

# Effective Old-Growth Conservation Requires Coordinated Actions Across Scales of Space, Time, and Biodiversity.

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## Abstract

Effective conservation of old-growth ecosystems, along with their unique biodiversity and climate benefits, requires coordinated actions from the scale of individual trees to broad regions. The US government is currently developing a conservation strategy for old-growth forest on federal lands, and similar efforts are occurring globally as nations implement the Kunming-Montreal Global Biodiversity Framework. An effective strategy must include elements at three spatiotemporal scales: immediate restrictions on harvest of old-growth and mature forests and old trees, standards to ensure management activities do not degrade old growth at the stand scale, and longer-term planning for old-growth restoration and recruitment across landscapes. Lessons from previous US forest policy, especially the Northwest Forest Plan, can inform efforts to strengthen each of these three components in the US old-growth conservation strategy. Ecosystem-based standards are needed to ensure protection of sufficient mature forest so that recruitment into the old-growth stage shifts ecosystems closer to historic proportions of old growth. In addition to clarifying existing goals related to ecological integrity, comprehensive old-growth policy must incorporate specific goals for recovering at-risk species based on empirical relationships across scales of biodiversity between forest habitat and species viability that are relevant across varied ecological contexts. Reversing extinction debt and ensuring long-term adaptation potential requires designation of large landscapes anchored by remaining old-growth stands, surrounded by areas managed for restoration of ecological integrity, native biodiversity, and ecosystem services including climate change mitigation.

## 1 Introduction

Halting and reversing global loss of biodiversity requires conservation strategies and policies coordinated across multiple spatial scales and levels of biological organization (IPBES, 2019). Within forest ecosystems, old trees and old-growth forests are key features supporting global biodiversity and ecosystem services whose conservation exemplifies the challenges of coordinating actions across scales (Lindenmayer et al., 2012; Mackey et al., 2014; Lindenmayer and Laurance

2017). Ecologically, old trees are “keystone structures,” defined as distinct spatial structures having a disproportionately large effect on the presence and abundance of other species (Lindenmayer and Laurance 2017). Old trees add significantly to the diversity of plants and animals because of their structural complexity, adding both vertical and horizontal heterogeneity to a forest stand and creating diverse niches that enhance species diversity.

Various definitions for old-growth forest have been proposed based on tree age or size but also the unique characteristics associated with older stands that maintain their array of native species, processes, and functions (DellaSala et al., 2022b; Barnett et al., 2023; USDA 2024b). By any definition, old-growth forests are rare in the US (<7% of the forested landscape in the conterminous US (Barnett et al., 2023)) and most other nations. The structural and ecological characteristics of old-growth forests differ substantially among forest types and associated tree species, spanning a range from closed-canopy forests to open-canopied woodlands and savannas (Noss, 2012), which makes formulation of universal management strategies and conservation policies challenging. Old-growth forest landscapes typically contain a distribution of tree sizes and patches of younger-aged trees reflecting recovery from natural disturbances such as wildfires, windstorms, and insect outbreaks.

Because large, old trees can be removed quickly by cutting, but require hundreds of years to be renewed, old-growth trees and stands (a spatial scale intermediate between tree and landscape, defined here as areas of relatively uniform site conditions, generally <40 ha) are classic examples of remnant biodiversity or ecosystem elements that require immediate conservation action (Lindenmayer and Franklin 2020). However, such efforts will be insufficient to restore ecological integrity (Table 3) unless coupled with recovery of old growth at the landscape scale via spatial planning that addresses current threats and the ecological legacies of past deforestation and forest degradation.

Here, we use the policy debate surrounding old-growth forest conservation in the US to explore the essential elements of a coordinated old-growth conservation strategy. The US government is developing a conservation strategy for old-growth stands and mosaics on federal lands in the United States via the National Old-Growth Amendment (NOGA; USDA, 2024a), which provides guidance on conservation of old-growth forest conditions on 122 National Forest (henceforth Forest) management plans throughout the contiguous US (USDA, 2024a).

We explain why an effective old-growth conservation strategy must include elements at three scales: immediate restrictions on harvest of old and mature trees, standards to ensure management activities do not degrade old growth at the stand scale, and longer-term landscape planning for old-growth restoration and recovery. We explain why the NOGA as currently drafted falls short in each of these three areas, and suggest changes that will allow the policy to achieve its stated goals (USDA, 2024a).

We compare the challenges to devising effective US old-growth conservation policy across spatial and temporal scales (Table 1) with analogous issues in Canada and globally as nations implement the recently adopted Kunming-Montreal Global Biodiversity Framework (CBD, 2023). Because the NOGA’s limitations are also characteristic of old-growth policies in other nations, our recommendations are relevant to the global conservation of old-growth forests, primary forests (unlogged forests of all age classes; Kormos et al., 2018), and intact forest areas (Watson et al., 2018).

## **2 Evolution of strategies for conservation of old-growth forest on US federal lands**

In the US, old-growth forest conservation has historically been the subject of extensive research and policy debate (Spies et al., 2019; DellaSala et al., 2022b; Johnson et al., 2024). In particular, the evolution of forest policy in the US Pacific Northwest (PNW) illustrates the challenges faced when developing effective old-growth conservation strategies. We categorize historic and current policy into three types of strategies (Table 2). First, procedural requirements can be implemented to promote consideration of old-growth conservation during planning processes. These policies are applied during the general planning process and are not referenced to specific areas of the landscape. Secondly, stand-level old-growth characteristics may be conserved by restricting logging of trees above a certain size or by protecting old growth at the stand level. Thirdly, in portions of the landscape, landscape-level conservation strategies can be implemented to constrain or prohibit certain management actions (e.g., timber harvest). In theory, these three approaches can be complementary but have more commonly been implemented separately.

For US federal land management agencies, the procedural approach has the longest history. The USDA Forest Service (henceforth Forest Service), the primary federal agency charged with management of forest ecosystems, has historically operated under the philosophy of “multiple use” management in which extractive and non-extractive land uses would be balanced in local project-level decisions by managers to meet Forest-level objectives. In the period from the 1950s to 1990s, management objectives emphasized timber harvest largely to the exclusion of ecological consequences (Johnson et al., 2024). However, by the 1990s this approach became legally untenable, particularly in the PNW, due to incompatibility with legal mandates to maintain viable populations of old-growth dependent species. Public acceptance of the multiple-use approach also diminished due to increased awareness of the ecological, recreational, and aesthetic values provided by standing old-growth forests (Johnson et al., 2024).

