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Review

Resolving conservation conflict through fire refugia: Integrating landscape resilience into forest management

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A B S T R A C T

Increasing wildfire activity and uncharacteristically severe fires in fire-prone forests have intensified long-standing tensions between biodiversity conservation and wildfire risk reduction. In the Pacific Northwest, USA, fire exclusion has been practiced for over a century, driven largely by the perception of wildfire as a destructive force to be minimized. Over the past 35 years, northern spotted owl (*Strix occidentalis caurina*) conservation has emphasized the protection of closed-canopy, structurally complex, older forests, which are habitat conditions associated with long-term population viability. Together, these approaches have inadvertently contributed to fuel accumulation and increased vulnerability to high-severity fire. This creates a conservation conflict: how to protect an old-forest species adapted to historical fire regimes that produced heterogeneous landscapes but sensitive to large, high-severity disturbances. We propose a spatially explicit management framework that uses the concept of fire refugia—areas that consistently burn at lower severity than the surrounding landscape—for aligning habitat conservation with wildfire resilience. Historically, spotted owl nesting forests were likely disproportionately located within fire refugia, yet fire exclusion has allowed nesting habitat to expand into uncharacteristic locations at greater risk of loss and can contribute to abnormal fire behavior. Identifying where owl habitat aligns with fire refugia can guide protective strategies, while fire-excluded habitat may warrant active restoration to improve resilience and reduce risk. We draw on spatial modeling, empirical case studies, and fire ecology to demonstrate how fire refugia can serve as a decision-support tool in forest planning. We conclude with policy alternatives for integrating refugia-based approaches into forest management frameworks.

1. Introduction

The increasing occurrence of uncharacteristically severe wildfires across forested landscapes and management responses to the threat (Agee and Skinner, 2005) has revealed growing tensions between biodiversity conservation and forest resilience goals (Kelly et al., 2020). In the western United States, more than a century of fire exclusion has dramatically altered fire-prone forest landscapes and contributed to widespread fuel accumulation through densification of existing forests and forest expansion that has resulted in more homogeneous landscape conditions (Fig. 1; Hagmann et al., 2021). These structural changes have increased the vulnerability of many forests to uncharacteristic high-severity wildfire, particularly under contemporary fire weather conditions (Boisramé et al., 2022; Hessburg and Agee, 2003; Kreider et al., 2024). The effects of uncharacteristically severe fire on societal, economic, and ecological values draw much attention. Less is given to the slow adverse effects of fire exclusion on habitats for species that evolved within frequent-fire landscapes (Brodie et al., 2023; Odion and Sarr, 2007; Stephens et al., 2019). Providing a spatial context for addressing these changes and effects is important because location is critical for applying ecological insights to management (Brown et al., 2004; Gaines et al., 2015; Prichard et al., 2020).

Managers worldwide are increasingly challenged with attempting to simultaneously protect habitat for species of conservation concern and reduce wildfire risk (Driscoll et al., 2010; McLauchlan et al., 2020). This challenge affects diverse ecosystems including, but not limited to, North American conifer forests, Australian eucalypt woodlands, South African fynbos, and Atlantic Forests of Brazil (Bradstock et al., 2012; Godoy et al., 2025; Kraaij and van Wilgen, 2014; Odion and Sarr, 2007). The result in the Pacific Northwest, USA is a mounting policy tension: how to

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Fig. 1. Landscape comparison illustrating vegetation and forest structure changes resulting from over 75 years of fire exclusion, using panoramas from Bethel Ridge (elevation 1915 m) in the eastern Washington Cascade Mountains, 52 km East-South-East of Mt. Rainier, Okanogan-Wenatchee National Forest, Washington, USA. The historical image from 1936 (upper photograph) shows a relatively open landscape with patchy, low-density tree cover characteristic of frequent, low-intensity fire regimes. By contrast, the 2012 image (center photograph) shows dense forest cover resulting from decades of fire suppression, increasing susceptibility to insect outbreaks and high-severity wildfires. The widespread tree mortality in the 2012 photograph was caused by a mountain pine beetle (*Dendroctonus ponderosae*) outbreak. Wildfire effects from Schneider Springs Fire of 2021 can be seen in 2024 image (lower photograph). The upper photograph was taken on July 31, 1936, by George B. Clisby, U.S. Forest Service/National Archives and Records Administration, Seattle, WA. The center photograph was taken on July 06, 2012, by John F. Marshall, Okanogan-Wenatchee National Forest and Pacific Northwest Research Station. The lower photograph was taken on June 24, 2024, by John F. Marshall, Okanogan-Wenatchee National Forest.

reconcile the conservation of complex, old forest structures with the increasing need for proactive fire management in landscapes that have been dramatically altered from historical conditions and undergoing rapid ecological change (Ager et al., 2016; Halofsky et al., 2024; Hessburg et al., 2015; Prichard et al., 2021).

