



Impacts of wildfire on spotted owls in California: a bioregional-scale data synthesis

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Funding information

U.S. Forest Service; U.S. Fish and Wildlife Service; Sierra Pacific Industries

Abstract

Wildfire has been a fundamental component of ecosystem dynamics for millennia. However, climate change, fire suppression, and land use practices have produced larger, more severe, and more frequent fires that threaten a range of wildlife species. Land managers in some fire-prone forest systems use fuels reduction treatments, including prescribed burning and mechanical thinning, to reduce vegetation density and the risk of large, high-severity fires. The strategy is to create forest landscapes that are more resilient to wildfire, which in turn will lessen the negative impact of uncharacteristically severe wildfire on wildlife. Yet there is uncertainty regarding the extent to which fire-adapted species are threatened by novel wildfire characteristics. The spotted owl (*Strix occidentalis*) has become a focal point for this controversy owing to its use of fire-suppressed forests that have been and will be vulnerable to changing fire regimes in the future. In this study, we attempted to address the question of how spotted owls respond to high-severity fire in California, USA, by leveraging 1) over 3 decades of detection–non-detection surveys in 1,514 historical spotted owl territories and 2) global positioning system (GPS) movement data from 171 individual spotted owls. Our study area included 7 national forests, 3 national parks, and extensive

privately owned forests in California. Dynamic occupancy analysis indicated that spotted owl territories were more likely to become vacant and less likely to be colonized if they experienced recent and extensive high-severity fire. Consistent with the occupancy analysis, our movement analysis indicated that individual spotted owls avoided using severely burned forest. Although spotted owl territory persistence was higher in pyrodiverse territories (i.e., those with a mixture of low, moderate, and high severity burned areas), foraging owls showed mixed responses to local pyrodiversity, with some evidence that use of severely burned forest increased when pyrodiversity was high. We conclude that large and severe wildfires threaten the persistence of spotted owls in California. That said, forest restoration and fuels reduction treatments that reduce the risk of large and uncharacteristically severe fires while promoting multi-scale heterogeneity and pyrodiversity will likely benefit spotted owls and other species that occupy mixed conifer forests in California.

KEYWORDS

California, disturbance, megafire, occupancy analysis, spotted owl, *Strix occidentalis*, wildfire

Impactos de los incendios forestales en el búho moteado en California: una síntesis de datos a escala biorregional **Resumen**

Los incendios forestales han sido un componente fundamental en la dinámica de los ecosistemas durante milenios. Sin embargo el cambio climático, la supresión de incendios naturales, y los cambios antropogénicos de la tierra han producido incendios más grandes, intensos y frecuentes que amenazan a una variedad de especies nativas. En algunos sistemas forestales propensos al fuego, los propietarios de tierras utilizan tratamientos de reducción de combustibles, incluyendo las quemas controladas y la limpieza mecánica, para disminuir la densidad de la vegetación y el riesgo de incendios extensos y de alta severidad. La estrategia consiste en crear ambientes forestales más resilientes al fuego, lo que a su vez reducirá el impacto negativo de incendios inusualmente severos sobre la vida silvestre. Aun así, existe incertidumbre al respecto al grado en que las especies adaptadas al fuego están amenazadas por características emergentes de los incendios. El búho manchado (*Strix occidentalis*) se ha convertido en un punto focal de esta

controversia debido a que su uso de bosques donde el fuego ha sido, y seguirán siendo suprimido, es vulnerables a los cambios en los regímenes de incendios en el futuro. En este estudio intentamos responder a la pregunta “¿Cómo responden los búhos manchados a incendios de alta severidad en California, EE. UU.?” aprovechando: 1) más de tres décadas de encuestas y de detecciones en 1514 territorios históricos de búhos manchados, y 2) datos de movimientos por GPS de 171 individuos. Nuestra área de estudio incluyó siete bosques nacionales, tres parques nacionales y áreas extensivas de bosques privados en California. El análisis de ocupación dinámica indicó que los territorios de búhos manchados tenían mayor probabilidad de quedar vacantes y menor probabilidad de ser colonizados si habían estado afectados por incendios recientes y extensos de alta severidad. De manera consistente con este análisis, nuestro estudio de movimiento mostró que los búhos solitarios evitaban usar bosques severamente quemados. Aunque la persistencia de búhos en los territorios fue mayor que en territorios “pirodiversos” (es decir, aquellos con una mezcla de áreas quemadas de baja, moderada y alta severidad), los búhos en forrajeo mostraron respuestas mixtas a la pirodiversidad local, con cierta evidencia de que el uso de bosque severamente quemado aumentaba cuando la pirodiversidad era alta. Concluimos que los incendios grandes y severos amenazan la persistencia del búho manchado en California. La restauración forestal y los tratamientos de reducción de combustibles que disminuyen el riesgo de incendios grandes e inusualmente severos, promueven la heterogeneidad y la pirodiversidad a varias escalas. Esta estrategia también beneficiará posiblemente a los búhos manchados y a otras especies que habitan los bosques mixtos de coníferas en California.

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INTRODUCTION

The importance of wildfire in ecosystems

Fire is a natural process that can drive spatial and temporal patterns of biodiversity (Bond and Keeley 2005, White et al. 2016). Disturbance regimes can also influence ecological processes and the evolution of life-history traits in species (Lytle 2001, Jones et al. 2023) because disturbance events can exert sufficient influence on species such that natural selection fosters adaptation (Connell 1978). The characteristics of a region's fire regime—severity, return interval, configuration, size, and seasonality—that are driven by elevation, latitude, climate, topography, and vegetation (Archibald et al. 2013, McLauchlan et al. 2020) provide this consistent selective force. Wildlife that inhabit fire-prone landscapes have evolved fire-adapted or fire-dependent traits (Nimmo et al. 2021, Jones et al. 2023). Species considered to be fire-adapted have evolved traits, often behavioral, that allow them to survive fires (Hovick et al. 2017, Matthews et al. 2017).

Climate, topography, vegetation, and productivity interact to drive and limit fire regimes, which in turn produces a range of forest types (van Wagtendonk et al. 2018) that are used by wildlife. Fire regimes of western North American forests are typically limited by either climate or fuels (Hessburg et al. 2019, Hagmann et al. 2021). Climate-limited fire regimes occur in forests where prevailing conditions are typically too cold or wet to carry fire (Wasserman and Mueller 2023). When climatic events like droughts occur, an abundance of dried vegetation in typically moist, dense stands facilitates large-scale and severe fires in which most or all of the live vegetation is killed (Hessl et al. 2004). In contrast, fuel-limited fire regimes occur in forests where the climate produces vegetation that is commonly dry enough to carry fire. As a result, fires in such forests burn frequently, and limited fuel accumulates between burns (Safford and Stevens 2017). These conditions typically result in a landscape dominated by low to moderate burn severity interspersed with small patches of high-severity or stand-replacing fire. Gradients in fire behavior and predictability—for example, from fuel-limited to climate-limited regimes—drove the accumulation of different types of behavioral, physiological, and other adaptive traits in animals across broad geographies (Pausas and Parr 2018). Such traits remain largely adaptive under a stable fire regime, but rapid changes to fire

regimes have the potential to produce fire-trait mismatches and erode fitness in fire-adapted species (Nimmo et al. 2021).

Changing fire regimes

Historically, fire drove ecosystem processes and maintained biodiversity in many systems, but Eurocentric land-use change, novel biotic assemblages, socio-economic drivers, and climate change resulting from human population growth and behavior have altered global fire regimes (Kelly et al. 2020). In western North American seasonally dry forests, fire suppression over the last roughly 150 years has resulted in broad-scale densification and homogenization of forests (Lydersen and Collins 2018), compositional shifts towards fire-sensitive tree species, and increased continuity of fuel loads (Safford and Stevens 2017). These effects were exacerbated by the repression of Indigenous management practices (Liebmann et al. 2016) and selective harvesting of large, mature trees (Hessburg and Agee 2003). As western North American dry forests have become more homogenized and prone to stand-replacing fire, climate change has led to rising temperatures, more frequent and extreme droughts, and more extreme fire weather (Westerling 2016). These factors, often interacting, have created a perfect tinderbox for ignitions—the majority of which are caused by humans (Balch et al. 2017)—resulting in large-scale, high-severity fires that are uncharacteristic for this ecosystem (Skinner and Chang 1996).