In response to the inadequacy of existing procedural safeguards to ensure viability of at-risk species, the Forest Service imposed new restrictions on the harvest of large, old trees. For example, the 1994 “Eastside Screens” sought to limit the harvest of old-growth trees by restricting logging on federal lands to trees >53 cm dbh (diameter at breast height) east of the Cascade crest in Oregon and Washington. Initial conservation strategies for the Northern Spotted Owl (*Strix occidentalis caurina*) also sought to maintain habitat conditions suitable for dispersal between stands of old forest by imposing tree- and stand-level constraints on timber harvest (e.g., the “50-11-40 rule” to retain 50% of every quarter-township (2300 ha area) in stands with a minimum average size and canopy closure)(Thomas et al., 1990; Noon & McKelvey 1996).

Ultimately, size-based and stand-level guidelines were seen as inadequate to address the cumulative effects of past logging practices and the subsequent regional decline in old-growth ecosystems and associated species of concern. In 1994, multiple federal land management agencies developed the Northwest Forest Plan (NWFP) to guide management of ~100,000 km<sup>2</sup> of federal lands in the PNW (Spies et al., 2019; Johnson et al., 2024). Two aspects of the NWFP were comparatively novel for US land management planning. First, the NWFP coordinated actions by 10 federal agencies across 17 Forests, plus dozens of areas managed by other federal agencies. Second, broad-scale management direction sought to maintain viability of species and sustain ecosystem services by partitioning the landscape into distinct land-use designations wherein different management objectives would be emphasized (e.g., Late Successional Reserves (LSR) and Riparian Reserves received greater protection, whereas Matrix areas between Reserves provided for the majority of timber harvest)(Murphy and Noon 1992; Johnson et al., 2024).

### **3 Landscape-scale strategies for biodiversity conservation**

US laws, including the National Forest Management Act (NFMA), historically required the Forest Service and other federal agencies that manage older forests to maintain viable populations of old-growth-associated species (Johnson et al., 2024). Successful legal challenges to forest management in the PNW focused on flagship species such as the Northern Spotted Owl, Marbled Murrelet (*Brachyramphus marmoratus*), and at-risk salmonids (*Oncorhynchus* spp.). The NWFP sought to resolve litigation and recover these species by means of a landscape-level reserve design (Thomas et al., 1990). The NWFP's focus was not limited to old growth, but sought to conserve late-seral stands more broadly, in part because Northern Spotted Owls occupy mature forests with residual large old trees (Johnson et al., 2024). The system of late-seral stands in the reserve were selected so as to be locally stable, a result of including stands in sufficiently close proximity to allow for connectivity via dispersal and sufficiently dispersed so as to achieve spatial independence from disturbance events.. This strategy significantly departed from the previous focus on individual old-growth stands to multiple stands dispersed broadly across the landscape (Noon and McKelvey, 1996).

Protecting entire landscape mosaics made up of old-growth reserves embedded and connected within a multi-aged forest matrix would theoretically ensure persistence of species associated with old-growth as well as those species that selected earlier successional habitats (Harris 1984). Landscape planning that resulted in “lines on a map” also created greater transparency in what management the public could expect to see in different areas, thus potentially increasing societal buy-in and reducing litigation around individual projects.

The NWFP's landscape planning approach was informed by foundational principles and concepts of conservation biology, including metapopulation dynamics, species-area relationships, and allometric scaling laws (Table 3)((Murphy and Noon, 1996). These principles describe how ecosystems are governed by universal patterns and processes that operate at the level of the individual organism and transcend species identities in shaping patterns of biodiversity. These quantitative and predictive ecological theories and concepts have extensive empirical support and provide insights broadly applicable to the conservation old-growth species in diverse regions (Table 3). Although our focus is the ecological science underpinning the NWFP, we acknowledge that on-the-ground implementation inevitably varied across the 17 Forests over time (Spies et al., 2019; Johnson et al., 2024).

Old-growth trees and stands have a positive effect on landscape-scale species richness due to their contribution to habitat heterogeneity. Old-growth-centered landscapes have emergent properties for biodiversity beyond those provided by individual stands. Given the scarcity and fragmentation of old-growth forests (both globally and within the US), populations of dependent species primarily persist as isolated small populations in remnant patches. Given small patch sizes, species richness is low and extinction rates high especially for species with large area requirements (e.g., apex predators, wide-ranging species) and those with limited mobility including range-restricted endemics. The effects of habitat loss on the viability of large-bodied, slow life history species may be delayed for decades. This slow decline eventually leading to the species absence is called an “extinction debt” (Kuussaari et al., 2009).

A hallmark of the NWFP, when compared to previous project-level forest management plans, is that it considered conservation goals over longer time horizons and greater spatial extents (DellaSala et al., 2015; Johnson et al., 2024). Under the NWFP, some proportion of areas between old-growth stands were to be restored to a mosaic of patches of different ages including mature, naturally disturbed, and naturally regenerated early seral stands that retain standing old living and

dead trees as biological legacies (Swanson et al., 2011). Because individual stands of old growth will eventually experience loss to disturbance or senescence, a conservation strategy focused on sustaining and increasing the amount of old growth must also protect a significant amount of mature forest, especially in areas adjacent to existing old-growth stands. Assuring that recruitment of mature forest, at the landscape scale, exceeds the rate of old-growth mortality will move Forest Service lands closer to their historic range of variability. Large, old trees occurring individually or in remnant patches outside designated old-growth reserves also merit protection due to their ecological role as keystone structures that buffer and connect old-growth stands.

The NWFP was both a species- and ecosystem-focused strategy, combining viability modeling of individual species with landscape planning to conserve ecological integrity and ecosystem services (Noon and McKelvey, 1996). At the time, public attention was particularly focused on cumulative effects of timber harvest and associated road construction on water quality for downstream communities and at-risk salmonid populations. At the watershed scale, old-growth forests maintain hydrological cycles critical to sustaining aquatic and other biodiversity elements (Johnson et al., 2024). The NWFP's Aquatic Conservation Strategy and Key Watersheds were designed to ensure protection and restoration of water quality and associated aquatic biodiversity at an appropriate scale.

In 2012, revisions to the regulations implementing NFMA de-emphasized the previous mandate for viability of individual species in favor of more general goals based on ecosystem integrity and a more limited group of species of conservation concern (USDA, 2012; Schultz et al., 2013). Though not defined in measurable terms, ecological integrity is a central component of the Forest Service 2012 Planning Rule (USDA, 2012). The foundational elements of ecosystem integrity – ecosystem processes, stability and adaptive capacity (Rogers et al., 2022) – are all derivatives of the underlying biodiversity of a forest ecosystem (Mackey et al., 2023). However, the more generalized goals of the 2012 Planning Rule allow agencies more discretion and insulation from litigation than did the previous requirement to sustain the viability of all native species. This is especially of concern given how much is not yet known regarding the complement of old-growth-associated species and their interactions.