Habitat conservation for the northern spotted owl (*Strix occidentalis caurina*), a federally listed species under the U.S. Endangered Species Act (ESA), exemplifies this challenge. While the spotted owl is strongly associated with nesting in older forests with large trees and moderate to closed canopies (Forsman et al., 1984; Lesmeister et al., 2018), throughout much of its range populations occupy landscapes that were historically shaped by frequent, mixed-severity fires (Baker, 2015; Franklin et al., 2000). In these frequent-fire landscapes, spotted owl nesting sites tend to overlap with persistent fire refugia—locations that normally experience lower fire severity compared to the surrounding landscape (Camp et al., 1997; Downing et al., 2021; Lesmeister et al., 2021; Meigs and Krawchuk, 2018; Meigs et al., 2020). These areas, shaped by topographic and microclimatic factors, are more likely to develop and retain essential nesting forests and may buffer spotted owl populations from severe fire events (Andrus et al., 2021; Davis et al., 2019; Frey et al., 2016; Krawchuk et al., 2016; Meddens et al., 2018). This spatial association suggests that the presence of fire refugia was an important evolutionary driver of spotted owl nesting behavior. Outside of these refugial nesting locations, fire effects tend to be more variable, resulting in heterogenous forest conditions. Within these frequent-fire landscapes, this pattern aligns well with empirical models of northern spotted owl fitness, which indicates fitness is highest in heterogeneous landscapes containing interspersed blocks of nesting and foraging habitat (Franklin et al., 2000).

It is important to recognize that not all forests within the northern spotted owl's range have the same fire history. For example, the coastal regions of the Olympic Peninsula and portions of the Oregon Coast Range have historically supported more mesic, closed-canopy forests characterized by long fire return intervals and a predominance of stand-replacing or low-frequency fire regimes (Agee, 1993; Spies et al., 2018). In these systems, the relevance of fire refugia-based strategies may be more limited or take different forms. However, these areas tend to be less impacted by fire exclusion or the increasing frequency and severity of wildfire, thus fire-related management conflicts are less pressing in the coastal portions of the owl's range. Accordingly, this review focuses primarily on the more fire-prone landscapes of the Klamath-Siskiyou region and eastern Cascades, where reconciling fire resilience and habitat conservation presents a more pressing challenge.

The ongoing impacts of fire exclusion in fire-prone landscapes has facilitated the expansion of nesting forest into uncharacteristic locations resulting in 'fire-excluded' nesting forest—stands that have missed multiple natural fire return intervals due to human intervention. These stands, while structurally suitable for spotted owl nesting, are also more vulnerable to loss from high-severity fire and may lack the underlying biophysical characteristics that allow them to persist under shifting fire dynamics (Hagmann et al., 2021; Lesmeister et al., 2019). This pattern has created a spatial mismatch between current spotted owl conservation priorities and future forest resilience.

In this review, we synthesize current ecological and fire modeling research to propose a management framework that distinguishes between spotted owl habitat within fire refugia and habitat outside of these zones. By distinguishing between spotted owl nesting forest that occurs within fire refugia (i.e., fire-tended nesting forest) and that which is fire-excluded, land managers can tailor conservation and restoration strategies to local fire risk and ecological resilience. We argue that integrating fire refugia into conservation planning can help resolve long-standing conflicts between species protection and forest restoration goals in the Pacific Northwest and in other fire-prone regions globally. Similar approaches have emerged in Southern California, USA, where multiple groups motivated by species conservation have developed landscape-scale refugia frameworks and management strategies that consider multiple stressors, including altered fire regimes, hydrology, and recreation pressure (Rojas et al., 2021; USDA Forest Service, 2019). In other ecosystems, incorporating refugial capacity into conservation planning has been shown to enhance biodiversity persistence in dynamic, disturbance-prone landscapes (Balantic et al., 2021; Lawler et al., 2025). These efforts underscore the global relevance of conservation strategies that are spatially explicit and resilience-based. We believe that by using these strategies, land managers can make place-based decisions that simultaneously support timber harvest goals, biodiversity conservation, and long-term landscape resilience.

2. Wildfire in the Pacific Northwest

Historically, many forests of the Pacific Northwest were shaped by frequent, low-to moderate-severity fires that created fine-scale heterogeneity in vegetation structure and distribution in response to the complex interactions between topography, vegetation, and climate (Agee, 1993; Hessburg and Agee, 2003). These fire regimes promoted fire-tolerant species, maintained low surface fuel loads, and sustained forest mosaics with high ecological resilience (Hagmann et al., 2021; Hessburg et al., 2005). The resulting fire patterns fostered conditions that supported both biodiversity and disturbance-adapted structural complexity within forest stands and created a heterogeneous landscape mosaic (Donato et al., 2009; Odion et al., 2014; Perry et al., 2011; Reilly et al., 2017). Patches of unburned or lightly burned areas within larger fire perimeters served as refugia for various old forest adapted species, including the northern spotted owl (Baker, 2015; Clark et al., 2011; Duchac et al., 2021). These refugia provided temporal continuity to suitable habitats, served as a ready seed source to facilitate post-fire recolonization, and as a place of refuge for wildlife during and after fire thereby contributing to the resilience and stability of forest ecosystems (Andrus et al., 2021; Hessburg et al., 2016).

However, fire exclusion policies implemented across the 20th century, combined with reductions in Indigenous burning and land use changes that began about a century earlier, have disrupted these natural disturbance regimes (Ager et al., 2016; Greenler et al., 2024; Knight et al., 2020, 2022). While initially effective in reducing wildfire occurrences, suppression policies led to the continued accumulation of fuels, increased forest density, shifts in tree species composition, and expansion of nesting forests (Boisramé et al., 2022; Kreider et al., 2024; Parks et al., 2015). These stressors, along with increasingly hotter, drier, and longer fire seasons have increased the likelihood of fires burning under extreme weather conditions, which has resulted in more frequent and uncharacteristically severe wildfires, posing significant threats to ecosystems and species adapted to historical fire regimes (Abatzoglou and Williams, 2016).

