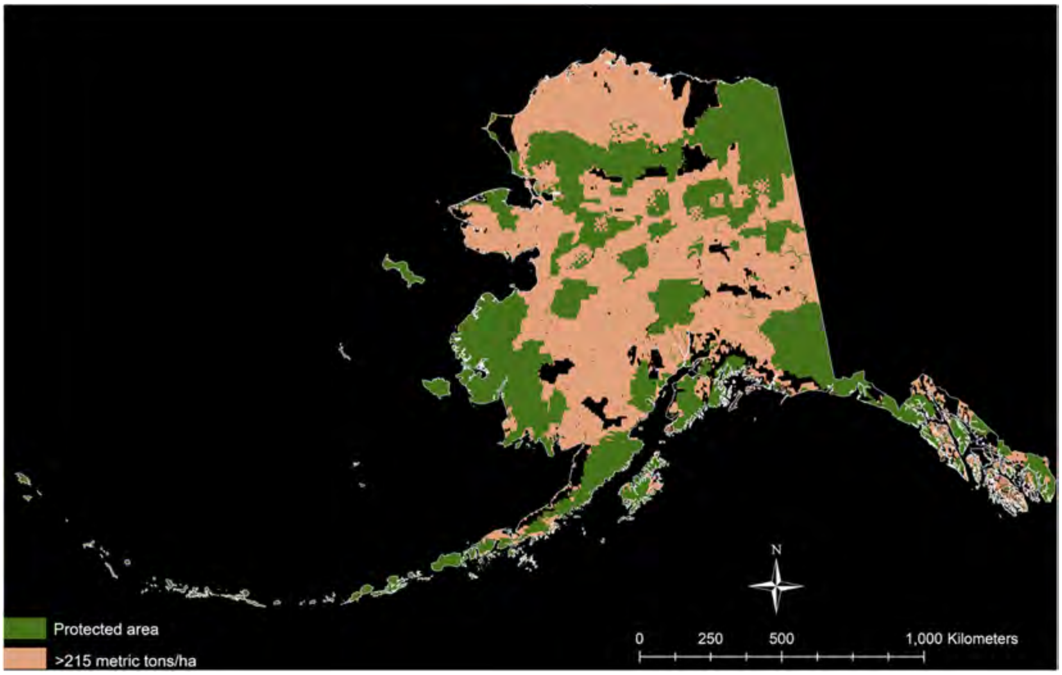

FIGURE 4 | IUCN I-VI Protected Areas in Alaska, according to the Protected Areas Database of the United States, maintained by the United States Geological Survey, and areas outside of the protected areas system where total carbon biomass is above the global median.