The NWFP's regionally coordinated landscape planning model informed subsequent ecosystem-focused plans including the Desert Renewable Energy Conservation Plan (DRECP) that coordinated biodiversity conservation in southeastern California to minimize conflicts with expansion of energy infrastructure (Kreitler et al., 2015). A zoning strategy was also implemented in 2001 for all Forest Service lands in the US. The National Roadless Area Conservation Rule added prohibitions on road construction and most timber harvesting on 237,000 km<sup>2</sup> of inventoried roadless areas that were >5,000 ha, to maintain these areas' unique ecological and recreational values (Talty et al., 2020). A more locally driven approach, in which individual Forests would adopt procedures to conserve their roadless areas, was initially considered for the 2001 Rule but rejected because potentially high variance in conservation strategies among Forests would undermine consistent application of the rule.

#### **4 Development of a national old-growth conservation policy**

Development of the NOGA results from increasing awareness that issues central to the NWFP (conservation of old-growth forests, at-risk species dependent on these forests, and ecosystem services) are relevant more broadly throughout the US and globally (White House, 2021, 2022). The amendment, currently issued in draft form for public comment, is scheduled for finalization by 2025

(USDA, 2024a). The federal effort to devise a national old-growth policy builds on previous US Executive Orders focused on old-growth conservation and climate change mitigation and adaptation (White House 2021, 2022). The NOGA includes the goal of ensuring long-term resilience and ecological integrity of old-growth forests under “rapidly changing climate conditions” (USDA, 2024a). The NOGA also states the intent to establish a clearer role for Indigenous Knowledge and tribal leadership in decision-making. Achieving these ambitious goals will require coordinated actions across disciplines and at a range of spatial and temporal scales.

The majority of the NOGA is devoted to adding and amending the procedures by which management planning occurs at the level of the 122 Forests and within their subunits, to ensure “a consistent management framework for conserving, stewarding, recruiting and monitoring old-growth forests” (USDA, 2024a). The NOGA’s approach favors procedural changes over prescriptive requirements and limitations on agency discretion, including decisions regarding timber harvest. The “top-down” approach that delineated management zones at the national scale, such as used in the 2001 Roadless Rule, was rejected by the NOGA’s authors because they concluded that “old-growth forests are dynamic systems and the intent is not to manage all of these areas in the same manner”; and that “strictly reserving mature and old-growth forest may not always ensure that it is protected from future losses” (USDA, 2024a).

Although the NOGA institutes new procedural steps to increase consideration of old-growth in Forest planning, it includes a broad exemption from these procedural requirements in “cases where it is determined that the direction in the amendment is not relevant or beneficial to a particular forest ecosystem type” (USDA, 2024a; section (b)(v.)). At the scale of old-growth stands, the NOGA does not restrict degradation of old-growth condition in contrast to provisions included in the NWFP. Instead, the NOGA emphasizes that “[t]here is no requirement that [old-growth forests] continue to meet the definition of old-growth when managed for the purpose of proactive stewardship.” (USDA, 2024a).

In place of a nationally coordinated landscape strategy, the NOGA calls for each of the 122 Forests (or groups of adjacent Forests) to develop an “adaptive strategy for old-growth forest conservation”. These adaptive strategies would set quantitative goals for old-growth forest conservation and determine if there is a need for changes in management practices to reach these goals. The NOGA lists among these goals ensuring adequate amounts, representativeness, redundancy, and connectivity of old-growth forest areas, as well as areas that function as climatic and fire refugia.

Because these criteria inherently involve mapped landscape elements, this suggests the need for landscape planning such as underpinned the NWFP. Although landscape plans do not necessarily involve reserves (i.e., areas where some forms of extractive use are restricted), “lines on a map” do by their nature limit the discretion of local managers. The NOGA’s emphasis on the widespread need for “proactive stewardship” suggests an aversion to establishment of designated landscape units with constraints on allowable actions (e.g., the NWFP’s LSR), in favor of an approach that permits intensive management and resource extraction, including commercial thinning and other timber harvest, wherever local managers deem it appropriate (Spies et al., 2018, 2019).

In the three decades since development of the NWFP, society has become more aware of the dynamic nature of forest ecosystems resulting from both historical disturbance processes and novel stressors (e.g., anthropogenic climate change, invasive species)(Newman, 2019). This awareness has led some to question whether an approach that uses “lines on a map” to encourage or prohibit certain

258 management practices is an appropriate and adequate management response to highly dynamic  
259 ecosystems (Spies et al., 2019).

260 At the same time as the NOGA is in development, the Forest Service is also revising the  
261 NWFP. The stated goals of the NWFP revision include facilitating active management for addressing  
262 fire disturbance and climate change, incorporating Indigenous knowledge, and ensuring a more  
263 predictable supply of timber from federal lands (USDA, 2023). A primary motivation for changes to  
264 the NWFP is the perception that the existing reserve-based strategy (e.g., the NWFP LSR) prevents  
265 fuels reduction via mechanical thinning and commercial logging from being implemented, and that  
266 these management activities are needed to avoid loss of biodiversity and ecosystem services due to  
267 high-severity fires (Spies et al., 2018, 2019). In the context of this ongoing debate, we address two  
268 related questions: (1) is a landscape-level conservation strategy involving reserves still appropriate in  
269 the PNW; (2) and more generally, to the diversity of old-growth forest types occurring across all  
270 Forest Service lands?

## 271 **5 Commonalities and contrasts in the context of old-growth conservation across ecosystems**

272 Given the diversity of forest types that support old-growth, across a range of ecological  
273 contexts and across multiple forest, woodland, and savanna communities in the United States and  
274 elsewhere our discussion is necessarily conceptual and illustrative rather than comprehensive. We  
275 propose that a landscape-level strategy analogous to the NWFP that identifies, protects, and connects  
276 old-growth trees and forest types remains broadly applicable.

277 Commonalities evident across US federal forestlands include the need for coordination  
278 among multiple land management units (e.g., Forests) within a region, a key element of the NWFP.  
279 Landscape planning is also broadly applicable to biodiversity conservation strategies in different  
280 ecosystems. Old-growth forest stands must form a minimum proportion of the landscape to recover  
281 old-forest-associated species such as the federally-listed Red-cockaded Woodpecker (*Dryobates*  
282 *borealis*) in the Southeast US (Noss, 2018). Populations of old forest-associated species outside the  
283 PNW may, like the Northern Spotted Owl, still be responding to historic loss of old-growth forest,  
284 leaving them vulnerable to additional cumulative losses absent rapid conservation actions to prevent  
285 further habitat loss. Within a given forest type, guidance to the target percent of the landscape to be  
286 old-growth forest can be based on the concept of the historic range of variation (Wiens et al., 2012).  
287 Coordinated landscape strategies also enhance the conservation of ecosystem services. The NWFP's  
288 Key Watershed approach, a zoning-based strategy for conserving water quality and associated  
289 aquatic species, is broadly relevant across ecosystem types.