In the case of the northern spotted owl, increases in the extent and severity of wildfires have been linked to declines in territory occupancy and survival, and loss of essential nesting forests (Lesmeister et al., 2019; Rockweit et al., 2024). Compounding the problem, fire-excluded forests now contain large areas of suitable spotted owl nesting forest that are increasingly vulnerable to stand-replacing fire (Baker, 2015; Jones et al., 2021). These forests often lack the structural and topographic characteristics that make persistent nesting forests more resistant to fire, such as those found in long-term fire refugia (Downing et al., 2021; Lesmeister et al., 2021).

The consequence is a paradox for both conservation and management: fire exclusion has preserved some spotted owl habitat in the short term, but it has also increased long-term vulnerability. Nesting forests that developed outside of fire refugia now face a heightened risk of loss to high-severity fire, threatening adjacent habitat persistence and complicating recovery timelines. Understanding these fire regime shifts is critical for identifying where protective or restorative actions are most urgently needed.

2.1. Wildfire effects on spotted owl habitat

Wildfires affect spotted owl habitat in complex ways, depending on fire severity, spatial pattern, and the occurrence of fire refugia. Low-to moderate-severity fires often preserve large overstory trees while reducing ladder fuels and dense understory vegetation, creating heterogeneous forest mosaics that support foraging without significantly degrading nesting and roosting conditions (Baker, 2015; Lee, 2018). These fires can also create canopy gaps that foster early seral vegetation and enhance prey availability (Franklin et al., 2000; Jones et al., 2020).

In contrast, high-severity wildfires, especially those occurring across large contiguous areas, can eliminate late-successional forest structure, including the large, decayed trees and complex canopy layers critical for nesting and roosting (Lesmeister et al., 2019; Sovern et al., 2019; Wilk et al., 2018). However, patches of high-severity fire, occurring at appropriate scales and locations within an owl's territory, may enhance foraging opportunities for spotted owls by resetting successional processes that lead to high quality prey habitat (Sakai and Noon, 1993). The extent of this impact depends on whether post-fire landscapes retain sufficiently large patches of old forest occurring in fire refugia, and the spatial pattern of post-fire vegetation. Spatial overlays of fire refugia models with maps of spotted owl nesting forest can reveal patterns of habitat persistence and loss that inform management priorities. For example, by overlaying a map of predicted refugial capacity with pre- and post-fire nesting forest models (Davis et al., 2022), we found that over the past 25 years, most of the spotted owl nesting forest that occurred outside fire refugia was lost to wildfire, whereas nesting forest within refugial areas was more likely to persist (Fig. 2).

2.2. Behavioral and demographic responses

Spotted owls across their range have consistently been found to continue to occupy burned areas when fires are lower in severity and sufficient amounts of the structural complexity required for nesting is maintained (Roberts et al., 2011; Rockweit et al., 2017). While lower severity fire appears essential for maintaining spotted owl nesting forest, higher severity burns may benefit spotted owls by enhancing foraging conditions in newly formed early seral habitats (Comfort et al., 2016; Jones et al., 2020; Kramer et al., 2021; Rockweit et al., 2024).

However, spotted owls tend to abandon territories predominantly affected by higher-severity fires, especially when nesting structures are lost. Post-fire displacement can lead to increased movement, shifts in home ranges, and use of lower-quality habitat (Rockweit et al., 2017, 2024). These responses may intensify competitive pressures from congeneric barred owls (*S. varia*), which are habitat generalists, increasingly occupy disturbed or transitional forest areas, and outcompete spotted owls for preferred sites (Jenkins et al., 2019; Lesmeister et al., 2018; Wiens et al., 2014). Increased turnover of territorial individuals reflecting reductions in territory quality have also been documented, highlighting the importance of spatial context for assessing impacts of fire (Clark et al., 2011; Rockweit et al., 2017).

2.3. Landscape context

At the landscape scale, the spatial distribution of fire severity and resulting habitat structure is presumed to play a critical role in determining spotted owl population outcomes (Franklin et al., 2000). Spotted owl persistence is more likely in landscapes characterized by a complex mosaic of fire severities, with nesting forests preserved in refugial locations that support nesting, roosting, and increased foraging opportunities (Rockweit et al., 2024; Schofield et al., 2020). Conversely, large, homogenous expanses of high-severity burns are strongly associated with territory abandonment and protracted recovery periods lasting decades or longer (Jones et al., 2016, 2017). This mosaic approach aligns with broader ecological findings in forest ecosystems that show prey populations and biodiversity benefit from enhanced pyrodiversity that results in a mix of burn severities and microhabitats (Bowman et al., 2016; Kelly et al., 2020).

While fire-excluded nesting forests may function as suitable spotted owl nesting habitat today, they are increasingly at risk of uncharacteristic, stand-replacing fire (Agee and Edmunds, 1992). These areas often lack microclimatic buffering, topographic protection, and historical fire-adaptation traits found in fire refugia (Davis et al., 2019; Downing et al., 2021; Frey et al., 2016). In many western US forest landscapes, the suppression-driven accumulation of ladder and surface fuels increases both the likelihood and severity of large fires, altering burn patterns and threatening habitat recovery (Mallek et al., 2013; Safford and Stevens, 2017). Recognizing this spatial mismatch between current habitat distribution and future fire risk is essential for prioritizing where management actions, either protective or restorative, are most urgently needed.