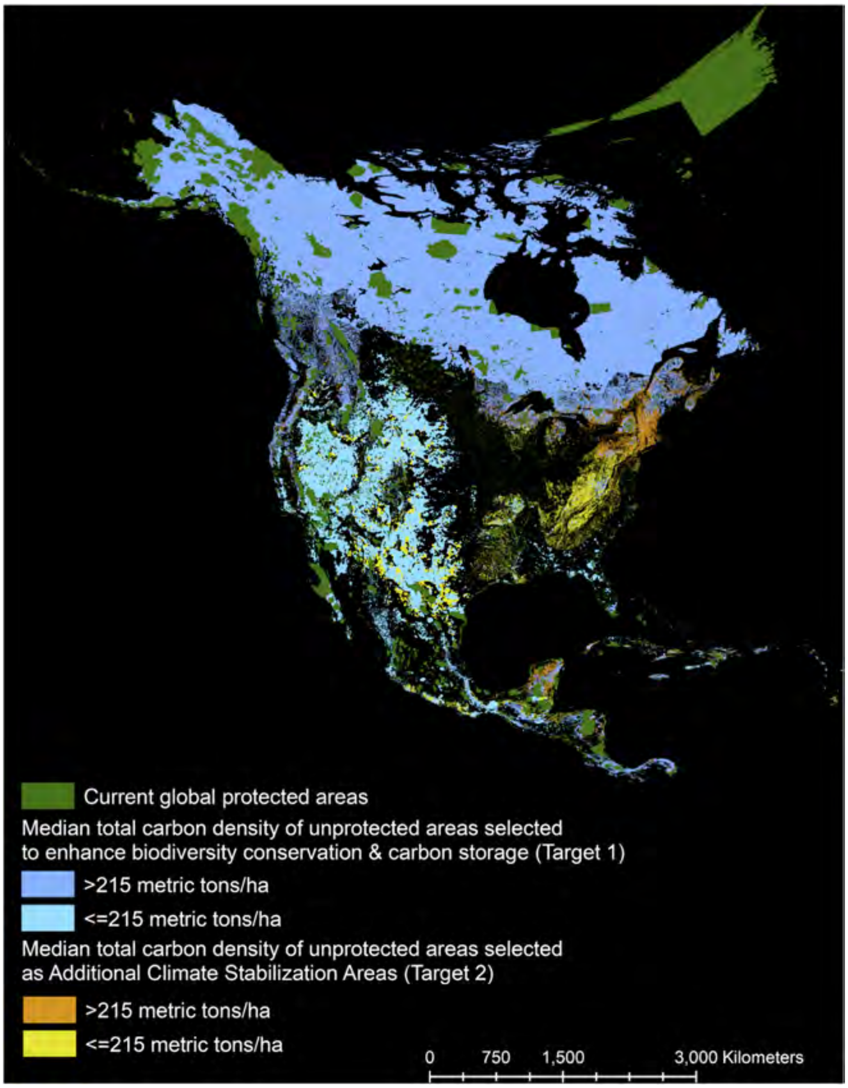

FIGURE 5 | Median total carbon distribution in the Nearctic realm [from Dinerstein et al. (2020)].

The amount of carbon stored on federal lands in Alaska is approximately 62% of the total carbon stored on all United States federal lands (Merrill et al., 2018). Average carbon storage in live vegetation and soils (2005–2014) was 131,675 MMT CO_2 Eq. on Alaska's federal lands, with 92 percent stored in soils and eight percent stored in live vegetation (Merrill et al., 2018). In the Tongass National Forest, 26 percent is stored in live vegetation (Leighty et al., 2006). Maps of total biomass carbon, which integrate above and below ground sources, indicate that nearly all of Alaska is above the global median (**Figures 4**, **5**). Protecting these carbon-storing intact systems in Alaska is important because the ability of these ecosystems to recover carbon once lost is very slow (Goldstein et al., 2020). It takes hundreds to thousands of years to accumulate carbon in trees and soils to their ecological potential, respectively, and it takes that long to regain that amount of carbon once removed, if ever (Sun et al., 2004; Luyssaert et al., 2008; Hudiburg et al., 2009). Ecosystem types that host large amounts of this "irrecoverable" carbon dominate much of Alaska, and include boreal forest, boreal peatlands, and seagrasses (Goldstein et al., 2020). Even partial "carbon recovery-ability" in the boreal and temperate peatlands could take millennia (Leifeld and Menichetti, 2018).

In a recent global analysis of remaining intact habitats and essential places to conserve to stabilize climate and avoid species extinctions, 93.6% of Alaska's lands were identified as essential (Dinerstein et al., 2020). Besides the existing protected areas (IUCN Category I-VI designations), the role of intact areas and high carbon storage areas were central to Alaska featuring prominently in this analysis (Dinerstein et al., 2020). Intact large mammal assemblages-places where rosters of the historically present (as of AD 1500) large mammals still remain-occur across much of Alaska (Morrison et al., 2007; Dinerstein et al., 2020). Presence of healthy populations of large mammals contributes to healthy ecosystem functioning and carbon storage

(Ripple et al., 2014; Cromsigt et al., 2018). Conserving and restoring robust populations of large mammals that occur in Alaska is an opportunity to maximize carbon storage, as well as to confer other benefits that the presence of large mammals brings for Indigenous, local, and visiting human communities (Colt, 2001; Colt et al., 2002; Chapin et al., 2004; Wolfe, 2004; Ballew et al., 2006).

Though this paper primarily focuses on synthesizing information on terrestrial systems, coastal systems are also a key component of Alaska's globally significant carbon storage capacity. Blue carbon refers to the carbon stored in coastal wetlands and estuaries. Seagrass and salt marshes can store up to 2.5 times the buried carbon as terrestrial boreal and temperate forests (Mcleod et al., 2011). Salt marshes and seagrass estuaries are losing up to 7% of their global distribution on an annual basis, however, most of the coastal seagrass estuaries in Alaska remain intact (Short et al., 2007). Alaska has among the largest eelgrass beds in the world (Ward et al., 1997). Though the blue carbon potential of peatlands, wetlands, and coastal estuaries has been studied in the Pacific coast region of Washington State (Kauffman et al., 2020), no such studies have been completed for Alaska.

CARBON EMISSION RISKS IN ALASKA

Wildfire is the dominant driver of ecosystem change in much of Alaska, particularly the boreal region, and is strongly linked to climate. The area that burns in Alaska has increased significantly in recent decades (Kasischke et al., 2010), and points to the importance of accounting for the potential changes in the Alaska fire regime with respect to carbon storage and fluxes. Recent large burns put Alaska as contributing to approximately half of United States fire carbon emissions in certain years (Veraverbeke et al., 2015, 2017). As the changes in future climate will affect the landscape configuration of vegetation types throughout fire-initiated secondary succession, there are potential feedbacks to the fire regime and hence differences in modeled projections (Wolken et al., 2011; Zhu and McGuire, 2016). In some cases, such as in white spruce forests of south-central and interior Alaska, old forests are better able to withstand fire than young forests due to their higher water content, taller canopies and thicker bark. However, in black spruce forests, old stands are highly fire prone. The extent to which mature forest stands can escape or withstand fire and other disturbances will therefore be a key factor in determining their near-term climate-change resilience. Hotter and more intense fires are also likely to burn more of the organic layer, further increasing emissions.