Disturbance events that deviate substantially from historical ranges of severity and extent can have lasting ecological consequences. While wildlife show varied responses to fire (Brunk et al. 2025), uncharacteristic fires often fail to yield fine-scale forest heterogeneity typical of historical fires, degrade habitat for forest specialists, and create novel interspecific dynamics in ecosystems (Delheimer et al. 2019, Jones et al. 2021, Steel et al. 2022). More homogeneous and severe fires can reduce foraging opportunities by eroding resource complementarity (Kelly et al. 2015), eliminate shelter or nesting opportunities, prevent recolonization in the subsequent years following a disturbance, and directly lead to wildlife mortality (Nimmo et al. 2019, 2021).

Disrupted disturbance regimes pose an existential threat to forest ecosystems and wildlife in the coming decades. In 2020 and 2021 alone, 100 vertebrate species had over 10% of their geographic range in California, USA, affected by large wildfires that contained uncharacteristically large patches of high-severity fire (Ayars et al. 2023). Climate change projections suggest that area burned in western North America may double or triple by 2050 (Westerling et al. 2011), which will also increasingly affect humans (Kolden 2020). While some animals appear resilient to change and exhibit adaptations or phenotypical plasticity to disturbance events like fire (Jager et al. 2021, Jones et al. 2023), others may become locally extinct in such dramatically altered landscapes (Jones et al. 2021).

Restoration as a solution to safeguard ecosystems

Many species that are vulnerable to the negative consequences of uncharacteristic fires may benefit from proactive management that modifies landscape structure to better resemble historical fire-adapted forests and creates forests that are more resilient to future fires (Hagmann et al. 2021). Fuels reduction treatments, which are the primary adaptation strategies for reducing the risk of uncharacteristically severe fire (Agee and Skinner 2005), have been shown to change fire behavior and mitigate the ecological impacts of wildfires (Vaillant et al. 2009, Prichard et al. 2020, McKinney et al. 2022, Ott et al. 2023).

Some uncertainties remain regarding the efficacy of fuels reduction treatments and their impacts to ecosystem processes (North et al. 2012, 2021; Franklin and Johnson 2012; Hessburg et al. 2020). Mechanical treatments and prescribed fire, the 2 main fuels management strategies in North America, have both been shown to mitigate extreme fire behavior and maintain fire-resilient forest structure, but such effects can be ephemeral if treatments

are only applied once (Stephens et al. 2012). Both mechanical treatments and prescribed fire can result in undesirable impacts to the ecosystems in which they are applied. For example, mechanical forest restoration can damage soils and impede nutrient cycling (Neary et al. 1999), fuel breaks can provide establishment sites for some nonnative plants (Merriam et al. 2006), and some combinations of fuels reduction techniques can harm standing trees (Collins et al. 2014). Nevertheless, there is widespread consensus that when applied appropriately, fuels reduction treatments can be highly effective in achieving ecological and social objectives (Hagmann et al. 2021, Hessburg et al. 2021, Prichard et al. 2021).

Forest restoration, high-severity fire, and spotted owls

Proactive management and forest restoration may have unintended consequences for sensitive forest-dependent wildlife species, though the benefits of modifying fire behavior can outweigh the risks (Pilliod et al. 2006, Kalies et al. 2010, Truex and Zielinski 2013). The spotted owl (*Strix occidentalis*) has been at the center of controversy regarding forest management in the western United States for nearly 5 decades (Forsman 1976, Verner et al. 1992, Gutiérrez et al. 1998, Franklin et al. 2021), with lingering uncertainty about the relative impacts of forest restoration and wildfire on this forest obligate (Lee and Irwin 2005; Tempel et al. 2014, 2015; Peery et al. 2019; Wood and Jones 2019; Kramer et al. 2021b). Spotted owls, which have experienced population declines since the mid-twentieth century because of a combination of many factors, have continued to decline across much of the 3 subspecies' (*S. o. caurina*, *S. o. occidentalis*, *S. o. lucida*) ranges (Jones et al. 2018, Wan et al. 2018, Franklin et al. 2021, Tempel et al. 2022). In the late twentieth century, much of the concern over the influence of forest management on spotted owls pertained to the effects of commercial logging (Jones et al. 2018). In recent years, concern has shifted to the potential for fuels reduction treatments to exacerbate long-term population and habitat declines (Gutiérrez et al. 2017).

Empirical studies on the effects of fuels reduction on spotted owls have been conducted, but they have been limited in various ways. In the Sierra Nevada, spotted owls (*S. o. occidentalis*) responded negatively to intensive and homogeneous defensible fuel profile zone (DFPZ) fuels treatments (Stephens et al. 2014, Gallagher et al. 2019). However, measurement of effects may have been confounded by a barred owl (*Strix varia*) invasion and the fact that the study did not account for imperfect detection. In the same region, a study by Tempel et al. (2014) showed statistically non-significant negative effects of medium-intensity mechanical treatments on spotted owl reproductive output and weak but positive effects of high-intensity mechanical treatments on spotted owl territory persistence. Another study showed that spotted owls across California preferentially foraged in areas with higher canopy base height, lower ladder fuel density, and lower canopy bulk density, which are conditions that can be created by fuels treatments (Wright et al. 2023). Finally, a study leveraging passive acoustic monitoring across the Sierra Nevada found evidence that a combination of low- and high-intensity fuels management—while retaining nesting and roosting habitat—can increase spotted owl occupancy (McGinn et al. 2025a). Generally, empirical evidence of the species' response to fuels treatments has been mixed and may depend on the intensity and spatial arrangement of the treatment and pre-treatment conditions on the landscape.

A key to understanding the net effects of fuels treatments on spotted owls is understanding the extent to which the species is adversely affected by increasingly large, high-severity fires. For example, fuels reduction treatments might be expected to provide indirect benefits to spotted owls and other species threatened by severe fire by modifying fire behavior and reducing the spread of stand-replacing fire (Figure 1). If spotted owls respond negatively to large, high-severity fires, then treatments could result in more resilient owl populations compared to others inhabiting untreated forests (Tempel et al. 2015, Jones et al. 2022). On the other hand, if spotted owls continue to occupy severely burned landscapes post-fire, then there would be little justification—from the perspective of the owl—to conduct fuels treatments in spotted owl habitat (Hanson 2021).

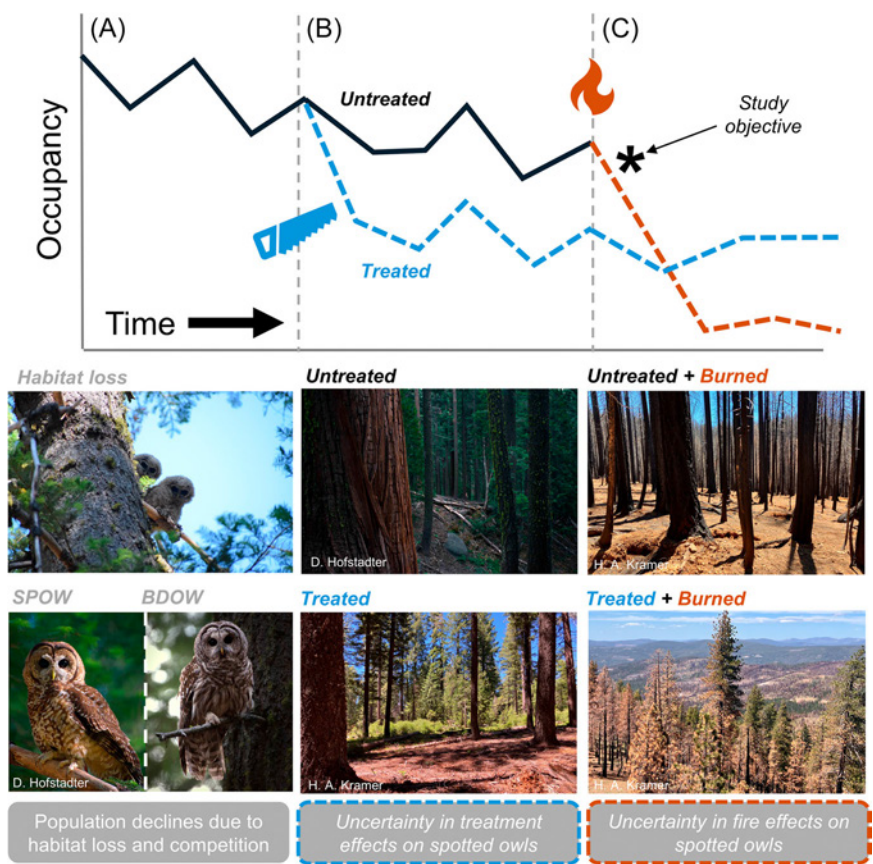


FIGURE 1 Conceptual diagram of key issues facing spotted owl persistence. Uncertainty in the literature is delineated by dashed lines. A) For the past few decades, northern and California spotted owls (SPOW) have declined across much of their range in response to habitat loss and fragmentation, often resulting in the loss of nesting and roosting habitat, and have faced threats associated with the encroachment of nonnative barred owls (BDOW; Lesmeister et al. 2018). B) Proposed fuels reduction treatments have uncertain impacts on spotted owls, and treatments that eliminate a relatively high proportion of canopy cover may have negative consequences for spotted owl nesting habitat. C) The impacts of fire on spotted owls in both treated and untreated habitat are also uncertain. In untreated habitat, there is lingering uncertainty that high-severity fire poses an existential threat to spotted owls in California. If uncharacteristically severe fire poses a sufficient threat to spotted owls, then the potential negative impacts of fuels treatments on spotted owls may be outweighed by the benefits of reducing the relative amount of high-severity fire that burns spotted owl territories. If high-severity fire does not pose a sufficient threat to spotted owls in California, then fuels treatments may not benefit spotted owls. The star indicates the uncertainty we attempted to address in this study.