This spatial heterogeneity is especially important for spotted owl foraging ecology. Recent studies have demonstrated that heterogeneity, which is often achieved through low- or moderate-severity fires or fuels treatments, can enhance prey availability and predation success. For example, Wright et al. (2023) showed that California spotted owls (*Strix occidentalis occidentalis*) in the Sierra Nevada Mountains selected foraging areas with increased canopy base height, lower ladder fuel density, and reduced canopy bulk, all outcomes associated with fuels reduction treatments. These structural conditions are beneficial both for fire resilience and for supporting key prey species. Similarly, Zulla et al. (2023) found that territories with greater landscape heterogeneity had higher hunting success and breeding output than more homogeneous

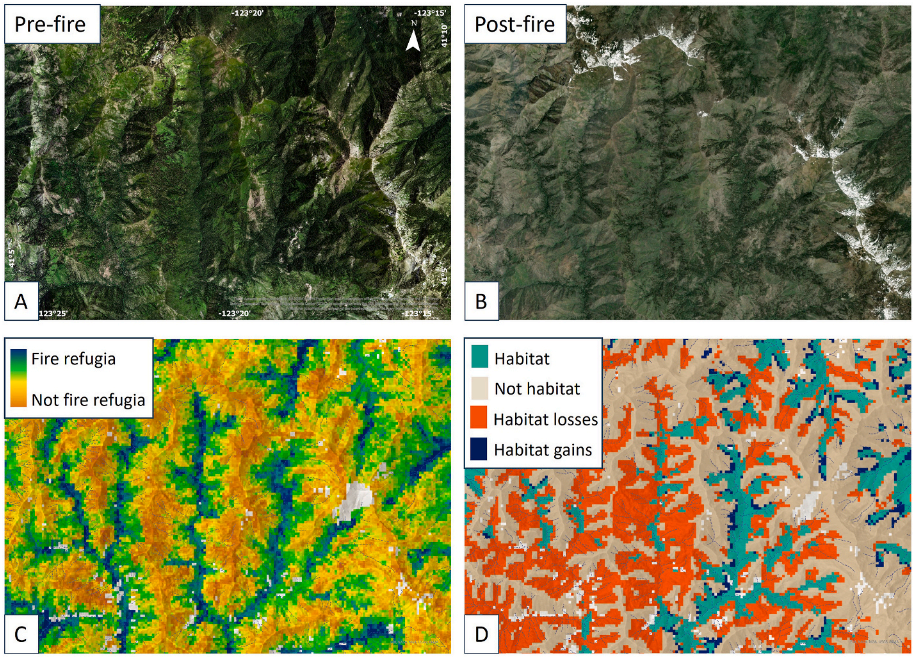

Fig. 2. Example landscape within the Trinity Alps Wilderness area of northern California, USA that was burned by the Red Salmon Complex in 2020, showing: (A) pre-fire satellite imagery, (B) post-fire imagery, (C) modeled fire refugia (Krawchuk et al., 2023), and (D) changes in northern spotted owl habitat (Glenn et al., 2017) post-fire. Teal areas represent spotted owl nesting habitat that persisted through fire; red shows habitat lost; dark blue indicates habitat gains from 1993 to 2017. Most nesting habitat loss occurred outside fire refugia and most of the habitat that had developed outside of it, owing to fire exclusion occurred on the western half of this picture (left half).

landscapes. These findings corroborate findings on fitness by Franklin et al. (2000) and work by Kuntze et al. (2023), who reported increased prey (dusky-footed woodrat; *Neotoma fuscipes*) captures in mosaics of mature and early-seral forest, highlighting the value of heterogeneous cover that fuels treatments can create. Together, these studies reinforce that targeted fuels reduction and restoration actions can directly benefit spotted owl fitness and population viability through improved foraging habitat, beyond reducing fire risk.

Incorporating a spatial assessment of fire mosaics into conservation planning aligns with landscape-scale approaches used in many fire-prone regions (Bowman et al., 2016; Pausas and Keeley, 2019). For example, in Mediterranean ecosystems, patch mosaic burning is recognized as an effective strategy for preserving biodiversity and reducing large, continuous burns (Moreira et al., 2011). Similarly, in savanna-woodland systems, models of fire-grazing interactions show that maintaining patch-level heterogeneity supports both wildlife and ecosystem function (Fuhlendorf and Engle, 2004). These parallels across ecosystems highlight the broad relevance of managing fire mosaics to balance risk and biodiversity, further reinforcing the rationale for spatially informed management in spotted owl landscapes.

3. Fire refugia

Fire refugia are areas that burn less frequently or at lower severity than the surrounding landscape due to interacting influences of topography, vegetation, and microclimate. These features moderate fire behavior that promotes persistence of older forests that supports species of conservation concern (Krawchuk et al., 2016; Meddens et al., 2018). Fire refugia commonly occur in north-facing slopes, drainage bottoms, riparian zones, and areas with high soil moisture or dense canopy cover that retains humidity and dampens fire spread (Fig. 2; Downing et al., 2021).

Importantly, fire refugia are not a binary feature of the landscape. Rather, they are probabilistic, representing a gradient of relative fire resistance shaped by both stable biophysical factors and dynamic conditions such as fuel moisture and fire weather (Krawchuk et al., 2020; Meigs et al., 2020; Moritz et al., 2010). Spatial models of fire refugia, including topo-climatic and holistic approaches, generate continuous probability surfaces indicating where refugial conditions are more or less likely to occur (Naficy et al., 2021). These gradients can help managers interpret model outputs not as fixed boundaries, but as tools for prioritizing conservation in areas with consistently high fire refugia probability while targeting lower-probability zones for resilience-focused management.