Despite short-term releases of carbon due to more intense and more frequent fires, shifts in dominant plant species catalyzed by severe fire could mitigate feedback to climate warming if future deciduous-dominated boreal forests are managed to reduce fire activity. Fast-growing deciduous trees that replace slow-growing black spruce following severe boreal forest burns has been shown to result in a net increase in carbon storage by a factor of five over the disturbance cycle (Mack et al., 2021).

A thorough review of baseline and projected future carbon storage and greenhouse-gas fluxes in Alaska was done by Zhu and McGuire (2016). They found that across upland and wetland ecosystems, Alaska will likely see substantial increases in carbon sequestration potential between now and 2099. This is due primarily to increases in net primary productivity and is predicted despite likely and substantial increases in carbon emissions due to wildfire. The temperate forests in south-central and southeast coastal Alaska, which store significant carbon in live and dead tree biomass, are also projected to increase storage potential. Susceptibility to climate change in lowland shrub tundra ecotypes is significant due to large amounts of soil organic carbon becoming available for loss by decomposition. It should be noted, however, that systems that are more intact and less disturbed are expected to maintain higher carbon storage levels (Martin and Watson, 2016).

ALASKA'S IMPORTANCE IN CLIMATE ADAPTATION AND RESILIENCE

Beyond biodiversity and carbon storage sequestration, Alaska's intact ecosystems provide other essential ecosystem functions such as regulating hydrological regimes or buffering against major storm events. These systems provide services directly essential to human health, including provisioning of clean air and water. Globally, intact ecosystems are especially important for many Indigenous communities (Watson et al., 2018; Plumptre et al., 2019). In Alaska, dependence on wild resources is cultural, social, and economic across communities. Rural residents harvest about 18,000 tons of wild foods each year, with fish making up about 56 percent of this harvest[5]. Rural communities in Alaska are geographically isolated by waterways, varied and steep terrain, and lack of road infrastructure, and hence are particularly reliant on wild foods.

For Indigenous peoples in particular, wild foods such as salmon are a central facet of culture and social relationships as well as subsistence[6]. Because of the conjunction of widespread intact ecosystems with Indigenous communities retaining their strong connections to place-based culture, Alaska provides opportunities for supporting healthy relationships between cultures, communities, and ecosystems that are rare in a global context (Fernández-Llamazares et al., 2021; Thornton and Moss, 2021). Even elsewhere in the temperate rainforests of the Pacific Northwest, many critical resources for these communities have become dramatically reduced in abundance, negatively impacting the resilience of human communities (e.g., Benner et al., 2021). Salmon, herring, and other marine foods are iconic in this regard (Thornton and Moss, 2021), but access to a diverse array of terrestrial and marine plant and animal foods contribute to nutritional health, cultural continuity, and resilience to modern crises (Moss, 1993; Hunn et al., 2003; Fernández-Llamazares et al., 2021).

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[5] https://www.doi.gov/subsistence; accessed 19 November 2020

[6] https://alaskasalmonandpeople.org; accessed 4 February 2021

Ecologically, Alaska could provide key refugia for species whose distributions will shift northward under climate change. Southeast Alaska will, for example, provide key refugia for temperate rainforest communities of the Pacific Coast (DellaSala et al., 2015), and future habitat for boreal species that presently occur further south and east (Stralberg et al., 2015). Land management decisions will affect how species, ecosystems and their services, and the people of Alaska and the nation as a whole, will adapt to climate-related changes. Conservation and informed management of areas of high refugia potential may help species and ecosystems persist, facilitate adaptation to new conditions, and allow for proactive management. This is consequential as many land managers are struggling to keep up with the accelerating consequences of climate change (Stralberg et al., 2020). Intact systems and the robust populations of species that occur in them can be viewed as an insurance policy against having to address the problems and associated costs that occur in trying to manage at-risk species in altered habitat in the future.

Leveraging the relatively intact nature of the Kenai peninsula in Alaska, the Kenai National Wildlife Refuge (KNWR) has been actively promoting proactive management to protect future anticipated ecosystem function (Magness and Morton, 2017). Leveraging climate envelope models developed for the region, managers at the KNWR have developed a portfolio approach that works with climate change trajectories to promote species more suited to future anticipated climates (Magness and Morton, 2018). Directing ecosystem change, in conjunction with resisting or accepting ecosystem change, is more attainable in intact ecosystems (Thompson et al., 2021).