290 The effects of climate, especially on increasing severity and frequency of fire disturbance,  
291 have been suggested as a reason for moving away from the 1994 NWFP's reserve-based strategy  
292 (Spies et al., 2018, 2019). In some respects, however, climate change makes landscape zoning and  
293 reserves even more relevant (DellaSala et al., 2015). Conservation of old-growth landscapes is  
294 increasingly seen as an essential contributor to climate mitigation, and enhancing the resilience of  
295 forest ecosystems and the adaptation potential of their components. Recovery of climate-stabilizing  
296 forest ecosystems is critical to long-term human well-being (Dasgupta, 2021). Comprehensive carbon  
297 budgeting on federal lands, including a focus on the value of old forest and its soils as long-term  
298 carbon stores, benefits from a zoning-based strategy for linking landscape pattern to ecosystem  
299 services (Law et al., 2021).

Protection and restoration of old-growth landscapes is also an effective climate change mitigation strategy via carbon sequestration and long-term storage due to accelerated carbon accumulation rates as trees and forest mature (Barnett et al., 2023). At the scale of individual trees, the largest trees in old-growth forests may represent just 1% of all stems yet store at least 40% of above-ground carbon as carbon stocks increases with tree size and age (Mildrexler et al., 2020; Stephenson et al., 2014). At the stand level, old-growth forests store 35 to 70% more carbon, including in the soils, compared to logged stands, highlighting their potential role in supporting natural climate solutions (Mackey et al., 2014, Law et al., 2021). In addition, unmanaged forests in the Northeastern US had higher carbon accumulation, increased structural complexity, and similar tree species diversity compared to managed forests (Faison et al., 2023).

The capacity of different portions of the landscape to act as climate change refugia also supports a landscape planning strategy that identifies and prioritizes refugia (a proposed but as-yet poorly defined element of the NOGA's adaptive strategies)(Carroll and Ray, 2021). Old-growth and mature stands, by creating microclimatic refugia, are ecosystem elements that inherently enhance the climate resilience of landscapes (Lesmeister et al., 2019). Fire disturbance frequency and severity differ widely across US forest ecosystems, but are typically influenced by landscape position, causing some stands to serve as transient or persistent topoclimatic fire refugia. Protection of such refugia via a zoning-based strategy can enhance pyrodiversity (landscape-scale variation in fire severity and frequency) and promote landscape resilience (e.g., by furnishing seed sources during post-fire recovery)(Krawchuk et al., 2016). Compared to younger forests, old-growth forests are expected to show considerable inertia in the face of climate change (Noss, 2001).

Independent of fire disturbance patterns, protection of old-growth stands situated in microclimatic refugia resulting from landscape position (e.g., via cold air pooling) can also promote ecological resilience and adaptive potential. Agency activities including timber harvest, wildfire suppression, and prescribed fire should incorporate refugia protection goals. However, implementing the NOGA's refugia protection goals will require substantial effort by agencies to develop and validate maps of refugia potential (Krawchuk et al., 2016; Stralberg et al., 2020; Keppel et al., 2024).

In addition to the commonalities described above, there are also important contrasts between the ecological context of old-growth conservation in different regions of the US. Many of these arise from contrasts in disturbance regimes, recovery trajectories, and the role of large trees and other vegetation layers in supporting biodiversity. There is wide variation among regions in the structural role of old trees in ecosystems. Although the closed-canopy forest of the coastal PNW is often used to illustrate "classic" old-growth forest, many old-growth "forests" are more accurately categorized as woodlands or savannas. For example, in eastside Cascades dry pine (*Pinus ponderosa*) and mixed conifer forests, large remnant trees are often scattered in small clusters across different age classes reflecting the consequences of recurring fires of mixed severity (Hessburg et al., 2015).

Although old-growth forests in many regions represent the latter age class of forest succession (Powell, 2012), the succession-to-climax model does not apply to all ecosystems. For example, longleaf pine (*Pinus palustris*) ecosystems in the southeastern US, which were once thought of as a "fire climax," are actually non-successional ecosystems, with different age classes of one dominant tree species but no discernable successional stages leading up to a climax state (Noss, 2018). Regeneration is limited to canopy gaps among patches of older trees due to higher temperatures of surface fires in areas with abundant fallen needles (Ellair and Platt, 2013).



Old trees in these ecosystems are keystone structures that facilitate development of herbaceous biodiversity by converting lightning strikes to surface fires (Platt et al., 1988). The spatial patchiness of old-growth trees in these savannas leads to relatively low densities of old pines required by Red-cockaded Woodpeckers and other old-growth dependent species. Thus, large blocks of pine savanna require protection to maintain viable populations of such species.

## **6 The role of mechanized vegetation management in old-growth forest conservation**

The NWFP reserve strategy was developed for a region where many forest ecosystems historically experienced infrequent, broad-scale fires. In contrast, the California Spotted Owl (*Strix occidentalis occidentalis*) Conservation Strategy for the southern Cascades and Sierra Nevada sought to preserve large trees without dividing the landscape into zones of differing management emphasis, due to the perceived need for continued fuels reduction including commercial logging throughout the landscape (Verner et al., 1992). This perceived contrast between appropriate strategies for mesic and xeric forest types still underpins much of the debate over the role of reserves in the conservation of US old-growth.

A broader spatial and temporal context is needed when discussing threats to old-growth ecosystems. The recent federal old-growth threat analysis focuses on amplification of fire and insect disturbance processes but mostly omits consideration of ongoing effects of historic forest loss and degradation, especially on non-federal ownerships within which federal forestlands are situated (USDA and USDI, 2023). Increasing disturbance frequency and severity (e.g., due to climate change) is a potential threat to some forest ecosystems, yet disturbance itself is an essential ecosystem process (Newman, 2019). The NOGA's goals of maintaining and restoring ecological integrity require a dynamic view of ecosystems that involves conserving key ecosystem processes such as fire and insect disturbances, which typically have effects distinct from anthropogenic disturbances such as logging (Swanson et al., 2011).

In ecosystems with a historic fire deficit (Ryan et al., 2013), the NOGA and associated policies should incentivize working with naturally occurring wildland fire for ecosystem benefits under appropriate conditions by preserving and restoring landscape-scale pyrodiversity within a the historic range of variability. This goal can be promoted by expanding opportunities for managed wildland fire and Indigenous cultural fire management, for example by eliminating current restrictions on use of fire suppression funds for managed wildland fire (Stephens et al., 2016). Landscape planning can facilitate increased use of managed naturally-occurring or prescribed fire (e.g., by designation of Strategic Fire Zones; North et al., 2024).