These fire refugia are not just ecologically distinctive, they also have critical implications for species conservation in fire-prone landscapes. In a synthesis of over 470 large wildfires spanning three decades and across the range of the northern spotted owl, Lesmeister et al. (2021) found that spotted owl nesting forests consistently burned at lower severity than the surrounding landscape. This consistent spatial association suggests that nesting habitat is more likely to occur in areas that have historically functioned as fire refugia. These areas, by burning less frequently or less severely, allow for the development and persistence of the closed-canopy, structurally complex, older forests required for nesting (Andrus et al., 2021; Lesmeister et al., 2021). While this pattern may not demonstrate strict co-evolution, it strongly suggests that spotted owls are evolutionarily adapted to landscapes shaped by frequent fire and spatial heterogeneity. Nesting and roosting typically occur in persistent fire refugia, while foraging behavior often extends into adjacent forest types that are more frequently disturbed or represent earlier seral stages. This spatial partitioning of ecological functions reflects a long-term adaptation to the dynamic structure of mixed-severity fire regimes.

Broader ecological theory and growing empirical evidence support the idea that vertebrate species, particularly those with strong site fidelity and low dispersal capacity, are often conditioned by the repeated presence of fire refugia in disturbance-prone systems (Nimmo et al., 2023; Robinson et al., 2013). This form of evolutionary conditioning suggests that species track and rely on landscape elements that consistently offer protection during disturbance events. Pausas and Parr (2018) argue that animal evolution in fire-prone ecosystems is often guided by spatial fire dynamics, with refugia serving as both survival and recolonization nodes. Keeley and Pausas (2022) further emphasize that persistent fire refugia can influence evolutionary pathways by maintaining lineage continuity in otherwise flammable systems. Lamont (2022) proposed that variability in fire regimes can shape species traits and constrain range boundaries. In this light, the consistent use of fire-sheltered areas by spotted owls for nesting may represent an ecological response that has been reinforced over evolutionary time. Recognizing this connection between species behavior, habitat persistence, and disturbance history is essential for developing conservation strategies that align with the spatial and temporal realities of fire-prone landscapes.

Despite the consistent spatial association between nesting locations and fire refugia, not all current spotted owl nesting habitat overlaps fire refugia. Some nesting habitat has expanded into areas where fire-excluded forests developed into suitable conditions due to suppression of natural fire regimes throughout the 19th and 20th centuries (Baker, 2015; Hagmann et al., 2021). These forests currently provide vegetation conditions that support spotted owl nesting but may lack the biophysical attributes that allowed them to persist under typical wildfire conditions. As such, they are more vulnerable to high-severity wildfire and post-fire habitat loss (Jones et al., 2021; Meigs and Krawchuk, 2018).

From a conservation and management perspective, fire refugia offer an ecologically grounded spatial lens through which to evaluate the long-term viability of spotted owl habitat. Identifying where nesting forest (a major component of habitat) coincides with fire refugia can help managers prioritize those areas for protective actions such as minimizing mechanical disturbance, limiting fuel treatments, or applying low-intensity prescribed fire to maintain refugial function. Conversely, nesting forest resulting from fire exclusion outside of fire refugia may benefit from ecological forestry practices that incorporate active restoration treatments to reduce the risk of stand-replacing fire, foster structural conditions associated with long-term persistence, and improve landscape scale resilience (Franklin and Johnson, 2012). Furthermore, restoration of fire-excluded nesting forests into historical cover types (e.g., oak woodland) that provided territorial heterogeneity and prey availability may result in improved spotted owl territory fitness (Franklin et al., 2000).

Fire refugia concepts can be operationalized within existing policy and planning frameworks. They offer a tangible way to incorporate landscape resilience into ESA recovery planning, U.S. National Environmental Policy Act (NEPA) ecological assessments, U.S. national forest plans, and nationwide fire management strategies such as the National Cohesive Wildland Fire Management Strategy (North et al., 2015). When combined with topographic templates, fire refugia models can inform spatial prioritization, helping land managers identify areas where high-value habitat overlaps with long-term fire resistance (Downing et al., 2021; Prichard et al., 2021). These concepts are also fully compatible with the revised recovery plan for the northern spotted owl which states (USFWS, 2011). In this way, fire refugia are more than a biophysical phenomenon, they represent a promising tool for resolving longstanding tensions between fire-adapted forest restoration and old-forest species conservation. With integration into policy-aligned planning processes, fire refugia may allow for more nuanced, spatially explicit management actions that increase both species persistence and forest resilience under shifting fire regimes (Enright et al., 2015; Hoecker and Turner, 2022).

3.1. Leveraging fire refugia in forest management

Fire refugia can serve as spatial anchors for differentiated management strategies, offering both an ecologically defensible rationale and a practical framework for aligning species protection with forest resilience goals. By prioritizing areas that have demonstrated persistence under past disturbance regimes, managers can hedge against future fire uncertainty and target investments in active management where the likelihood of long-term ecological benefit is highest (Andrus et al., 2021; Kreider et al., 2024). Identifying potential fire refugia across the landscape begins with spatial modeling techniques that incorporate historical fire severity, topographic position, canopy structure, and soil moisture indices (Downing et al., 2021; Meddens et al., 2018). When overlaid with species-specific habitat models (e.g., Davis et al., 2022; Glenn et al., 2017), these data layers can reveal where high-value nesting habitat coincides with persistent lower-severity fire patterns (Fig. 2). Such overlap identifies priority zones for protective or minimal-intervention strategies, including the reintroduction of low-intensity surface fires that retain large-diameter trees and snags and maintain dense canopy cover, thereby preserving conditions for nesting forest structure and microclimatic buffering.

Topography further refines the strategic placement and intensity of these treatments. South-facing slopes and other exposed positions tend to experience more intense fire behavior, while north-facing slopes and topographically sheltered areas such as riparian corridors are more likely to act as fire refugia (Downing et al., 2021; Krawchuk et al., 2016). Incorporating topographic context allows managers to anticipate variation in fire effects across the landscape and adjust fuel reduction strategies accordingly. This template-based approach improves the ability to target areas for passive protection or active restoration, depending on fire exposure and ecological resilience, while minimizing unintended impacts to sensitive species and habitat features (Hessburg et al., 2015).