Alaska is home to many of the last remaining intact and largely unaltered Pacific salmon (genus *Oncorhynchus*) producing ecosystems. The persistence of salmon and their supporting habitats has sustained the connection between Alaskans and salmon for over 10,000 years (Halffman et al., 2015). In contemporary times, salmon support multi-billion industries in Alaska through harvest by commercial fishermen and recreational anglers (Johnson et al., 2019). Salmon are harbingers of climate change and are increasingly observed in Arctic regions where Indigenous Peoples have little or no experience interacting with salmon (Dunmall et al., 2013) and where community reception to the newcomers is mixed (Carothers et al., 2019). Although Alaska is in a prolonged period of low abundance of the large-bodied and iconic Chinook salmon (*O. tshawytscha*), the numbers and biomass of wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean are as high as they have been since the 1920s (Ruggerone and Irvine, 2018).

Evidence points to major ocean changes as the primary drivers of these shifts in abundance (e.g., Cunningham et al., 2018), though changes in streamflow and freshwater discharge also play a role. Restoring and maintaining intact landscapes and flexible options for salmon to adapt in the future will determine where and how salmon are distributed across the state moving forward. In the rainforest region of Southeast Alaska, it is a priority to understand the efficacy of forest restoration from historical logging and if and how this can improve. For example, restoration and management to buffer against higher frequency flooding events, drought, and variability has been prioritized by disciplinary experts (Shanley et al., 2015). Maintaining flexible options for salmon—by maintaining a diversity of habitats and keeping these as intact as possible—will increase the likelihood that salmon productivity can be maintained despite large-scale shifts that will occur (Cline et al., 2017; Schoen et al., 2017).

Mitigating climate change and maintaining flexible options into the future will be essential to minimize forced migration of human populations as climate refugees, loss of access to food resources, and other uncertain risks (Hamilton et al., 2016). This is particularly important in Alaska as communities deriving significant elements of their daily needs from subsistence economies and ecologies are particularly at risk from climate change (Savo et al., 2016). In Alaska, climate change could add \$5–6 billion to future costs for public infrastructure from now to 2080 (Larsen et al., 2008; Melvin et al., 2016). A recent report estimates that some of the most certain consequences of climate change in Alaska will cost between \$340 million and \$700 million per year over the next three to five decades (Berman and Schmidt, 2019), and this estimate included only a limited set of costs. Such costs may be borne by United States taxpayers more generally as well as Alaskans. Rural Alaskans will be disproportionately affected by changes to subsistence harvest cycles and reduced barge service as rivers become too shallow. Implementing plausible adaptation strategies could offset impacts by up to 45% over the long-run (Larsen et al., 2008).

THE IMPORTANCE OF ALASKA TO A UNITED STATES STRATEGY FOR CLIMATE STABILIZATION AND BIODIVERSITY CONSERVATION

The sheer size of Alaska and proportion of intact systems, much of which is public land, makes Alaska a singularly important and opportune place for the United States to consider natural climate solutions within its own borders. Approximately 60% (900,000 km^2 of 1.5 M km^2) of Alaska's terrestrial surface area is federal land (**Figure 1**). Nearly 2/3 of this is within an IUCN protected category I-VI, with management ranging from protections for wildlife and recreational values [e.g., Fish and Wildlife Service (FWS) Refuges, National Park Service (NPS)], to managing lands for some oil and gas, mineral, and timber development [e.g., United States Forest Service (USFS), Bureau of Land Management (BLM)]. The State of Alaska manages another 100 million acres (404,685 km^2), an area the size of the State of California, for an equally wide range of purposes. Together, 88% of Alaska is managed either by the federal or state government. No United States state has a larger amount of public lands nor the combined intactness, carbon storage, and native biodiversity importance of Alaska.

As noted, ANCSA, enacted in 1971, transferred 44 million acres (178,062 km^2) of land (nearly 12% of the State) to newly created Alaska Native regional and village corporations. These lands are managed for the benefit of the corporations' Alaska Native shareholders. In addition, the Alaska National

Interest Lands Conservation Act (ANILCA), passed in 1980, provided varying protections to 157 million acres of land set aside as National Parks, National Forests, and other conservation areas. It also established subsistence priority in hunting, fishing, and gathering activities for rural residents, Alaska Native or otherwise, stating that, "the continuation of the opportunity for subsistence is essential to Native physical, economic, traditional, and cultural existence." Roughly 80% of the population of remote rural Alaska residents are Indigenous People[7], and federal and state public lands comprise much of the traditional territory of Alaska's 229 federally recognized tribes—creating an unusual opportunity for a small number of landowners and sovereign tribes to work together on coordinated land management strategies across large regions of the state. Only about 1% of Alaska is in general private land ownership.

Many intact systems in Alaska face a variety of proposed industrial land uses that either increase carbon emissions through the extraction and production of fossil fuels or diminish carbon storage values and system intactness through degradation or conversion of natural areas. Among these are expanded fossil fuel development in the Brooks Foothills and Beaufort Coastal Plain (**Figure 6**), clear-cut old-growth logging in forest systems in southeast Alaska, and large-scale, fossil-fuel based mining operations and associated infrastructure in otherwise intact regions such as the Bristol Bay watershed. Land conversion from forest to agriculture in Alaska's boreal region would be likely to result in net carbon release (Grünzweig et al., 2004). In Canada, agricultural conversion is the greatest source of historical loss of boreal forests, and remains an important driver of deforestation in some boreal zones (Hobson et al., 2002). Such conversion is not however, occurring at anything approaching large scales in Alaska (**Figure 3**).