The NOGA defines "proactive stewardship" as vegetation management (including commercial timber harvest) that "promotes the quality, composition, structure, pattern, or ecological processes necessary for old-growth forests to be resilient and adaptable to stressors and likely future environments" (USDA 2024a). However, the appropriateness of considering vegetation management via commercial and non-commercial thinning depends on several factors, including the type of ecosystem, its fire and other disturbance ecology, the site-specific disturbance history, and current stand structure. Thinning of small-diameter understory trees (coupled with retention of old or large diameter trees) can be beneficial for biodiversity and ecosystem services, especially at the stand scale, in some forest types, although it may be less effective at addressing fire behavior or insect outbreaks at the landscape scale (DellaSala et al., 2004; DellaSala et al., 2022).

Increased fire frequency and severity due to climate change are most relevant to dry forests of the western US, but the effects of historic and ongoing fire suppression are evident in other forest types. For example, many pine (*Pinus* spp) ecosystems of the southeastern US have experienced declines in biodiversity due to fire exclusion and subsequent invasion by mesic hardwood tree species, which shade out the species-rich herbaceous layer (Noss, 2018). Restoration of these pine ecosystems may benefit from understory thinning and prescribed and cultural burning practices analogous to those implemented in western dry forests. Among the benefits are reduced risk of severe fire and accompanying carbon loss (Hurteau et al., 2008).

The NOGA's bias towards "proactive" vegetation management does not acknowledge that "passive" (i.e., non-mechanized) management may often be the most appropriate strategy. In ecosystems where fire is the dominant disturbance process, the appropriate role of thinning is as a pretreatment for prescribed burning or wildfire to restore natural stand structure and groundcover biodiversity. In such cases, the objective is to segue to fire treatments alone as quickly as possible (Rickey et al., 2013). Thinning is not an optimal strategy for restoring historic fire regimes where fire can be introduced without thinning, or when large fire-resistant trees are removed to financially support thinning projects (DellaSala et al., 2022a).

Given existing budgets and cultures of US land management agencies, there are significant challenges to implementing landscape-scale thinning strategies in a "nature-positive" manner. As in medicine, restoration treatments should be guided by the rule of "first do no harm" (Marker and Lindstrom 2017). Especially in mountainous regions, federal lands that retain old-growth stands are primarily areas costly to access and log, compared to previously harvested federal forested lands and private timberlands with extensive road networks (DellaSala et al., 2022b; Barnett et al., 2023). Subsequent to the initial harvest of primary forest, thinning of small trees is often not economically feasible unless remnant large old trees are harvested or funding is dedicated to restoration (e.g., "stewardship contracts" without a commercial logging component or additional road construction). Road construction to enable commercial thinning and fuels reduction of old-growth stands may have significant negative effects on watershed and aquatic species (Forman et al., 2003).

A comprehensive review of optimal management practices to restore beneficial fire regimes in different forest types goes beyond the scope of our paper. However, we note that there is greater societal and scientific consensus concerning positive effects of 1) fuels reduction around human communities, 2) changes in fire suppression strategies to facilitate managed wildland fire, 3) increased agency support for prescribed fire, and 4) restoration of Indigenous cultural fire practices that were historically suppressed by US land management agencies (Stephens et al., 2016; Spies et al., 2018, North et al., 2024).

All four approaches are compatible with an "adaptive strategy for old-growth forest conservation" which includes reserves as a major component. Support for Indigenous cultural fire practices forms part of our evolving concept of "reserves" as places where beneficial human activities are supported (Eisenberg et al., 2024). Although Indigenous peoples hold diverse perspectives on appropriate "land relationship" frameworks, Indigenous-led regional planning processes in Canada and elsewhere have designated extensive reserves where industrial activities are restricted to limit negative impacts on ecological and cultural resources (ICE, 2018). These examples demonstrate that reserve-based landscape conservation is compatible with Indigenous co-management and knowledge including cultural fire. Recent progress has been made at the global level in coordinating conservation goals with empowerment of Indigenous peoples via new

429 paradigms for Indigenous Protected and Conserved Areas (IPCA) and ‘other effective area-based  
430 conservation measures’ (OECM)(IUCN, 2019).

## 431 **7 The role of local discretion and national direction**

432 The NOGA includes a broad exemption from its new procedural requirements in “cases  
433 where it is determined that the direction in the amendment is not relevant or beneficial to a particular  
434 forest ecosystem type” (USDA, 2024a). The stated intent is to recognize that not all ecosystem types  
435 have the capacity to reach an old-growth forest development stage. This broad exemption to the goals  
436 of the NOGA is problematic. First, the exemption as written is not limited to certain ecosystem types  
437 and could be broadly applied by local managers. Although all forest types cannot be managed in an  
438 identical fashion, we are concerned that such broad discretion at the level of individual Forests may  
439 undermine the effectiveness and limit the national consistency of the strategy.

440 Federal land management agencies do not have a strong record of assessing cumulative  
441 effects absent coordinated policy direction such as seen in the NWFP or Roadless Conservation Rule.  
442 In the past, the majority of National Forests failed to comply with similar legal requirements that  
443 ultimately led to the lengthy litigation resulting in the NWFP. This failure is the result of multiple  
444 factors including: (1) a “philosophical” bias and educational focus in forestry to favor active  
445 management; (2) a desire to maximize agency discretion; (3) bureaucratic incentives tied to timber  
446 volume targets; (4) internal economic incentives that tie budgets to timber harvest (e.g., Knutson-  
447 Vandenberg Act funds); and (5) pressure from external industry and community groups that receive  
448 economic benefits from logging federal lands (DellaSala et al., 2022). The key challenge in designing  
449 a successful national old growth conservation strategy lies in balancing the flexibility to sustain and  
450 restore old-growth forest ecosystems across diverse forest types with a strong national policy that  
451 ensures consistency and effectiveness, and counters historic tendencies of agencies to ignore  
452 cumulative effects and respond primarily to socioeconomic factors that promote unsustainable  
453 logging practices including the harvesting of old-growth stands.

454 The second reason that the NOGA’s exemptions are problematic is that the ecological value  
455 of old growth is evident even in ecosystems that do not conform to classic successional models,  
456 including some of the specific exemptions mentioned in the NOGA. The NOGA would benefit from  
457 a more inclusive and ecologically informed definition of old-growth, and by incorporation of the  
458 concept of historic range of variability (HRV) as a starting point (Table 3). Each Forest should  
459 estimate the proportion of its landscape that would have historically been old-growth. This estimate,  
460 sets landscape-scale targets for forest composition, structure, and subsequent management actions,  
461 based on a commitment to protect and restore old growth representing all relevant ecosystem types,  
462 including by retention of mature forest that is ageing into the old-growth category via proforestation  
463 (Moomaw et al., 2019). HRV should typically be considered on an ecoregional scale. If management  
464 on non-federal lands favors shorter rotations, this implies that federal lands will have to be managed  
465 primarily for recovery of now-rare categories (typically including old growth and naturally disturbed,  
466 unsalvaged, and regenerating younger forests; Swanson et al., 2011) to compensate for shortfalls on  
467 non-federal lands.