Nesting forest that occurs outside of long-term fire refugia, particularly in fire-excluded forests, may require proactive restoration designed to emulate historical fire patterns and reduce the risk of uncharacteristically severe fire. In these areas, fuel treatments such as mechanical thinning, prescribed fire, and the selective removal of fire-excluded trees can help reintroduce structural heterogeneity by restoring a more natural arrangement of tree clumps, gaps, and variable canopy layers that reflect historical patch dynamics (Hessburg et al., 2015; Prichard et al., 2021). While such treatments often involve removing small and medium-sized trees that contribute to fuel loading, they can be designed to retain key structural elements, such as large, fire-tolerant trees and coarse woody debris that support wildlife habitat and ecological function (Brodie et al., 2024; Hessburg et al., 2015). Treatments could be tailored to local topoedaphic conditions to foster spatial heterogeneity that enhances forest resilience. Importantly, to ensure no harm to resident spotted owls, surveys prior to active management would be necessary. Further, restoration treatments would need to be conducted outside of the breeding season in areas with enough nesting forest within fire refugia, or in fire excluded forests not currently occupied by spotted owls.

Edge management is another critical consideration because forest stands with diffuse or gradual structural transitions at their boundaries, rather than abrupt edges, can support higher biodiversity (Duelli et al., 2002; Pöpperl and Seidl, 2021; Pryke and Samways, 2012; Schlegel, 2022). These gradual transitions buffer microclimatic extremes, reduce wind exposure, and support a richer and more stable understory community compared to sharp forest edges (Chen et al., 1995; Harper et al., 2005). In the Pacific Northwest, low-contrast forest edges of old forests enhance spotted owl occupancy and movement across landscapes (Comfort et al., 2016). These edge characteristics support structurally complex vegetation with multi-layered canopies and dense shrub cover, which in turn promotes spotted owl foraging success with higher prey abundance and movement (Linnell and Lesmeister, 2019; Sakai and Noon, 1997).

Maintaining or restoring diffuse edges around refugia, nesting forest, and treatment zones can improve habitat connectivity, reduce ecological fragmentation, and buffer interior forest structure from the effects of wildfire (Lesmeister et al., 2021). Edge conditions can influence fire behavior, where variations in fuel load and vegetation structure near forest edges may alter fire spread and intensity (LaCroix et al., 2008). Gradually transitioning fuel treatments outward from the core of refugial areas can reduce fire severity while maintaining key habitat features.

Finally, integrating fire refugia into U. S. forest management policy mechanisms, such as National Forest land management plans, ESA recovery actions, and NEPA analyses, can help institutionalize these approaches. Spatial fire refugia models and topographic templates provide science-based tools that can inform environmental assessments, prioritize areas for fuels reduction, support habitat conservation goals under changing disturbance regimes, and help meet the goals outlined in the National Cohesive Wildland Fire Management Strategy (Ager et al., 2016; North et al., 2015; Prichard et al., 2021). Taken together, these strategies illustrate how fire refugia can serve as a linchpin concept, both ecologically and operationally, for managing at-risk species and fire-prone landscapes in a unified, spatially explicit framework. Ultimately, this framing may help bridge the policy divide by shifting conversations from fire exclusion versus biodiversity protection to a resilience-oriented paradigm.

3.2. Little White Salmon project

The Little White Salmon Forest Resilience and Wildfire Risk Mitigation Project offers a compelling case of how fire refugia concepts can be integrated into forest management planning. Located in the Gifford Pinchot National Forest of southwestern Washington, USA, the Little White Salmon project spans over 68,000 acres of transitional mixed-conifer forests at the interface of the eastern and western Cascade ecoregions (USDA Forest Service, 2024). The region includes mature and old-growth forests, steep topographic variation, and areas with significant wildland-urban interface. To support risk-informed planning, managers incorporated advanced spatial models of fire refugia that estimate the likelihood of areas acting as low-severity fire refugia under varying fire weather scenarios (Downing et al., 2021; Krawchuk et al., 2023). These models were developed in collaboration with researchers and applied using interactive tools to overlay refugia probabilities with other resource values such as wildlife habitat, infrastructure, and vegetation condition (Naficy et al., 2021).

A unique strength of the Little White Salmon project lies in its use of two complementary modeling approaches: topo-climatic refugia and holistic refugia. Topo-climatic refugia identify areas where biophysical characteristics, such as north-facing slopes, riparian corridors, and areas with cool, moist microclimates, moderate fire behavior and reduce burn severity. These areas are derived from terrain and climate variables and represent long-term fire buffers that persist across fire events (Downing et al., 2021; Meigs et al., 2020). In contrast, holistic refugia models also integrate layers of ecological, cultural, and management values, including forest structure, vegetation composition, biodiversity, and Indigenous knowledge or local priorities. This broader lens allows land managers to identify not only where fire is likely to burn less severely, but also where the maintenance or restoration of fire refugia will most contribute to ecosystem function, biodiversity conservation, or community resilience (Krawchuk et al., 2023).