RECOMMENDATIONS

While the tundra, forests, and other ecosystems of Alaska all face some degree of risk, there is potential for these to be managed through local land-use decisions and actions (Grünzweig et al., 2004; Goldstein et al., 2020). Managing for climate stabilization and adaptation benefits in Alaska may provide an opportunity to scale land conservation and augment management on the rapid timescale that is necessary to meet global climate and biodiversity objectives (Dinerstein et al., 2019). Land management has a significant role to play in how Alaska's systems, species, and people contribute to climate stabilization and adapt to climate change. For example, forest carbon storage potentially could triple with management focused on limiting harvest in the high biomass forests of Southeast Alaska (Zhu and McGuire, 2016). Further, processes internal to an ecosystem can lead to a decoupling from regional temperature and moisture regimes, and relatively undisturbed systems can confer resistance to climate change (Stralberg et al., 2020). Management of fire in Alaska has also been suggested as a potentially important climate mitigation strategy, as well as being important to directly protect human communities (Phillips et al., 2019). New evidence that shifting species dominance following severe burns in boreal forests is important as this has the potential to reduce likelihood of future fires, increase the tenure of this carbon on the landscape, and provide negative or stabilizing feedback to climate warming (Mack et al., 2021).

The singular opportunity that Alaska's relatively intact systems present, particularly the irreplaceability of its accumulated carbon stores, merits consideration of an approach to the management of Alaska's public lands that prioritizes climate stabilization, adaptation, and resilience. Such an approach might include a wide range of management actions. The identification and designation of areas important for climate stabilization and resilience could provide an opportunity to increase the use of nature-based approaches to mitigating climate change. These designations could include large intact areas and areas that are essential carbon storehouses, particularly vital in climate mitigation, and which could be managed to maintain and enhance conditions (e.g., vegetative cover, soil condition) for carbon storage and sequestration. Co-developing ideas and means to manage these areas with local people, particularly federally recognized tribes, could also increase stewardship and the efficacy of these areas in meeting not only conservation and climate objectives but also local economic, social, and cultural concerns.

Though additional IUCN-defined protected areas (categories I-VI) may be warranted in specific places, climate stabilization designations may simply shape management plans in a way that maximizes carbon storage and biodiversity conservation. Achieving expanded conservation objectives may also be achieved through other effective area-based conservation measures (OECMs) and Indigenous and Community Conserved Areas (ICCAs; Wells et al., 2020). Long-term or indefinite-termed withdrawal of areas of public land and waters from specific activities that directly contribute to emissions (e.g., expanded fossil fuel development) or that diminish carbon storage, intact systems, and biodiversity values through significant degradation or conversion of natural areas (e.g., clear-cut old growth logging and large-scale hard rock mining) could be considered (Wells et al., 2020). Such targeted withdrawals provide near-term biodiversity and climate stabilization benefits while still meeting other human needs and retaining the option to adjust management in the future.

Targeted withdrawals or designations may be area-based or they may be ownership-based, such as withdrawals of categories of federally-owned or managed lands and waters from fossil fuel extraction, for example. The Northern Bering Sea Climate Resilience Area[8] (NBSCRA) is an example of an area-based, targeted withdrawal of oil extraction activities. This designation, created in partnership between regional Indigenous entities, including over 70 federally recognized tribes, and the federal government, was also an example of a collaboratively-developed designation that increases authority, recognition, flexibility,

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[7] https://iseralaska.org/static/legacy_publication_links/researchsumm/UA_RS10.pdf; accessed 4 February 2021

[8] https://obamawhitehouse.archives.gov/the-press-office/2016/12/09/executive-order-northern-bering-sea-climate-resilience; accessed November 20, 2020