The impact of fire on spotted owls is understood to vary across subspecies, regions, and ecological context (Wan et al. 2019, Jones et al. 2020a). Across their entire geographic range, spotted owls evolved under a range of fire regimes including infrequent, high-severity fire regimes in the western Cascades of Washington and Oregon, USA. In California, spotted owls evolved under a lower severity but frequent fire regime, and individuals exhibit behaviors that reflect apparent adaptations to such fires (Kramer et al. 2021b, Jones et al. 2023). Despite many studies that have examined this species' response to fire, the role of fire as a driver for the distribution, demographic rates, and behaviors of spotted owls has generated controversy (Gutiérrez 2020). This controversy may originate from variation in spotted owl responses based on their ecological contexts or pre-fire management history

of the landscapes in which they occur. For example, spotted owls tended to use areas of high pyrodiversity (i.e., areas characterized by a mixture of burn severities) following the King Fire where pre-fire forests were a patchwork of National Forest System and private lands (Jones et al. 2020b), but owls did not select similar burn characteristics across several national parks that were more frequently treated with prescribed fire and had a greater background level of vegetation heterogeneity (van Wagtenonk 2007, Kramer et al. 2021b).

Fire's effect on spotted owls varies across space, time, and ecological scales and, accordingly, may influence scale-dependent and spatially partitioned behaviors (e.g., nesting versus foraging behaviors) in different ways. Historical fires, which created burn mosaics, likely preserved areas of persistently unburned, late-seral forest constituting one type of fire refugia (Meddens et al. 2018) that may have contributed to generating suitable nesting and roosting habitat in proximity to a variety of foraging habitats (Jones et al. 2025a). Extensive severe fire that eliminates the majority of live canopy leads to a long-term loss of nesting habitat for spotted owls, which primarily limits where the species can occur on the landscape (Ganey et al. 2017, Jones et al. 2021). Severe fire can also kill large trees, which play a role in the species' nesting, roosting, and foraging behaviors (Barrows 1981, Zulla et al. 2022, McGinn et al. 2023a). On the other hand, there is some evidence that when burn severity in a fire is spatially heterogeneous and patchy, fire may improve hunting success of spotted owls in mixed-conifer forests by creating edges between forest age classes (Jones et al. 2020b, Zulla et al. 2022, McGinn et al. 2024). Spotted owls will sometimes forage along the edge of even very large patches of high-severity burn but will not travel far into them, rendering much of their area inaccessible (Jones et al. 2020b).

Spotted owl responses to fire may also reflect variation in methodological approaches. Following the 2013 Rim Fire, a study using data from unmarked spotted owls collected during the subsequent breeding season showed no apparent impact of high-severity fire on occupancy rates (Lee and Bond 2015). Another study using a before-after-control-impact framework with individually marked owls revealed immediate and persistent negative effects of high-severity fire on spotted owl occupancy following the 2014 King Fire (Jones et al. 2016a 2021). These differences in the effect of high-severity fire may be due to studying unmarked versus marked individuals, where estimating occupancy of unmarked birds could mask fire effects (Berigan et al. 2019). At the same time, an individual-agnostic acoustic study investigating the effects of fire over a 30-year period showed that spotted owls were unlikely to occupy sites that experienced high-severity fire that burned up to 2 decades prior (McGinn et al. 2025b). Studies of spotted owl foraging habitat selection have shown positive, neutral, and negative responses to severe fire. Positive responses have been shown in studies that do not control for high-severity patch size and configuration (Bond et al. 2009, 2016). In contrast, studies that explicitly model high-severity patch size and configuration have found that individual owls avoid large and homogeneous patches (Jones et al. 2020b, Kramer et al. 2021b).

For these reasons, a more complete understanding of the response of spotted owls to fire is needed and should be derived from robust longitudinal data and analytical techniques. Hopefully, such analyses will offer greater certainty regarding spotted owl responses to fire, allowing forest managers to proceed in developing adaptive strategies for conserving spotted owls as the climate warms and fire regimes continue to change (Moritz et al. 2012). If large, predominantly high-severity fires threaten the persistence of spotted owls across their range, then forest restoration may be necessary to limit an existential threat to the species. If uncharacteristically severe wildfires do not pose a substantial threat to spotted owls, then forest restoration may not be necessary from the perspective of owl conservation.

Data synthesis to address key issues of uncertainty and controversy

To resolve long-standing uncertainty in spotted owl responses to high-severity fire (Figure 1), we examined spotted owl responses to high-severity fire and pyrodiversity across an entire bioregion, multiple decades, and multiple ecological scales. First, we integrated multiple long-term, longitudinal detection–non-detection datasets across

5 national forests, 2 national parks, and privately owned land in California to examine the impact of fire on the occurrence dynamics of 2 subspecies of spotted owls that occur in California (*S. o. caurina*, *S. o. occidentalis*). Notably, we only examined northern spotted owl occupancy at the southern periphery of their range. We structured the data to reflect a before-after-control-impact framework to enable a robust analysis (Popescu et al. 2012, Conner et al. 2016) of the direct impacts of fire on spotted owls. We used a Bayesian approach (Royle and Kéry 2007) to examine results within a probabilistic framework rather than approximating the presence or absence of a statistically significant effect. We predicted that fire characteristics typical of severe megafires (i.e., extensive areas of high-severity fire) would result in individuals abandoning previously occupied territories, while frequent fire characteristics typical for the region (i.e., lower-severity fire and higher pyrodiversity) would be correlated with individuals persisting on the landscape. We predicted that territories experiencing more high-severity fire would be less likely to be colonized by owls, and owls inhabiting those territories would be less likely to persist. We also predicted that spotted owls would be more likely to colonize and remain in territories that experienced higher local variation in burn severity (i.e., higher pyrodiversity).

Second, we integrated data from multiple global positioning system (GPS) tagging projects to examine the movements and foraging behaviors of 171 individual spotted owls relative to post-fire territory characteristics. These owls occurred across 7 national forests, 2 national parks, and privately owned land. We expected that individual habitat selection would reflect the foraging opportunities afforded by mixed-severity fire and the degradation of nesting and roosting habitat caused by high-severity fire. Specifically, we predicted that individuals would avoid severely burned forest and preferentially select forests characterized by higher fine-scale pyrodiversity. For managers to make decisions that effectively conserve spotted owls and manage frequent-fire forests in a rapidly changing climate, a better understanding of this species' relationship to high-severity fire—specifically one that reconciles discrepancies across regions, populations, ecological scales, and prior studies—is necessary.

STUDY AREA

We combined detection–non-detection data from 9 study areas for our occupancy analyses. The Lassen (LAS), Eldorado (ELD), and Sierra (SIE) were long-term demographic study areas with typical landownership patterns in the Sierra Nevada, consisting mainly of public land managed by the United States Department of Agriculture (USDA) Forest Service but overlapping some privately owned land (Figure 2). The Sequoia-Kings Canyon (SKC) study area was located entirely within 2 national parks of the same name. The RIM, CHIPS, and MOONLIGHT study areas comprised spotted owl territories within the perimeters of the Rim Fire (2013), Chips fire (2012), and Moonlight fire (2007), which burned approximately 100,000 ha, 30,000 ha, and 25,000 ha, respectively. In study areas consisting mainly of public land managed by either the USDA Forest Service or the National Park Service (LAS, ELD, SIE, SKC, RIM, CHIPS, and MOONLIGHT), surveys were for California spotted owls. In study areas that occurred in or adjacent to land owned and managed by Sierra Pacific Industries (SPI_CS0 and SPI_NS0), surveys within the Sierra Nevada targeted California spotted owls and surveys in Northern California were for northern spotted owls.