In the Little White Salmon project, fire refugia maps helped stratify management actions into distinct zones. Areas where both the topo-climatic and holistic refugia models scored high were prioritized for conservation-oriented strategies that minimize disturbance and preserve structural complexity, particularly in old forest patches with strong natural fire resistance. In contrast, areas with low refugia probability under both models were targeted for proactive fuel treatments, including thinning and prescribed fire. Notably, locations that scored high under the topo-climatic model but lower under the holistic model were identified as opportunities for ecological restoration to enhance forest structure and resilience in otherwise favorable terrain (Krawchuk et al., 2023). This differentiated strategy supports a nuanced form of landscape planning, recognizing which areas would be prioritized for protection, restoration, or strategically treated based on both fire exposure and ecosystem value.

This case illustrates the embedding of fire refugia modeling into collaborative planning processes, especially the use of interactive platforms to visualize treatment tradeoffs and explore refugia-based planning in real-time with stakeholders. The Little White Salmon project demonstrates how fire refugia can serve not only as landscape features to better understand ecosystem function but also as operational tools to guide investment, restoration, and conservation priorities. The ability to identify and protect habitat features most likely to persist through future disturbance aligns with previous research highlighting the importance of persistent landscape elements for sustaining northern spotted owl populations and guiding adaptive forest management under increasing fire risk (Davis et al., 2017; Lesmeister et al., 2021).

3.3. Southwestern Oregon fire refugia and spotted owl nesting forests

The 2013 Douglas Complex fire in Klamath Mountains of southwestern Oregon offers an example of how fire refugia can mediate the impacts of wildfire on northern spotted owl habitat. The mixed-severity fire burned nearly 20,000 ha during severe fire weather conditions across a mixed-ownership landscape, including the U.S. Bureau of Land Management lands managed for old forest conditions and intensively managed private industrial forests. This contrast in ownership and management created a natural experiment to evaluate how forest structure, topography, and prior land use influenced fire severity and ecological outcomes (Lesmeister et al., 2019; Zald and Dunn, 2018).

Two different studies highlight the variability in fire effects that may occur as a result of landscape position, prior land use, pre-fire forest structure, and ownership patterns. Lesmeister et al. (2019) used lidar-derived forest structure and owl demographic data collected before and after the Douglas Complex to show that spotted owl nesting forests experienced significantly lower burn severity compared to adjacent forest types. These nesting areas frequently overlapped with modeled fire refugia and were situated in north-facing slopes, riparian corridors, and other topographically sheltered settings with high canopy cover and large live trees. These features contributed to microclimatic buffering and reduced fire intensity. Notably, spotted owl occupancy persisted in many of these refugial areas after the fire, demonstrating that landscape position and structural complexity can buffer critical habitat even during large wildfire events. In parallel, Zald and Dunn (2018) analyzed fire severity within the same complex and found it was significantly higher on private industrial lands with homogenous, young plantations compared to older, structurally diverse forests on public lands. These results emphasize that both biophysical setting and land management history influence the likelihood that a forest will act as fire refugia.

The Douglas Complex has since played a formative role in shaping fire-adapted management strategies in the region. For example, in the South Fork Sacramento project, fire refugia maps that were partially informed from the Douglas Complex were used in the design of alternative treatments aimed at maintaining high-quality northern spotted owl habitat and persistent nesting forests (USDA Forest Service, 2023). This planning effort integrated spotted owl habitat models (Lesmeister et al., 2021) and persistent habitat layers (Davis et al., 2022) to co-develop treatments with federal wildlife agencies. The Bioregional Assessment of Northwest Forests (USDA Forest Service, 2020) also references fire refugia, including those derived from the Douglas Complex, as foundational to planning reserve networks that can persist under future climate and fire regimes. These applications demonstrate how spatial fire refugia science, grounded in empirical studies of fires like the Douglas Complex, is informing real-world management decisions aimed at integrating biodiversity conservation with fire resilience.

3.4. Sierra Nevada Conservation Strategy

Although focused on the California spotted owl, the U.S. Forest Service's 2019 Conservation Strategy for the California Spotted Owl in the Sierra Nevada demonstrates a structured approach to incorporating fire refugia into species conservation. The strategy explicitly recognizes that some nesting forest has persisted in fire refugia and prioritizes these areas for protective management (USDA Forest Service, 2019). Simultaneously, it calls for active restoration in fire-excluded stands, using thinning and prescribed burning to reduce future wildfire risk while retaining habitat structure.

The strategy offers valuable insights into the application of fire refugia concepts in forest management. One key lesson is the recognition that topographic position of many older, structurally complex forests can function as natural fire refugia due to their inherent resistance to high-severity fires. Protecting these areas would be important for maintaining habitat for old forest species through multiple fire events. Additionally, the strategic use of fuel reduction treatments, such as thinning and prescribed burns, can enhance the resistance of fire refugia by reducing the likelihood of active crown fire encroaching upon these critical habitats. Furthermore, adopting a landscape-scale approach that incorporates fire refugia into broader conservation planning ensures that management actions are contextually appropriate and support long-term ecosystem resilience. The strategy's operational guidance offers a replicable model for northern spotted owl management in the Pacific Northwest. Importantly, it also demonstrates how refugia-based thinking can be embedded within formal agency conservation frameworks.

3.5. Lessons learned

Together, these case studies highlight the practical relevance and flexibility of a fire refugia-informed approach to forest and species management. They show that refugia mapping, when coupled with species habitat models and topographic data, can inform where protective versus restorative actions are most appropriate. However, they also underscore challenges, such as the need for institutional support, inter-agency coordination, and the capacity to integrate spatial tools into planning processes.

From a policy standpoint, the key lesson is that fire refugia offer a bridge concept, linking ecological knowledge with operational forest planning in ways that support both biodiversity protection and wildfire resilience. As fire regimes shift, landscape-scale conservation strategies that incorporate this spatial nuance will be increasingly necessary to avoid blunt, one-size-fits-all management that fails to account for future fire exposure.