468 The success of the NOGA’s “adaptive” strategies is contingent on developing improved  
469 methods for monitoring the status and trends of biodiversity across scales of space and time (Noss  
470 1990; Lindenmayer et al., 2012; Kuhl et al., 2020). Adaptive management implies long-term data  
471 collection across a system of controls and treatments, i.e., lines on a map with differing management  
472 in different areas. The NOGA includes aspirational goals regarding ecological integrity and

connectivity but does not provide guidance on how to establish control groups, baselines, measurable indicators, metrics, and targets to monitor achievement towards goals (Schultz et al., 2013; Brown and Williams, 2016; Mackey et al., 2024).

Recent progress on mapping mature and old-growth forest at multiple spatial scales (DellaSala et al., 2022; Barnett et al., 2023; USDA, 2024b) is highly relevant to the goals of the NOGA. Progress towards achieving the goals of the NOGA are dependent on the Forest Service developing an old-growth monitoring network (USDA, 2024a). To be useful in estimating temporal trends and management effectiveness, site-level monitoring information will need to be integrated with remotely sensed data sources. In turn, data on old-growth status and trends can be integrated into more broadly focused analyses such as federal lands carbon budgeting and the US National Nature Assessment (Carroll et al., 2023).

## **8 Analogous policy issues in old-growth conservation globally**

Despite global focus on the general goal of protecting old trees and old-growth forests (along with primary forests and intact forest landscapes), many specific old-growth policy issues remain unresolved in the US and other nations. For example, in the province of British Columbia, Canada, which encompasses extensive areas of coastal and interior old-growth forest (DellaSala et al., 2021), temporary deferral of logging has been implemented in a subset of priority remnant old-growth stands. The provincial government implemented these “emergency” deferrals in response to advocacy by communities, Indigenous peoples (termed First Nations in Canada), and non-governmental organizations, and in response to the threat of federal intervention to protect at-risk species (Northern Spotted Owl and mountain caribou (*Rangifer tarandus caribou*)) under the Canada’s Species At Risk Act (SARA). Concurrently, longer-term regional planning processes have been initiated in coordination with First Nations but have progressed at a slow pace in comparison to ongoing loss of old-growth forest (Carroll and Ray, 2021). Coordinating immediate stand-level and long-term landscape-level strategies is challenging in Canada as in the US.

Unlike the US, Canada is party to the Convention on Biological Diversity (CBD, 2023). In 2022, parties to the CBD adopted the Kunming-Montreal Global Biodiversity Framework (KMGBF), consisting of goals, targets, and indicators designed to reverse the decline of biodiversity and ecosystem services via transformative societal change that also addresses equity issues (CBD, 2023). The US, the only nation not a formal party to the CBD, nevertheless has endorsed many elements of the KMGBF, as well as related international pledges and agreements such as the Glasgow Leaders Forest Declaration and Paris Climate Agreement (White House, 2021, 2022).

Although provinces control most land-use decisions under Canada’s federalized governance structure, British Columbia’s old-growth deferrals and regional planning have received support from the federal government, in part to fulfill national-level commitments to KMGBF targets. Understanding the goals, targets, and indicators that make up the KMGBF is key in evaluating efforts by Canada and other CBD parties to implement meaningful old-growth policy. Although the KMGBF commits nations to halting the extinction of species (analogous to the mandates of the US Endangered Species Act and Canada’s SARA), many KMGBF targets focus on concepts such as ecological integrity that remain poorly defined (analogous to the NOGA)(Carroll et al., 2022).

KMGBF target 1 calls for expansion of biodiversity-aware spatial planning to halt the loss of “areas of high biodiversity importance, including ecosystems of high ecological integrity” (CBD, 2023). KMGBF targets 2 and 3, respectively, establish goals for restoring the ecological integrity of

at least 30% of degraded areas and establishing protected and conserved areas (the “30x30” commitment to protect 30% of the globe by 2030) in landscapes of particular importance for biodiversity and ecosystem services. These three targets in turn support KMGBF target 4’s biodiversity-element-based objectives to halt anthropogenically caused species extinctions and significantly reduce extinction risks. KMGBF target 8 (promoting climate adaptation and mitigation), and target 10 (ensuring sustainable forestry practices) are also highly relevant. Lastly, several targets focus on policy and planning processes: target 14 calls for better integration of biodiversity conservation into policy, target 21 for strengthening monitoring and data from both Western and Indigenous knowledge systems, and target 22 for ensuring participation of Indigenous peoples and historically unrepresented groups in decision-making.

The history of the CBD suggests that nations have struggled to implement individual targets in a holistic manner (Hughes and Grumbine, 2023). For example, although target 3 and its 30% goal for protected areas (30x30) has received most attention, protected areas are most effective when situated within sustainably managed landscapes (Carroll and Noss, 2022; Carroll et al., 2024). This suggests that global and national strategies focused on conservation of keystone ecosystem elements, such as old trees, should be embedded in broader landscape-scale strategies supporting viability of threatened species and ecosystem restoration efforts (Lindenmayer and Franklin, 2020; Carroll et al., 2022). An inclusive paradigm of “land relationship” planning, guided by integration of Western and traditional knowledge, as set forth in KMGBF targets 21 and 22, will be a key element of such strategies (ICE, 2018).

## **9 Conclusion**

Effective conservation of old-growth forests, along with their unique biodiversity and climate benefits, requires coordinated actions from the scale of individual large, old trees to entire landscapes. A comprehensive multi-scale strategy should include immediate restrictions on harvest of old trees, standards to ensure management activities do not degrade existing old-growth stands, and long-term landscape planning for old-growth restoration (Table 1). The draft US National Old-Growth Amendment requires major changes to address forest management across scales and to comply with legal requirements to manage forest so as to promote their ecological integrity. Our essay aims to propose changes needed before the NOGA is finalized, but also to inform long-term development of effective policy in the US and elsewhere.

Due to broad exemption and omissions, the NOGA lacks substantive protection for remnant old growth at the tree and stand scale. The current scarcity and long regeneration timelines of old trees make old-growth forests inherently vulnerable to cumulative impacts from active management (DellaSala et al., 2022). This vulnerability needs to be addressed immediately via two policies acting at the relevant scale of trees and stands: 1) an immediate moratorium on commercial harvest of existing old-growth trees, and 2) a standard requiring activities within old-growth stands to not degrade or impair old-growth condition, similar to standards included in the NWFP in relation to LSR and Key Watersheds, and in earlier draft NOGA language.

In developing effective policy in the US and globally, a focus on protection of old-growth trees and stands as keystone ecosystem elements is necessary but not sufficient absent coherent landscape strategies. Immediate actions to protect old-growth stands must be complemented by planning at broader spatial and longer temporal scales. Ecosystem-based standards should be developed to ensure sufficient extent of mature forest is protected so that recruitment of these stands into the old-growth stage, minus cumulative loss of old growth due to mortality and other factors,

560 shifts ecosystems towards to the approximate proportion of each forest ecosystem type that would  
561 have historically been old growth.