We examined the movements and foraging ecology of spotted owls based on GPS data from individuals on both public and private lands. Specifically, we GPS-tagged California spotted owls on the LAS, ELD, SIE, the Plumas National Forest (PLU), the Tahoe National Forest (TAH), the Stanislaus National Forest (STA), the San Bernardino National Forest (SBN), Yosemite National Park (YOS), SKC, and land owned by Sierra Pacific Industries (SPI) in the Sierra Nevada. We GPS-tagged northern spotted owls on the Shasta-Trinity National Forest (SHA) and adjacent private land owned by SPI.

Elevation in these study areas ranged between 300 m and 2,500 m, where spotted owls occurred at higher elevations farther south. Most spotted owl territories in our study were in the Sierra Nevada, where forests were dominated by ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). Generally, hardwood species were California

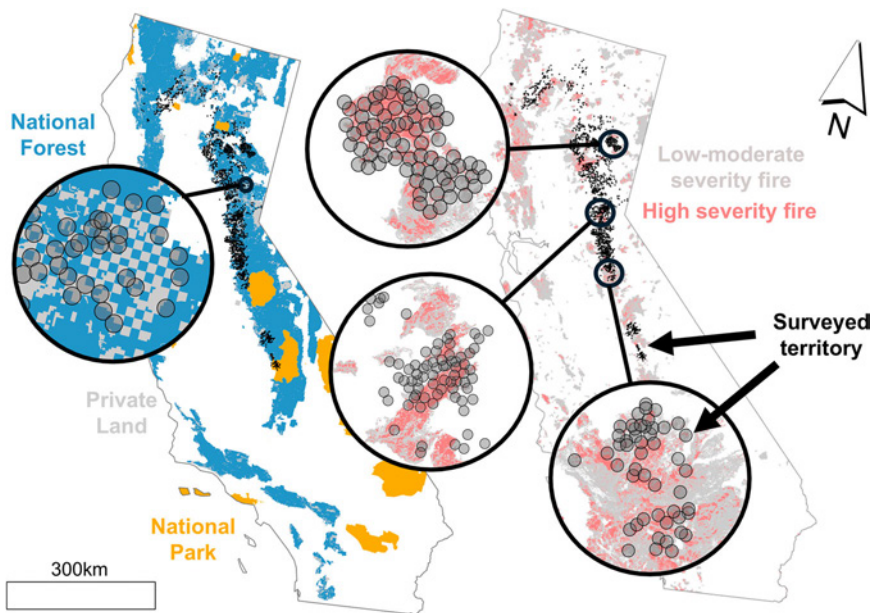


FIGURE 2 Spotted owl territories surveyed across California, USA, ($n = 1,514$ territories) between 1989 and 2022 on both public and private land. Territories overlapped 7 national forests, 2 national parks, and land owned by Sierra Pacific Industries. Of the surveyed territories, 796 (52.3%) experienced fire at some point between 1984 and 2021.

black oak (*Quercus kelloggii*), tanoak (*Notholithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), and bigleaf maple (*Acer macrophyllum*). At higher elevations in the Sierra Nevada, the vegetation type was dominated by red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*). In Southern California, where some individuals were GPS-tagged for movement analyses, territories were composed of big cone Douglas-fir (*Pseudotsuga macrocarpa*) and canyon live oak (*Quercus chrysolepis*) interspersed with chaparral vegetation. In Northern California, where northern spotted owl territories were surveyed and individuals were GPS-tagged, mixed-conifer forests were composed of similar overstory and understory species to the Sierra Nevada, with the addition of Pacific madrone (*Arbutus menziesii*) in the overstory and California huckleberry (*Vaccinium ovatum*) in the understory.

METHODS

Surveying historical spotted owl territories

We conducted surveys in 1,514 spotted owl territories across 5 national forests, 2 national parks, and in areas occurring on and adjacent to private land owned by SPI from 1989 to 2022 (Figure 2; Table S1). Spotted owl summer breeding seasons (Gutiérrez et al. 2017) were our primary sampling periods. We divided these periods into 14 2-week-long secondary sampling periods, beginning at the start of March and ending at the end of September (Tempel et al. 2014). Territories surveyed by SPI generally included detections obtained at the temporal scale of the primary sampling period, reporting an average annual detection probability of 0.971 (K. Roberts, SPI, unpublished data). In our statistical model, we applied estimates of detection probability obtained from non-SPI territories to the SPI territories that lacked secondary sampling periods. This simplifying assumption (that the detection process is constant across ownership) allowed us to use these valuable sources of data in our models. In some cases, the same

territory occurred in multiple study areas in a given year. This occurred when a territory was surveyed near a boundary of 2 study areas. In these cases, to avoid pseudoreplication (Hurlbert 1984), we used only data that were collected as part of the non-SPI study (typically long-term demography studies).

Field crews detected owls (singles or pairs) at night by imitating owl vocalizations at call stations and along survey routes within owl territories. Field crews conducted diurnal or twilight surveys at territories with recent nocturnal detections to assess occupancy with visual sightings (LaHaye et al. 2004, Tempel et al. 2022). To reduce false positive responses from non-territorial floaters or individuals in neighboring territories (Berigan et al. 2019), we did not consider single-night detections in our analysis and prioritized diurnal or twilight detections. We considered nocturnal detections of individual birds only if they had occupied the territory during the previous year (i.e., if we resighted color bands on previously captured birds), which we discerned by unique color banding of individuals (Franklin et al. 1996). Field crews determined reproductive status by feeding live mice to owls and observing if they took mice to an active nest or juvenile (Franklin et al. 1996).

GPS tagging individual spotted owls

We GPS-tagged 171 individual spotted owls in 2015–2023 (Figure 3). We used 7 types of GPS units that we installed with either a backpack or tail-mount attachment (Table 1). Owls were captured using snare poles, hand-grabs, or bal-chatri traps. All relevant state and federal permits were obtained before capturing and handling birds. GPS tags were deployed during summer breeding seasons (April–August), and units were programmed to record locations at varying intervals for specific, independent projects (Table 1). We filtered final locations to include those

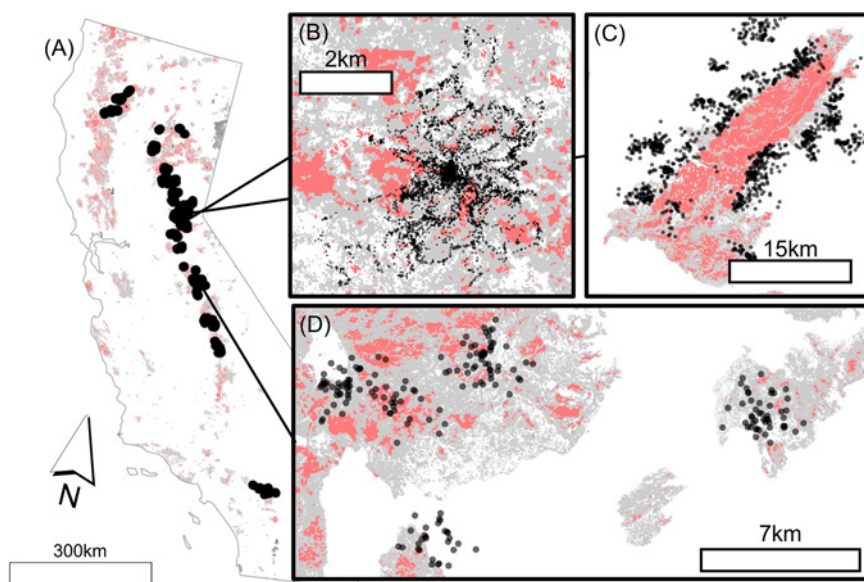


FIGURE 3 Locations of spotted owls across the Sierra Nevada, California, USA (A) We GPS-tagged 171 individuals between 2015 and 2023, tracking movement at 3 temporal sampling scales. We examined fine-scale foraging movements with resampled locations that were 6 minutes apart (B), shown here for one individual that occurred within the boundaries of the Caldor Fire. We examined foraging habitat selection with resampled locations that were 2 hours apart (C), shown here for multiple individuals that overlapped the boundaries of the King Fire. We examined general habitat selection with resampled locations that were 24 hours apart (D), shown here for 4 individuals that either occurred within or overlapped the boundaries of the Rim Fire.