4. Discussion

This review addresses the perceived trade-off between conserving late-successional species and their habitat and reducing wildfire risk. This dilemma reflects broader tensions that affect fire-prone landscapes around the world. In the Pacific Northwest, conservation strategies for the northern spotted owl have traditionally focused on protecting old forest structure while limiting disturbance. While this approach has been instrumental for preserving habitat in the short term, it has also contributed to long-term vulnerability, particularly in frequent fire landscapes where forest stands have become denser and landscapes more structurally homogeneous due to fire exclusion, resulting in increased susceptibility to fire-induced loss (Hagmann et al., 2021; Hessburg et al., 2016; Kreider et al., 2024).

Overlaying fire refugia maps with high-value spotted owl nesting forest offers a promising strategy for addressing this conservation conflict. By identifying the spatial co-occurrence of fire refugia and critical habitat, managers can develop conservation strategies that reflect differences in ecological resilience and fire exposure. Where habitat overlaps with persistent fire refugia, protective management that maintains structural integrity and microclimatic stability may be most appropriate. In contrast, where nesting habitat occurs outside of fire refugia, particularly in fire-excluded forests, active restoration such as ecological thinning or prescribed fire may be necessary to reduce risk while maintaining key habitat features. This spatially informed approach aligns with growing calls for landscape-scale management that accounts for historical disturbance patterns and contemporary risk profiles (Hessburg et al., 2015; Prichard et al., 2021).

Importantly, fire refugia is not only an ecological concept, but also offer a practical tool for spatially informing conservation decisions and forest management. Recent advances in spatial modeling, coupled with improved data on topography, vegetation, and fire history, allow managers to predict refugial areas with increasing accuracy. These models can be incorporated into existing planning mechanisms, including NEPA environmental analyses, ESA recovery plans, and land management decision-support systems (Ager et al., 2016; Downing et al., 2021). Integrating refugia-based planning into these tools can support more proactive, risk-informed management strategies that enhance both species conservation and fire resilience.

The integration of fire refugia into forest planning is consistent with broader calls for ecologically based, landscape-scale forestry. Franklin and Johnson (2014) emphasize the importance of aligning management with disturbance-adapted forest dynamics and creating mosaics that better reflect historical fire regimes (Hessburg et al., 2015, 2016). These perspectives are well-aligned with fire refugia concepts as spatial anchors for management differentiation, allowing managers to protect structurally complex areas while applying restoration treatments in more vulnerable zones. They are also well-aligned with our knowledge of spotted owl habitat associations in frequent fire landscapes. Kramer et al. (2021) found that California spotted owls are well adapted to fire-managed landscapes with a mix of stand conditions, lending empirical support to the idea that restoration and conservation are not mutually exclusive. Koontz et al. (2020) further demonstrated that forests with large, fire-resistant trees and heterogeneous structure are more likely to withstand high-severity fire, reinforcing the value of treatments that promote such conditions.

In California's Sierra Nevada, North et al. (2007) showed that combining thinning and prescribed fire in historically frequent-fire forests helped restore structural complexity and reduced future fire intensity. These findings are directly applicable to parts of the spotted owl's range that have missed multiple fire return intervals and now support fire-sensitive habitat in uncharacteristic locations. Together, these studies suggest that the strategic integration of fuel reduction and habitat restoration, informed by spatial models of fire refugia, can support both resilience and conservation objectives.

Despite these opportunities, institutional and policy challenges remain. Many existing land management frameworks are not yet designed to accommodate probabilistic concepts like fire refugia, nor are they flexible enough to incorporate evolving fire behavior models into conservation targets. Coordination across jurisdictions is particularly challenging in the Pacific Northwest, where multiple federal, state, tribal, and private stakeholders manage interspersed forest lands with differing mandates. These complexities mirror those described by Hessburg et al. (2016), who highlighted the necessity of navigating ecological and social trade-offs in mixed-severity forests.

To overcome these barriers, managers may elect to embed fire refugia concepts in collaborative governance structures that include scientists, land managers, and community stakeholders. Informed co-production of management plans, bolstered by ecological forecasting tools and adaptive feedback loops, will likely be most successful. Lessons from previous policy efforts, such as the limitations of the Northwest Forest Plan's adaptive management areas, show that without institutional support, even ecologically robust strategies may fail to achieve long-term outcomes (Franklin and Johnson, 2014; Spies et al., 2019).

5. Conclusions

As land managers seek to balance wildfire risk reduction with habitat conservation, fire refugia can provide a critical planning tool that is both ecologically grounded and operationally practical. The findings presented in this review echo broader calls for a shift toward ecologically based, place-specific forestry that reflects natural disturbance regimes (Franklin and Johnson, 2014; Hessburg et al., 2015). By identifying fire refugia and overlaying them with species-specific habitat models, land managers can better inform proactive conservation that anticipates disturbance impacts and leverages ecological resilience.

Moving forward, the success of fire refugia-based strategies will depend on their integration into policy frameworks such as active forest management, NEPA planning, ESA recovery plans, and broad-scale wildfire risk reduction initiatives. Ongoing investments in ecological modeling, public engagement, and cross-jurisdictional collaboration will be necessary to institutionalize these approaches and ensure that the lessons learned from past forest policy efforts translate into actionable, durable solutions.

CRediT authorship contribution statement

Damon B. Lesmeister: Writing – review & editing, Writing – original draft, Visualization, Resources, Conceptualization. **Raymond J. Davis:** Writing – review & editing, Visualization, Conceptualization. **Jeremy T. Rockweit:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

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

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