562 Bedrock US environmental laws such as the ESA and NFMA contain a fundamental  
563 responsibility to prevent species' extinctions, with habitat protection as the principal foundation of  
564 this effort. Compared to the 1994 NWFP, the NOGA and proposed NWFP revisions deemphasize the  
565 linkages between forest landscape composition and species viability, instead referencing as-yet  
566 poorly defined goals such as ecological integrity and resilience. The lack of specific goals for  
567 recovering at-risk species dependent on old-growth forests is a striking omission in the NOGA that  
568 must be addressed so that biodiversity is conserved across all scales from populations and species to  
569 ecosystems (Carroll et al., 2022)

570 Conserving and restoring ecological integrity is a foundational goal and legal requirement for  
571 the Forest Service (USDA, 2012; section 219.9a), and at the global scale is an element of multiple  
572 KMGBF targets (CBD, 2023). Because of their physical dominance and structural complexity, old-  
573 growth trees are a key biological entity in conserving ecological integrity (Brown and Williams,  
574 2016). The NOGA acknowledges that conserving old-growth stands and native species is central to  
575 conserving the ecological integrity of forest ecosystems (Wurtzebach and Schultz, 2016; Rogers et  
576 al., 2022). However, the ecological integrity goal suffers from a lack of specific metrics for its  
577 measurement. If a legal requirement is not measurable, how is it possible to assess attainment of that  
578 goal? Absent measurable targets, standards, and indicators, the commitment to ecological integrity  
579 will remain a purely aspirational goal (Brown and Williams, 2016; Mackey et al., 2024).

580 The NOGA's landscape-level planning element (the adaptive strategies for old-growth forest  
581 conservation) is still nascent and poorly defined, and lacks the strong guidance needed to shift  
582 management emphasis towards a vision for restoration of old-growth landscapes. Reversing  
583 extinction debt and ensuring long-term adaptation potential requires designation of large areas  
584 anchored by remaining old-growth stands, surrounded by areas managed for restoration of ecological  
585 integrity (appropriately defined in measurable terms), native biodiversity, and ecosystem services  
586 where management objectives explicitly include recruitment of additional old growth by allowing  
587 mature forests to develop over time (i.e., proforestation; Moomaw et al., 2019). The breadth of  
588 exemptions and discretion present in the NOGA as now written is inconsistent with such an  
589 ambitious and coordinated strategy.

590 National-level policies such as the NOGA should be coordinated with development of  
591 regional landscape conservation plans and complement ongoing revision of existing regional plans.  
592 The 1994 NWFP's insights that spatial landscape design is essential for effective conservation of  
593 species, services, and processes associated within old-growth forest ecosystems remains broadly  
594 relevant. Systematic conservation planning and landscape design are widely accepted fundamentals  
595 of conservation science and practice (Margules and Pressey, 2000; Kukkala and Moilanen, 2013). In  
596 place of the NOGA's broad generalizations regarding the need for "proactive stewardship",  
597 substantive discussion is needed of the varied ecological contexts presented by diverse old-growth  
598 types (including non-successional examples such as longleaf pine and other savanna ecosystems) and  
599 their implications for spatial landscape design. In most contexts, reserves in the broad sense (IUCN,  
600 2019) are necessary and compatible with practical strategies for ecosystem restoration and  
601 Indigenous co-management practices (e.g., cultural fire). Such areas can also help nations fulfill  
602 "30x30" commitments to conserve at least 30% of the landscape by 2030 (Carroll and Noss, 2022;  
603 CBD, 2023). In grappling with these conceptually and practically challenging questions, US  
604 conservation policy can be strengthened by consideration of the parallels between US and global

605 policy development as the world's nations work to implement the KMGBF by coordinating targets  
606 regarding inclusive spatial planning, protected areas, species viability, and ecosystem integrity.

607         The ultimate impetus for old-growth conservation efforts arises not only from our increased  
608 scientific understanding of these forests' contributions to biodiversity, climate, and ecosystem  
609 services. The impetus also lies in the evolution of society's vision for the role of forest lands,  
610 especially those held in the public trust by the federal government. Ongoing conflict between  
611 ambitious aspirational goals for restoration of nature and continued support for extractive industries  
612 by most national governments has also undermined efforts at the global level including  
613 implementation of the KMGBF. Conservation science cannot resolve this values-based debate but  
614 can help inform society as to the rising costs of the status quo and the ecological and social benefits  
615 of maintaining, recovering, and restoring functioning old-growth ecosystems.

616 **10 Tables**

617 Table 1. Examples of correspondence between spatial and temporal scales of policy action for old-growth conservation.

618

Spatial scale	Temporal scale		
	Immediate	Multi-year	Multi-decadal
Tree	Old-growth harvest moratorium, size limits		
Stand/site		Non-degradation standard for old-growth stands	
Landscape			Landscape planning, landscape-level restoration strategies
Regional		Ecosystem-specific old-growth recruitment goal	Monitoring
National		Non-ecosystem-specific goal	National status and trends monitoring



619 Table 2. Spatial scales of implementation of old-growth conservation, including past and current old-growth management policies and  
 620 corresponding laws and mandates. Acronyms used: ESA (Endangered Species Act), FLPMA (Federal Land Policy and Management Act),  
 621 KMGBF (Kunming-Montreal Global Biodiversity Framework), NEPA (National Environmental Policy Act), NFMA (National Forest  
 622 Management Act), NOGA (National Old-Growth Amendment), NWFP (Northwest Forest Plan), SARA (Species At Risk Act).

623

Spatial scale	Historic US strategies	US mandates	Canadian mandates	Global KMGBF targets
Procedural (aspatial)	Forest-level planning	NEPA, NOGA	Reconciliation-based planning	1, 14, 21, 22
Tree	Eastside screens			4, 10
Stand/site	California Spotted Owl recovery Strategy, 50-11-40 rule, Survey and Manage standard.	ESA, NFMA	SARA, province-level old-growth deferrals	3, 4, 8, 10
Landscape	NWFP	NFMA, ESA, FLPMA	SARA (national), Modernized Land Use Planning, Forest Landscape Planning (British Columbia), Reconciliation-based planning	1, 2, 3, 4, 8, 10

624

625 Table 3. Ecological concepts and theories relevant to old-growth forest conservation. The NWFP’s landscape planning approach was  
626 informed by these ecological theories and concepts which continue to provide insights broadly applicable to old-growth ecosystems in  
627 diverse regions.