TABLE 1 Types of global positioning system (GPS) tags used to monitor movements of spotted owls in California, USA, in 2015–2023. Individuals tracked in this study were tagged with one of 7 tag types. Tags were programmed to record locations at different intervals during the summer breeding season to accomplish specific objectives for other studies. In our study, we resampled filtered locations to standardize resource and step selection analyses.

Tag type	Mass (g)	Attachment	Pre-filtering	Post-filtering	Years used	Time interval	Start-end time (PDT)	Study
Pinpoint 100 ^a	7.0–10.0	Backpack	1,263	311	2015	1–3/night	2200–0300	Jones et al. (2020b)
Pinpoint 120 ^a	7.0–10.0	Backpack	1,338	345	2016	1–3/night	2200–0300	Jones et al. (2020b)
Pinpoint 120 VHF ^a	6.0–10.0	Backpack, tail-mount	22,592	8,199	2017–2018	5/night	2200–0300	Jones et al. (2020b), Kramer et al. (2021a, b)
Swift Pinpoint 120 ^a	6.0–10.0	Tail-mount	20,290	16,930	2019–2023	2–4 min	2000–0600	McGinn et al. (2023a, b)
Pinpoint Argos 240 ^a	9.0	Tail-mount	7,836	6,598	2023	20 min	2200–0800	
Alle-300 Ecotone ^b	10.0	Tail-mount	74,260	66,158	2019–2022	2 min	2000–0630	Wilkinson et al. (2022), Zulla et al. (2022, 2023)
Vesper 3.2 ^c	11.6	Tail-mount	31,860	31,860	2019–2020	1 min	2000–0600 ^d	Reid et al. (2022)

^aLotek, Wareham, United Kingdom; Lotek, Newmarket, Ontario, Canada.

^bEcotone, Gdynia, Poland.

^cASD, Haifa, Israel; encapsulated in epoxy by Lotek, Wareham, United Kingdom.

^dDelayed start time to account for capture disturbance

with a high degree of spatial accuracy, which depended on tag type (H. A. Kramer, University of Wisconsin-Madison, unpublished data). Specifically, we considered only GPS points obtained with Pinpoints that had a horizontal dilution of precision (HDOP) of less than 5 and were obtained with at least 5 satellites, which were both correlated with error in initial testing ($r_{HDOP} = 0.42$, $r_{SATS} = -0.16$). We filtered points obtained with Ecotones by battery life (>3.7 V; Zulla et al. 2022). Across all tag types, we retained an average of 63.3% of GPS locations after filtering. For this study, we did not analyze any locations recorded during diurnal hours (0800 to 2000).

Environmental data for dynamic occupancy models

We compiled covariates for occupancy analyses at a home-range scale, which we defined as 1,500-m buffers around territory centers; this accounted for the breadth of spatial covariates that may influence spotted owl behavior, and subsequently, site occupancy (Tempel et al. 2014, Jones et al. 2021). We determined territory centers by calculating the geometric mean between locations across sampling years, prioritizing nest locations, juvenile locations, adult roost locations, and protected activity centers. These activity centers, which surround active nests or suspected nest stands, have been established on public lands by the USDA Forest Service since 1993. We eliminated presumed duplicate territories surveyed by different research groups—determined by greater than 50% overlap of territory buffers for different studies—and prioritized the sites for which we had more complete detection histories.

We obtained fire severity information for all fires that occurred in the study area from 1985–2022 from the Monitoring Trends in Burn Severity (MTBS) project (MTBS 2022). The Thematic Burn Severity dataset calculates the (relativized) differenced normalized burn ratio (RdNBR) and then classifies the results into 4 classes: unburned or unchanged, low severity, moderate severity, and high severity. To obtain fire severity information for our occupancy analysis, we used the package *exactextractr* (version 0.10.0; Baston 2024) to estimate the proportion of 4 burn categories within the buffers around each owl territory center: unburned or unchanged canopy structure (within fire perimeters), low severity ($<25\%$ canopy mortality), moderate severity ($25\text{--}75\%$ canopy mortality), and high severity ($>75\%$ canopy mortality). We calculated the Shannon diversity index of all severity classes for each year in our study, which is a widely used approach to quantify pyrodiversity (Jones and Tingley 2022).

Environmental data for resource and step selection analyses

To prepare used and available data for resource and step selection analyses applied to GPS-tagged individuals, we used the package *amt* (version 0.2.2.0; Signer et al. 2019) in the R statistical programming environment (version 4.4.0; R Core Team 2024). First, we removed any points that were too far away from the previous location to be biologically plausible. In this case, we removed points that were indicative of movements >3 km/hour (C. J. Zulla, University of New Mexico, personal communication). Second, we resampled the remaining fixes for all territories at 3 temporal scales (Table S2). Specifically, we examined 1) fine-scale movement with a sampling rate of 6 minutes and a tolerance of 4 minutes using step selection functions (Avgar et al. 2016), 2) foraging resource selection with a sampling rate of 2 hours and a tolerance of 15 minutes, and 3) broader scale resource selection with a sampling rate of 24 hours and a tolerance of 2 hours. For our step selection analysis, we created steps from our final tracks for the finest temporal scale (6-minute), and for every used step, we created 10 random steps. For the resource selection analyses, we estimated 95% fixed kernel home ranges for each tagged individual with at least 15 remaining locations after filtering and resampling at the 2-hour and 24-hour temporal scales. Within each 95% kernel home range buffered by 400 m, estimated separately for both temporal scales, we established 10 available locations for every used location.

We used the Google Earth Engine (Google, Mountain View, CA, USA) environment to calculate fire characteristics around each used and available location. We first created a 100-m buffer around each used and available

location, which corresponds to all possible spatial error for GPS tags (H. A. Kramer, unpublished data). For any buffered points that intersected a fire (MTBS) that occurred in 2005–2021 (10 years prior to the first GPS tagging year), we clipped the fire area to the buffered area. Within each clipped fire, we calculated the percentage of the clipped area that burned at each severity class. We calculated pyrodiversity as the Shannon diversity index of burn severities. We then assigned each location these calculated metrics and the year of the fire. We removed any fire attributes from fires that occurred after tagging occurred. For example, we tagged multiple individuals in the SIE in 2019 and 2020 and did not include fire variables from the Creek Fire, which occurred after tagging was complete in 2020. We also considered locations that were repeatedly burned within our study's time frame; 58 of 3,877 locations resampled at the 24-hour rate, 0 of 1,113 locations resampled at the 1-hour rate, and 32,114 of 146,310 locations resampled at the 6-minute rate were burned multiple times. For these locations, we considered the cumulative proportions of burn severity class and the average pyrodiversity index.

We examined the effects of fire severity and pyrodiversity in occupancy, step selection, and resource selection models for several reasons. First, these variables that describe fire characteristics are broadly used to examine the impact of fire on spotted owls at an ecologically meaningful scale (Jones et al. 2021, Jones and Tingley 2022). Second, we did not exhaustively examine all potential variables that may impact spotted owl occupancy—such as topography, vegetation, and climate—because our objective was to make targeted inferences about the impact of fire characteristics on spotted owls and not to develop a predictive model or exhaustively describe all factors influencing spotted owl occupancy. We had *a priori* hypotheses in mind with both fire characteristics and made inferences on those hypotheses by depending on the influence of each effect in our *a priori* model (Tredennick et al. 2021). Finally, we used random effects to account for other non-focal effects like pre-fire vegetation that varied across study areas and across individual territories (Muff et al. 2020).

Long-term, bioregional-scale dynamic occupancy models

We used a Bayesian dynamic occupancy model (MacKenzie et al. 2003, Royle and Kéry 2007) to test hypotheses about spotted owl response to wildfire in California (Figure 1). We fit 2 models with the same general structure with fire covariates (high-severity fire and pyrodiversity) calculated across 2 different timeframes (a 5- and 15-year time lag for fire effects). The proportion of high-severity fire and pyrodiversity were correlated at the territory scale ($r_5 = 0.73$, $r_{15} = 0.73$), so we calculated pyrodiversity as a binary covariate (Figure 4). The models contained parameters for initial occupancy ($\psi_{i,1}$), colonization ($\gamma_{i,t}$), persistence ($\phi_{i,t}$), and detection probability ($p_{i,t,j}$), where i was the site, t was the primary sampling period (year), and j was the secondary sampling unit (survey). The primary sampling periods t were breeding seasons (March–September), and the secondary sampling periods j were 2-week sampling periods within each breeding season (1–15 March, 15–31 March, 1–15 April, etc.). For each site i and year t , we determined whether a spotted owl was detected (see above) and the number of secondary sampling periods that were surveyed.