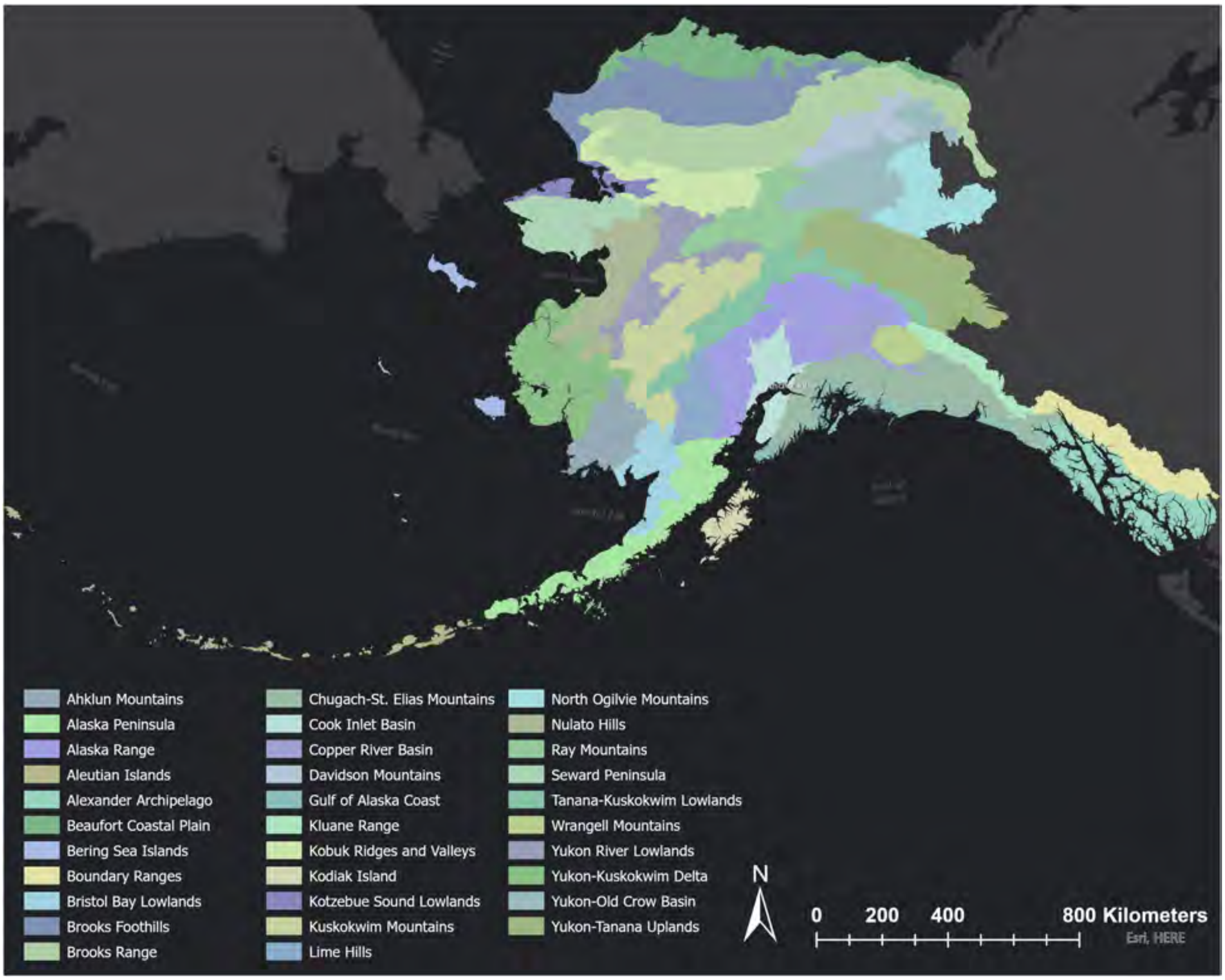

FIGURE 6 | Ecoregions of Alaska [from Nowacki et al. (2003)].

and benefits to local stakeholders, particularly Indigenous peoples. Notably, the NBSCRA required for the first time that Indigenous knowledge be included in federal decision-making. Co-development of climate stabilization and resilience designations and approaches with federally-recognized tribes could provide a means of recognizing tribal sovereignty, tapping Indigenous knowledge and governance, addressing the needs of Indigenous communities, and achieving climate and biodiversity objectives in an effective and socially just manner (Artelle et al., 2019). Designations might also include or be complemented by programs designed to be expanded to ensure multiple resource management benefits–such as water and food security and economic and educational opportunities–for resource users.

Prioritization of a climate stabilization, adaptation, and resilience approach may also be attractive to Alaska Native corporate landowners if the benefits to shareholders were to outweigh the benefits of resource extraction that diminishes carbon storage and biodiversity conservation but currently provides needed economic activity. Sealaska, the regional Alaska Native corporation for Southeast Alaska, established a carbon bank of 165,000 acres (667.7 km^2) of its lands in Southeast Alaska. No commercial timber harvest will occur on those lands for 100 years. Federal programs could be designed in partnership with Alaska Native corporate landowners, federally-recognized tribes, and Alaskan communities that complement market-based actions and further incentivize climate stabilization and resilience investments on Alaska Native corporate lands and federal lands. These programs could also provide economic opportunities related to stewardship of carbon, food security, and other ecosystem services. Similarly, federal, state, and private partnerships may incentivize state climate stabilization investments and enable coordinated climate stabilization strategies over intact systems with fragmented land ownership.

Based on the information synthesized above, such an approach in Alaska should consider:

1. Maintaining intactness values: evaluate costs and benefits of developing industrial projects in intact areas as maintaining intact landscapes helps mitigate climate change as well as buffer its impacts.

2. Promoting proforestation—letting forests grow—as a forest management strategy and a component of ecosystem-based management.
3. Conserving forests with old trees.
4. Together with local communities, addressing and developing wildfire response strategies and stewardship and restoration strategies that promote carbon storage.
5. Prioritizing conservation and restoration of intact large mammal faunas and healthy salmon streams; presence of viable populations of these species confer systems-level carbon storage, and a myriad of other benefits for people and nature.