Concept	Definition
Allometric Scaling Laws	Many studies have demonstrated that vertebrate species uniquely scale their spatial environment and that patterns of space-use (area requirements) are strongly correlated with differences in body mass (LaBarbera 1989). The non-linear relationship between body mass (M) and area requirements (Y) is best expressed as a power function of body mass (West et al., 1997), a general model for the origin of allometric scaling laws in biology. In addition, large-bodied species generally use more energy than small-bodied ones (Peters 1986). These relationships suggest that species occurring in old-growth forest with large area requirements and slow life histories, will occur at lower densities and be vulnerable to local extinctions.
Ecological Integrity	The US Forest Service uses ecological integrity as the fundamental concept to guide its assessment, land-use planning, and monitoring of forest ecosystems (Wurtzebach and Schultz 2016). Ecological integrity has been defined as a measure of the composition, structure, and function of an ecosystem in relation to the system’s <b>natural range of variation</b> (Mackey et al., 2023). For forest ecosystems, Rogers et al., (2022) propose key foundational elements including: (1) dissipative structures – especially forest structural complexity and carbon sequestration in late seral forests; (2) productivity (e.g. nutrient cycling) and regenerative capacity following disturbance; and (3) ecosystem resistance/constancy, resilience and persistence in the context of environmental variation.
Extinction Debt	Many animal species that select old-growth forest ecosystems have slow life histories (i.e., delayed age at first reproduction, low reproductive rates, and high survival rates). Species with slow life histories often show a delayed response to declines in the quality and extent of their focal habitats. For old-growth dependent species experiencing habitat loss, the expectation is that many will eventually become extinct as the forest reaches a new equilibrium. The number of extant specialist species of the focal habitat expected to eventually become extinct as the community reaches a new equilibrium is called the “extinction debt” (Kuussaari et al., 2009).

Habitat Heterogeneity Hypothesis	This hypothesis proposes “... that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity” (Tews et al., 2004). MacArthur’s classic study of warblers in late seral coniferous forests in the northeastern US provides empirical evidence of the roles of vertical and horizontal habitat heterogeneity in promoting bird species diversity (MacArthur 1958). At these diverse scales, heterogeneity develops from multiple factors including complex vertical and horizontal canopy structures, canopy gaps, extensive branching patterns, large cavities, deeply fissured bark, standing dead trees, downed logs, and extensive forest floor leaf and litter cover.
Historic Range of Variation (HRV)	The HRV concept is widely cited by the Forest Service as a useful metric to guide the management of forest ecosystems. The concept is based on the premise that keeping ecosystems within their historic bounds of variation will ensure their <b>ecological integrity</b> . Many definitions of HRV exists, but one closely tied to sustaining ecosystem integrity states that HRV is “...the spatial and temporal variation in composition, structure, and function experienced in an ecosystem from about 1600 to 1850 when the influence of European-American were minimal” (Dillon et al., 2005). Based on this definition, estimates of composition and structure could provide a rough approximation of the proportion of the landscape that was old-growth within the time period preceding Euro-American settlement. For biodiversity objectives, management might focus on the distribution of stand structural classes most likely to support native species and reflect environmental conditions prior to extensive harvest of mature and old-growth forests. 3Guidance provided by HRV estimates will need to reflect constraints imposed by data limitations, human land-use impacts and accelerating climate change (Romme et al., 2012).
Keystone Ecological Structures	As a consequence of their size, geometric complexity, and distinct spatial structure, old-growth trees provide critical resources for other species (Manning et al., 2006). For example, standing dead wood in mixed beech-maple forests may be a keystone structure, as the removal of this structure (through e.g., forest management) would significantly reduce the diversity of many species’ groups. A forest ecosystem type (e.g., old-growth coastal forests) may be dominated by a single type of keystone structure (e.g., old-growth Douglas fir trees). Several species groups may depend on this one keystone structural element which may positively affect biological diversity at multiple spatial scales (e.g., an individual tree, a forest stand, or ecosystem type).
Metapopulation Theory	Currently, old-growth forests of all types are rare and highly fragmented. For a given species, individual old-growth patches may provide colonists to other old-growth patches (source patches), or act as a receiver of colonists from source patches (sink patches) (Pulliam 1988). This group of spatially separated populations of the same species, interacting at some level via local colonization and extinctions, is called a metapopulation (Levins 1969). In general, for a metapopulation to be stable requires that dispersal be sufficient to recolonize vacant

	<p>patches. Because of the fragmented distribution of old-growth patches across the landscape, many old-growth species appear to be distributed as a metapopulation. Subpopulations can persist over time in a dynamic balance of extinction and recolonization events provided patches are sufficiently connected.</p>
Niche Theory	<p>The niche is that set of environmental resources and physical conditions essential for the survival, reproduction and persistence of a given species in the presence of biotic interactions. Species that occupy similar niches may compete when resources are limiting, leading to niche differentiation as an adaptive response to interspecific competition. By characterizing a species' niche, managers can predict how changes in environmental conditions, vegetation composition, or resource availability will affect species occurrences, abundances, and distributions. The theory also suggests that the diversity of species in an ecosystem is a result of the variety of niches available for species to occupy. High species diversity is essential to sustain the integrity and functioning of ecosystems.</p>
Population Viability	<p>In stable environments, the theoretical mean time to extinction (MTE) of local populations, subject only to demographic stochasticity, increases exponentially with abundance (Ovaskainen &amp; Meerson 2010). However, under conditions of environmental stochasticity (e.g., wildfire, timber harvest), MTE increases more slowly (as a power function) with increases in a species' abundance. As a result, high levels of environmental stochasticity can lead to high extinction risk even for large populations, particularly if their population growth rates are small. As for body size-abundance relationship, large bodied species selecting old-growth forests will be most vulnerable to population declines at both the local scale (as stand sizes decrease) and the landscape scale (as the number of old-growth forest patches decline).</p>
Species-Abundance Distribution	<p>In general, across taxonomic groups, most species within a given ecosystem type are rare. Because persistence likelihood of a given species scales positively with its abundance, most old-growth dependent species that have experienced habitat loss will be subject to increased probabilities of local extinction.</p>
Species-Area Relationship	<p>The relationship between species richness (S) and habitat area (A). S scales non-linearly with increases in the area of suitable habitat, and is often described by the power function <math>S = cA^z</math>, where, <math>c</math> and <math>z</math> are estimated parameters (MacArthur and Wilson 1967, Harte et al., 2009). One explanation for this positive relationship is based on the habitat heterogeneity hypothesis—that is, larger areas provide more habitat types. The importance of this theory is illustrated by an example concerning the loss of old-growth forests for late-seral obligate forest birds breeding in the Douglas-fir forest type. Pre-1900 estimates of the percent of the forested landscape in old-growth Douglas-fir were approximately 40% (Spies 2009). The current estimate (FS and BLM lands) is 17% (USDA, 2024a). This</p>

	decline in the extent of old-growth in the Douglas-fir type predicts an ~ 36% decline in number of breeding bird species.
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632            The authors declare that the research was conducted in the absence of any commercial or  
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