We constructed a model to describe site occupancy dynamics across the Sierra Nevada and portions of Northern California. Within our model, we assumed observations were imperfect representations of the latent state, or presence, of a site $z_{i,t}$. A detection was considered a success, and we modeled it with a binomial distribution; if the site was occupied ($z_{i,t} = 1$), the probability of a success was p , but if it was not occupied ($z_{i,t} = 0$), the probability of a success was 0. The model also included the number of trials (n) or, in this case, secondary sampling visits:

$$y_{i,t} \sim \text{Binomial}(p_{i,t}z_{i,t}, n_{i,t})$$

The biological model described the latent variable observed from detection histories, with parameter $z_{i,t} = 1$ if site i was occupied in year t and 0 if unoccupied, and parameter $n_{i,t}$ as the number of secondary sampling periods

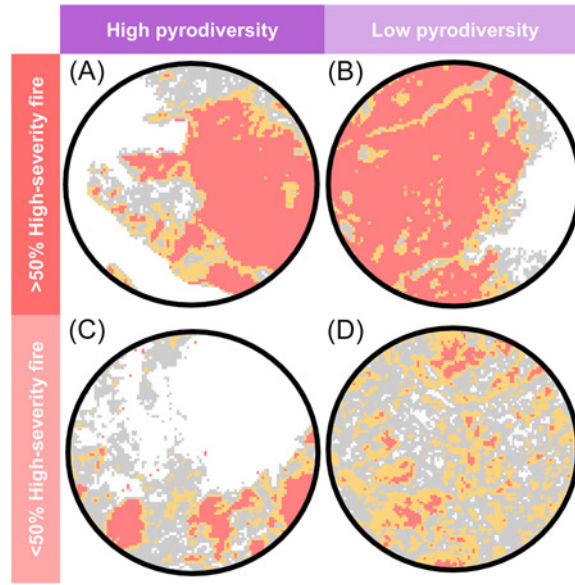


FIGURE 4 In our investigation of fire effects on spotted owl occupancy in California, USA, 1989–2022, high-severity fire and pyrodiversity were correlated at the territory scale, so we examined pyrodiversity as a binary covariate. We provide examples of A) a territory with a higher-proportion of high-severity fire and high pyrodiversity, B) a territory with a higher-proportion of high-severity fire and lower pyrodiversity, C) a territory with a lower proportion of high-severity fire and higher pyrodiversity, and D) a territory with a lower proportion of high-severity fire and lower pyrodiversity.

that were surveyed for site i in year t . For this model, $z_{i,1}$ was drawn from a Bernoulli distribution with probability parameter $\psi_{i,1}$. For the subsequent years, $z_{i,t}$ was drawn from a Bernoulli distribution where the probability of site occupancy depends on the probability of colonization and persistence:

$$z_{i,1} \sim \text{Bernoulli}(\psi_{i,1})$$

$$z_{i,t} \sim \text{Bernoulli}(z_{i,t-1}\gamma_{i,t} + [1 - z_{i,t-1}]\phi_{i,t-t})$$

We modeled detection probability as a logit-linear function of covariates that varied between sites and years. We included covariates to account for factors that could influence spotted owl detection probability (Kelly et al. 2023). First, we examined the effect of reproductive status on detection probability, where $repro_{i,t}$ took the value of 0 for non-reproductive territories and 1 for territories that produced young. We additionally examined the effect of the presence of barred owls on detection probability (Bailey et al. 2009), where $BDOW_{i,t}$ took the value of 0 where and when barred owls were not detected within territory boundaries and 1 where and when barred owls were detected within territory boundaries during spotted owl surveys. Finally, we included a random effect for year to control unmodeled temporal heterogeneity and a random effect for study area to control for unmodeled spatial heterogeneity in detection probability. Thus, we modeled detection as:

$$\text{logit}(p_{i,t}) = a_0 + a_1 repro_{i,t} + a_2 BDOW_{i,t} + a_{\text{year}_t} + a_{\text{study}_i}$$

We modeled initial occupancy during the first year of our study (1989) at each territory ($\psi_{i,1}$) as a logit-linear function of covariates that varied between sites, where f_i was an indicator variable for territories that experienced

fire at any point in 1984–2021, and P_i was a binary value that took a value of 1 where >50% of a territory overlapped privately owned land and 0 where ≤50% of a territory overlapped public land. For the subsequent years ($t > 1$), we modeled annual occupancy as the process dependent on true occupancy status ($z_{i,t}$) and affected by the probability that a vacant territory would become colonized ($\gamma_{i,t}$), or that an occupied territory would persist ($\phi_{i,t}$). Thus, we modeled initial occupancy as:

$$\text{logit}(\psi_{i,1}) = b_0 + b_1 f_i + b_2 P_i$$

$$\psi_{i,t} = \gamma_{i,t-1}(1 - z_{i,t-1}) + \phi_{i,t-1}z_{i,t-1},$$

where colonization and persistence patterns were altered through the effects of site- and time-varying covariates. We modeled colonization and persistence as logit-linear functions of covariates that varied between sites and years:

$$\text{logit}(\gamma_{i,t-1}) = c_0 + c_1 f_i + c_2 y_{i,t} + c_3 f_i y_{i,t} + c_4 f_i y_{i,t} H_{i,t} + c_5 f_i y_{i,t} SDI_{i,t} + c_6 f_i y_{i,t} SDI_{i,t} H_{i,t} + c \cdot \text{year}_{t-1} + c \cdot \text{study}_i$$

and

$$\text{logit}(\phi_{i,t-1}) = d_0 + d_1 f_i + d_2 y_{i,t} + d_3 f_i y_{i,t} + d_4 f_i y_{i,t} H_{i,t} + d_5 f_i y_{i,t} SDI_{i,t} + d_6 f_i y_{i,t} SDI_{i,t} H_{i,t} + d \cdot \text{year}_{t-1} + d \cdot \text{study}_i,$$

where f_i was an indicator variable for fire-affected territories, and $y_{i,t}$ was an indicator variable for survey years, either 1–5 years post-fire or 1–15 years post-fire; $H_{i,t}$ was a variable representing the cumulative proportion of a territory that was affected by high-severity fire, and $SDI_{i,t}$ was a binary variable representing pyrodiversity (Shannon diversity index). If multiple fires affected a territory in either timeframe, then $H_{i,t}$ was the sum of those proportions and $SDI_{i,t}$ was the mean index value. If $SDI_{i,t}$ was greater than that of a territory with an equivalent distribution of 3 burn categories, $SDI_{i,t}$ took the value of 1 (high pyrodiversity). Otherwise, $SDI_{i,t}$ took the value of 0 (low pyrodiversity). The terms c_{t-1} and d_{t-1} were annual, normally distributed random effects that allowed annual unmodeled heterogeneity in colonization and persistence parameters, including that which may be related to climatic variation. The terms $c \cdot \text{study}_i$ and $d \cdot \text{study}_i$ were normally distributed group-specific random intercepts that allowed unmodeled spatial heterogeneity across study areas in colonization and persistence parameters, including that which may have been related to unmeasured post-fire management strategies or differences in vegetation and topography among sites.

We fit the above model to the data using the package *rjags* (version 4.15; Plummer 2019) and *jagsUI* (version 1.6.2; Kellner 2024) in the R statistical programming environment (v4.4.0; R Core Team 2024). All coefficients were assigned diffuse Gaussian priors with $\mu = 0$ and $\alpha = 0.5$ (Northrup and Gerber 2018). We ran 3 chains of 1,000 iterations, an adaptation phase of 1,000, and a thin rate of 10, yielding 300 posterior samples for each parameter across all chains. We tested for goodness of fit using posterior predictive checks (Broms et al. 2016, Kass et al. 2020) (Figure S1). Specifically, we calculated the proportion of posterior predicted values that were higher or lower than observed values, which represented mean frequencies of each occupancy state either predicted or observed across all years. Bayesian p-values > 0.05 and < 0.95 indicated no lack of fit for each occupancy state. We removed sites with missing years of data from this test. We tested for convergence using Gelman-Rubin statistic (where $\hat{R}$ values < 1.1 indicated convergence) and made inferences about parameters by examining the direction and magnitude of the mean effects, and the extent to which posterior distributions overlapped zero. We considered variables from both full models to have support if the value of their posterior distribution evaluated at $\theta = 0$ was less than their prior evaluated at the same point, resulting in a Savage-Dickey Bayes factor > 1 (Hobbs and Hooten 2015).