A climate stabilization and resilience approach could also involve greater focus of public resources and funding for a research agenda to better inform land managers in stewarding Alaska's systems. Such an approach should also facilitate greater support and funding for Indigenous-led research and co-production of knowledge with Indigenous Peoples. According to a recent report assessing natural climate solutions across the United States, priority areas to maintain in Alaska comprise 29% of total carbon storage across all ecosystems, and are extremely important in terms of the United States commitment to draw down greenhouse gas emissions[9]. Filling key research gaps, particularly related to how the role of wildfire and ecosystem shifts may affect the carbon balance in Alaska, is particularly important. We elaborate on this and other research priorities in the next section.

RESEARCH PRIORITIES

Indigenous-led research and research needs prioritized by Indigenous Peoples in Alaska should be a central component of research priorities. Collaboration with Indigenous knowledge-holders is consistent with internationally recognized Indigenous rights and generates more impactful research outcomes (Ban et al., 2018). Such cooperation among scientific and Indigenous perspectives will both improve understanding of system dynamics and better inform both scenario planning and the design of any climate stabilization and resilience approach to Alaska's lands and waters.

Fire is a key ecosystem driver across the boreal region of Alaska. In this century, it has increased in range, with more frequent fires occurring further north, west, and south, as compared to historical records. Fire has also increased in frequency (leading to shorter average fire return intervals), intensity and severity, leading to more complete burning of biomass in trees and in soils, associated greater losses in carbon, and slower post-fire recouping and regenerating (Turetsky et al., 2011). Model results suggest that the boreal forest is particular at risk of carbon losses *via* fire, and that changes in fire regime will cause net carbon loss from deep organic soils and near−surface permafrost (O'Donnell et al., 2011; Genet et al., 2013). Carbon is lost to the atmosphere not only during fire events, but for years afterward, as well—but this effect is poorly understood. Postfire changes in absorption of solar radiation and organic decay in soils alter rates of carbon turnover in boreal forests. These post-fire releases may have been vastly underestimated, in part due to poor understanding of "mass wasting" and carbon decomposition in the mineral soil layer in the 2 years post-fire (O'Neill et al., 2003; Potter, 2018). The magnitude of these changes, their overall impact on carbon balance, and the practical ability of human management strategies to alter their trajectory all merit additional research and modeling.

While it has already been noted that the increased temperatures and permafrost thaw associated with past and ongoing climate change have already accelerated carbon loss from soils *via* decomposition, the magnitude of past and future carbon losses are far from clear—as are potential management strategies that might limit or mitigate such losses. Decay rates and rates of carbon loss are temperature sensitive and occur differently at different depths and locations. More data are needed on the effects of climate change on soil organic carbon in boreal permafrost soils, especially from depths greater than one meter (Kane et al., 2005; Johnson et al., 2011). A meta-analysis of existing literature on the anticipated response of Alaska's ecosystems to climate change is a research priority. Synthesizing scientific conclusions and quantifying how projected changes are likely to influence boreal forest and tundra ecosystems, in particular, would benefit the research community and land managers. This meta-analysis could help inform a quantitative assessment of the potential for Alaska's natural climate solutions to help the United States meet national and global climate commitments, as was recently assessed for Canada (Drever et al., 2021).

Ecological shifts have seen some recent research, but much remains to be examined with regard to the impacts of shrub encroachment in tundra systems and increases in forest biomass in areas previously sparsely forested, particularly on land areas where permafrost has recently thawed (Loranty et al., 2018). Complex patterns of soil drainage, currently unmapped for the state, add to the difficulties of predicting these land cover changes. Of particular importance is to understand and monitor how shrub species in tundra ecosystems will vary in response to climate and environmental change, and how herbivores and their shifting distributions may limit this change (Myers-Smith et al., 2011). Filling data gaps so that analyses such as that of Fargione et al. (2018) on natural climate solutions for the United States may be completed for Alaska is a priority. Similarly, filling gaps and completing mapping and inventorying of blue carbon networks is also a pressing research priority so that Alaska's blue carbon potential can be adequately assessed.

The ecoregions of Alaska have many close parallels in the ecoregions of Canada, particularly with regard to permafrost tundra, vast boreal forests underlain with discontinuous permafrost southern boreal forests (aspen parkland), and temperate coastal rainforests (**Figure 6**). While in some cases the management of these lands has been similar in Alaska and in Canada, in many cases there have been key differences. For example, in Canada, there has been a policy of active clear-cutting and regeneration (large-scale forestry) in much of the

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[9] https://www.audubon.org/conservation/climate/naturalsolutions; accessed 9 July 2021

boreal zone, while the same has not been true in Alaska. Research focused on the differing outcomes of these differing strategies, with regard to carbon storage and uptake, is a little-explored avenue. Another parallel is a shift from large-scale clearcutting in coastal rainforests of British Columbia to ecosystem-based management. Most of the coastal rainforest of British Columbia's central and north coast—which are ecologically similar to the rainforests of southeast Alaska—are now managed under an ecosystem-based regime.

Besides basic research, there is a need to conduct more work on scenario planning to inform policy-making and management. Scenario planning can identify opportunities to shift land management and to meet desired states, or to avoid, mitigate, or enhance certain outcomes. Geodesign is one potential approach to move this type of integrated carbon futures assessment forward. Based upon deep stakeholder engagement (Steinitz, 2012), geospatial science, and scenarios that are socially and environmentally plausible (Trammell et al., 2018), geodesign futures can identify priority landscapes for a range of carbon storage solutions. Currently, the International Geodesign Collaborative is exploring the feasibility of the Trillion Trees Initiative using the geodesign principles of stakeholder-informed landscape planning. Regardless of the tool, the early involvement of local communities and stakeholders in identifying options for developing a climate stabilization and adaptation approach is likely to result in stronger, more durable outcomes for both biodiversity conservation and community wellbeing (Salomon et al., 2018). Additionally, and as information becomes available, quantitative assessments of how nature-based solutions can contribute to sequestration targets will be helpful to help guide investments and decision-making.

DISCUSSION

Avoiding the worst effects of climate change requires rapid decarbonization and improved ecosystem stewardship. Alaska, with its intact ecosystems and ecoregions with full rosters of native species—many with relatively healthy populations—provides a globally exceptional opportunity for protecting biodiversity in a context linked to natural climate solutions. As climate warms, intact systems will become more valuable as they have greater potential to provide superior resilience to climate change and will help buffer against frequent droughts and other disturbance events. Analysis of vegetation cover data for Alaska shows that significant changes are occurring, with implications for both the biodiversity and carbon storage potential of the nation. Natural climate solutions offer win-win solutions to the linked crises of biodiversity loss, accompanying cultural and traditional losses, and climate change. Managing lands for climate stabilization, adaptation, and resilience provides an opportunity to prevent degradation of ecosystems and to increase the ability of ecosystems to remove CO_2 from the atmosphere. Because Alaska is also globally significant for its large contribution to carbon storage, incentivizing land management to conserve and enhance this storage presents a significant opportunity for the United States to lead in natural climate solutions.

Quantification of the near-term contribution of various land management scenarios to climate emissions reduction and to long-term climate stabilization in Alaska is difficult due to significant data gaps. In 2018, researchers identified and analyzed 21 natural climate solutions in the contiguous United States and found that combined they could reduce global warming emissions by an amount equivalent to nearly 21% of United States net emissions in 2016 (Fargione et al., 2018). No such study has been performed for Alaska, which accounts for 19.3% of the United States land mass (US Census Bureau, 2012). Given the size and importance of Alaska's lands and waters and the magnitude of its accumulated carbon stores and potential climate stabilization services over time, however, it is clear that Alaska must play a prominent role in any knowledge-based, United States climate stabilization strategy.

Design of a natural climate solutions approach for Alaska should consider both western-scientific and Indigenous perspectives and be developed within a framework that acknowledges the value of human-environment relationships in fostering ecosystem integrity and human well-being. The early involvement of local communities and stakeholders in identifying options is likely to result in stronger, more durable outcomes. In particular, collaboration with Alaska's Indigenous communities, tribes, and landowners is necessary to develop an effective and socially just approach. Worldwide, there is a growing recognition that ecological knowledge and stewardship practices of Indigenous peoples can offer pathways for conservation and resources management that is not only effective but also socially just (Atlas et al., 2020). A stewardship approach that acknowledges the value of human-environment relationships in fostering ecosystem integrity and human well-being provides a framework for such collaboration (Chapin et al., 2015).

New research from the World Economic Forum ties half the world's GDP—$44 trillion dollars—directly to nature and its services[10]. The recent COVID-19 crisis has demonstrated the ability of the world's governments to mobilize trillions of dollars and there are a number of proposals emerging to tie environmental restoration and climate response to economic recovery. A climate stabilization and adaptation approach offers one framework to move beyond the incrementalism of protected area designation over the past couple of decades and to incentivize protection of intact lands that are already providing a myriad of benefits for biodiversity and humanity. Alaska, with its largely intact landscapes, wildlife values, and high carbon storage potential, is an opportunity for the United States to lead both in global climate and biodiversity conservation efforts.

AUTHOR CONTRIBUTIONS

CV and ED conceived of and drafted the manuscript. NF, ND, AJ, BL, KL, SR, FS, and ET contributed to ideas, writing, and editing of the manuscript. AJ and ET produced the figures. All authors contributed to the article and approved the submitted version.

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[10] https://www.weforum.org/press/2020/01/half-of-world-s-gdp-moderately-or-highly-dependent-on-nature-says-new-report/

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The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.