For each site and each year, we simulated 300 occupancy estimates using the process described above for the occupancy model that considered fire impacts up to 15 years after a disturbance. First, we obtained a mean occupancy estimate for each year across all sites. Then, we categorized territories into 3 groups: territories that, at some point during the study period, experienced >50% high severity fire; territories that, at some point during the study period, experienced <50% high severity fire; and territories that experienced no high-severity fire during the study period.

Analyses of habitat use at multiple temporal scales

To test our hypothesis about the effect of fire characteristics on the fine-scale movement of spotted owls, we estimated the relative probability of use with mixed conditional Poisson regression models with stratum-specific intercepts, which allowed Bayesian inference with integrated nested Laplace approximations (INLA; Muff et al. 2020). For our step selection analysis, for which location data were resampled using the protocol described above, we examined the movement of 55 individuals. The model was formulated as:

$$E(y_{ijk}) = \mu_{ifk} = \exp(\alpha_{ifk} + \beta^T x_{ijk} + u_i^T z_{ijk})$$

$$y_{ifk} \sim \text{Poisson}(\mu_{ifk}),$$

where $i = 1, \dots, I$ individuals, $j = 1, \dots, J$ indexed used or available locations at a given time, $k = 1, \dots, K$ strata, α_{ifk} was the stratum-specific intercept with $\alpha_{ifk} \sim \text{Normal}(0, \sigma^2_\alpha)$, and σ^2_α fixed to a very large value (i.e., 10^4) to help model fitting and prevent shrinkage to an overall mean (Muff et al. 2020), β^T was the vector of coefficients being estimated, and u_i^T was the vector of individual-specific random effects.

To test our hypothesis about the effect of wildfire on foraging habitat selection, we used mixed-effects logistic regression models (1 = used, 0 = available). For our resource selection analyses, for which location data were resampled using the protocol described above, we examined foraging habitat selection at the 2-hour temporal scale for 62 individuals and habitat selection at the 24-hour temporal scale for 121 individuals. As in the step selection function above, we allowed intercepts to vary by individual owl. We modeled the probability π_{if} that a used or available point $y_{if} \sim \text{Bernoulli}(\pi_{if})$ was used by an individual $i = 1, \dots, I$ at location $j = 1, \dots, J_i$ as

$$\text{logit}(\pi_{ijk}) = \mu + \alpha_i + \beta^T x_{ij} + b_i^T z_{ij},$$

where μ was the overall mean (intercept), α_i was the individual-specific random deviation from the intercept, β^T and x_{ij} were vectors of fixed-effects coefficients and covariates, b_i^T was the vector of individual-specific random slope coefficients, and z_{ij} was a design vector (Muff et al. 2020). For the step and resource selection analyses, we examined the proportion of high severity fire, pyrodiversity, and an interaction between the 2. At this scale, high-severity fire and pyrodiversity were not highly correlated with one another (Pearson's r coefficient = 0.41).

In addition to fixed effects, we estimated random slope effects for each additive main effect (excluding interactions) that varied by individual owl to account for individual variation and provide less-biased estimates of population-level selection (Duchesne et al. 2010). These individual random effects enabled us to account for potential variation due to subregion, subspecies, tag type, capture method, and sex. As above, we made inferences about parameters by examining the direction and magnitude of the mean effects, and the extent to which posterior distributions overlapped zero. We fit the step-selection model and the resource selection models using the package R-INLA (Lindgren and Rue 2011, Verbosio et al. 2017).

RESULTS

Effects of high-severity fire on occupancy

During 1985–2021, 795 of 1,514 territories (52.5%) in our study area experienced at least one fire. Both the 5- and 15-year models included coefficients for fire variables that did not overlap zero, suggesting both temporal scales were meaningful with regard to fire (Table S3). Additionally, Savage-Dickey Bayes factors for fire coefficients suggested evidence in favor of both full models (Table S4). Occupancy declined in 1989–2022 (Figure 5), and initial occupancy was higher in territories that overlapped privately owned forest ($b_2 = 2.41$).

According to the 5-year model, the mean odds of an unoccupied territory becoming occupied (i.e., colonization) the following year tended to decrease by 19.7% for every 10-ha increase in high-severity burned forest within territory buffers ($c_4 = -1.34$). Although the 95% Bayesian credible intervals overlapped zero, 89% of the posterior density was negative, indicating there was an 89% chance that high-severity fire reduced colonization. The odds of an occupied territory persisting decreased by 24.4% for every 10-ha increase in high-severity burned forest ($d_4 = -1.71$), and the posterior density indicated there was a 99% chance that high-severity fire reduced persistence. Territories with high pyrodiversity (indices equal to or greater than that of a territory with an equivalent distribution of 3 burn categories) were 27% more likely to be colonized than territories with low pyrodiversity ($c_5 = 0.24$), and the posterior density indicated that there was a 91% chance that pyrodiversity increased colonization. Territories with high pyrodiversity were also 105% more likely to persist than territories with low pyrodiversity ($d_5 = 0.72$), and the posterior density indicated that there was a 100% chance that pyrodiversity increased persistence.

According to the 15-year model, the mean odds of an unoccupied territory becoming occupied the following year decreased by 21.4% for every 10-ha increase in high-severity burned forest within territory buffers (Figure 6; $c_4 = -2.05$), and 99.3% of the posterior density was negative. The odds of an occupied territory persisting decreased by 13.5% for every 10-ha increase in high-severity burned forest (Figure 6; $d_4 = -1.24$). While the 95% Bayesian credible intervals overlapped zero, the posterior density indicated there was a 94% chance that high-severity fire reduced territory persistence. Territories with high pyrodiversity were 132% more likely to persist

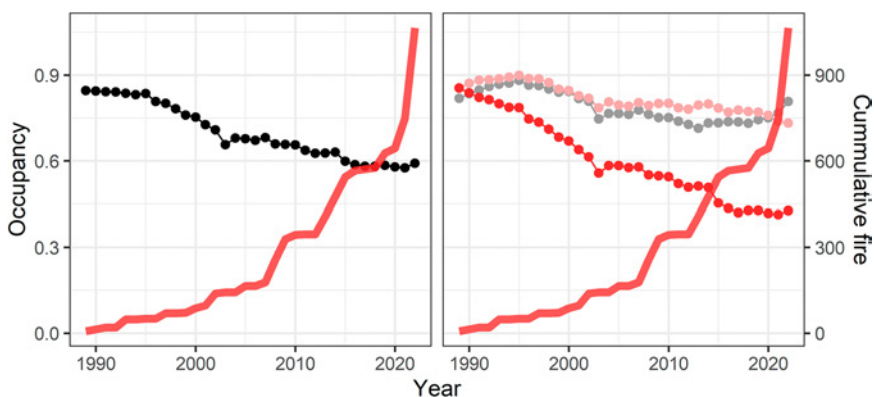


FIGURE 5 Predicted occupancy, indicated by solid dots, according to the 15-year model in which we examined the effect of high-severity fire and pyrodiversity on colonization and persistence of spotted owl territories in California, USA, 1989–2022. In the left panel, occupancy was averaged across all territories. In the right panel, occupancy was averaged according to burn characteristics. Specifically, red indicates territories where at least 50% of the territory burned at high-severity, light pink indicates territories that burned where less than 50% of the territory burned at high-severity, and grey indicates territories that never burned during the study period. Finally, the thick red line indicates the cumulative number of territories that experienced fire across the study area.

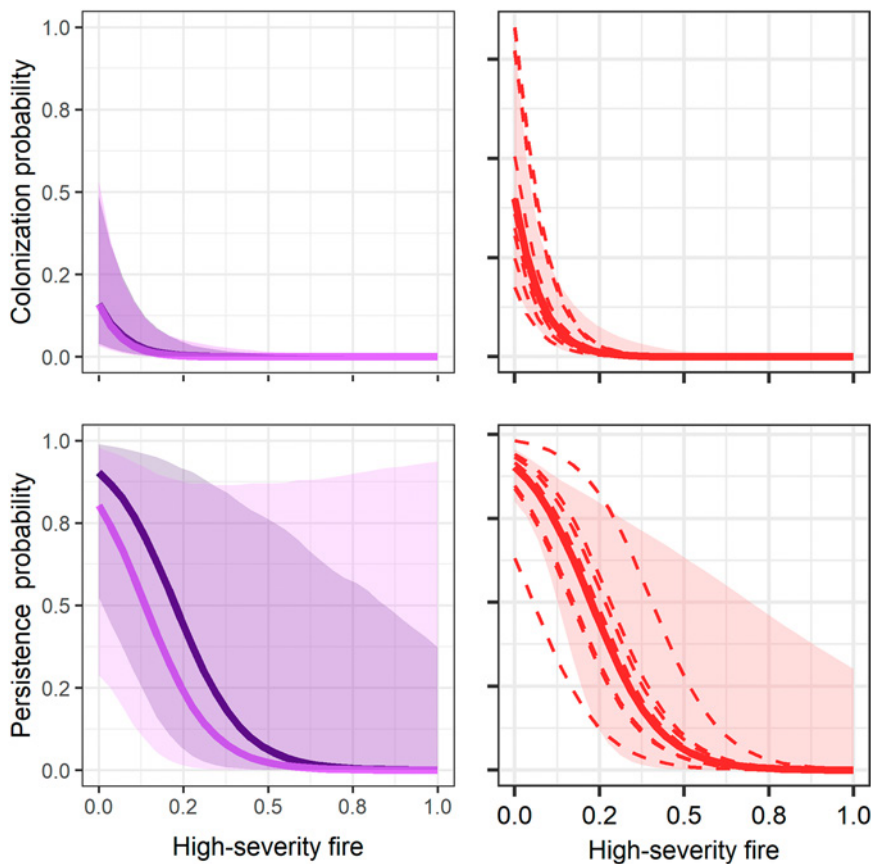


FIGURE 6 Predicted relationships between fire covariates and occupancy rates (persistence and colonization) of spotted owl territories in California, USA, 1989–2022. Mean effects were calculated from the model that assumed fire impacts lasted 1–15 years. In the left panels, thick lines indicate the prediction of the posterior mean across all study areas, where dark purple indicates sites with high pyrodiversity and light purple indicates sites with low pyrodiversity. On the right panels, thick lines indicate the prediction of the posterior mean across all study areas and dashed lines indicate predictions of the posterior means for each study area. Shaded regions show the upper and lower 95% Bayesian credible interval of the mean effect.

than territories with low pyrodiversity (Figure 6; $d_5 = 0.84$), and the posterior density indicated there was a 100% chance pyrodiversity increased persistence.

Effects of fire on step selection

Of the 55 individuals tagged and resampled for the 6-minute interval analysis, 15 used or had access to forests that had burned in 2005–2021. Individuals were less likely to use areas with a higher proportion of high-severity fire, such that the mean odds of use decreased by 22.2% for every additional 1 ha that burned at high severity in buffered areas around locations (Figure 7; $\beta_H = -0.057$). Nearly 100% of the posterior density was negative, indicating there was nearly a 100% chance that high-severity fire decreased the probability of use. There was insufficient evidence for an overall mean effect of pyrodiversity or an interaction between pyrodiversity and high-severity fire. Random slopes ranged from -0.034 to 0.048 for pyrodiversity, -0.10 to 0.009 for high-severity fire, and -0.041 to 0.042 for the interaction between pyrodiversity and high-severity fire.

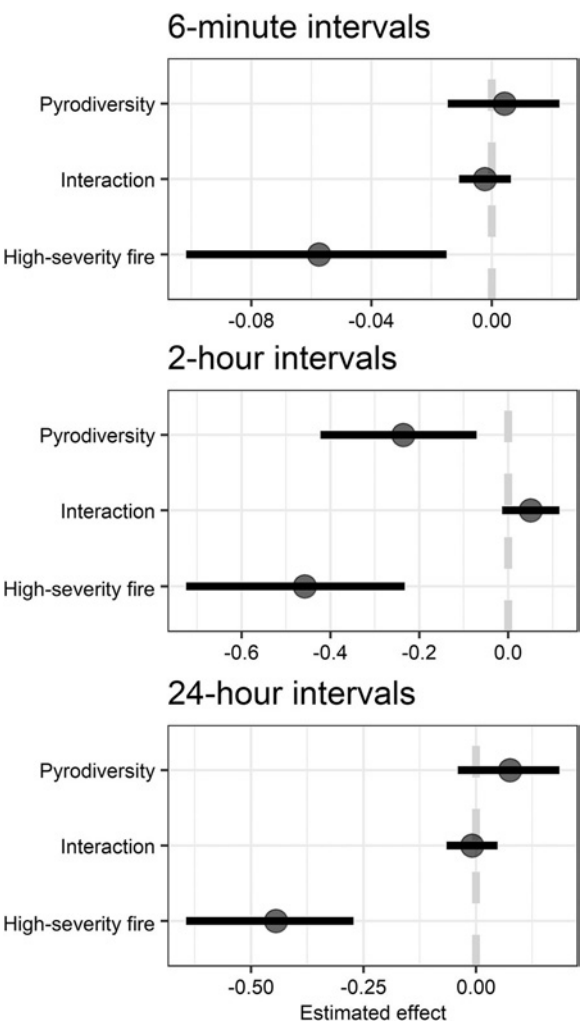


FIGURE 7 Posterior means and 95% credible intervals of coefficients in the 6-minute scale step selection model and the 2-hour and 24-hour resource selection models for spotted owls in California, USA, 2015–2023. Each model included the proportion of high-severity fire and the Shannon diversity index of fire severity classes (pyrodiversity) within 100-m buffers around locations as fixed-effects coefficients, and an interaction between the 2 variables. Each model also included an individual-specific random slope.

Effects of fire on resource selection

Of the 121 individuals tagged for the coarsest temporal analysis (24-hour), 56 had home ranges that burned between 2005 and 2021. Of the 62 individuals tagged for the 2-hour analysis, 22 had home ranges in previously burned forests. At both temporal sampling scales, individuals were less likely to occur where there was a higher proportion of high-severity fire. Specifically, at the 24-hour scale, the mean odds of use decreased by 56.6% for every additional 1-ha that burned at high severity around locations (Figure 7; $\beta_H = -0.44$). Based on the posterior density, there was a 100% chance that high-severity fire reduced the probability of use. There was insufficient evidence for an overall mean effect of pyrodiversity or an interaction between pyrodiversity and high-severity fire. Random slopes ranged from -0.49 to 0.54 for pyrodiversity, -1.26 to 0.12 for high-severity fire, and -0.58 to 0.45 for the interaction between pyrodiversity and high-severity fire.

At the 2-hour sampling scale, the mean odds of use decreased by 74.7% for every additional 1-ha that burned at high-severity around locations (Figure 7; $\beta_H = -0.46$). The probability of use decreased by 62.5% with every 1-point increase in pyrodiversity (Figure 7; $\beta_{SDI} = -0.24$). The posterior densities of the covariates indicated there was nearly a 100% chance that high-severity fire and pyrodiversity decreased the probability of use. There was evidence for a positive interaction between high-severity fire and pyrodiversity (Figure 7; $\beta_{SDI \times H} = 0.050$), suggesting that individuals were more likely to forage in patches of high-severity fire where there was a high diversity of other severity classes in proximity. While the 95% Bayesian credible intervals for this interaction effect overlapped zero, 94% of the posterior density for the effect was positive. Random slopes ranged from -0.61 to 0.19 for pyrodiversity, -0.77 to -0.25 for high-severity fire, and -0.33 to 0.48 for the interaction between pyrodiversity and high-severity fire.

DISCUSSION

One of the most controversial wildlife conservation issues in western North America has become the management of spotted owls and their habitat in increasingly fire-prone forest landscapes (Gutiérrez 2020). Numerous studies have examined the impact of fire on spotted owls, but the species' relationship to burned forests varies across environmental gradients and studies. In contrast, a recent meta-analysis suggested no effect of high-severity fire on spotted owls (Lee 2018, but see Jones et al. 2020a). In this study, we sought to reconcile existing scientific uncertainty. We found that high-severity fire—across decades, landownership boundaries, and subspecies—was correlated with the local extinction of historical spotted owl territories and decreased the probability of unoccupied sites becoming occupied (i.e., being colonized) for up to 15 years after a wildfire. On the other hand, fires that produced a mixture of burn severities (i.e., had high pyrodiversity) were related to an increased probability of spotted owls persisting in previously occupied territories. The GPS data revealed that individuals affected by fire consistently avoided using severely burned forest, except when high-severity fire occurred in the context of a mosaic of burn severities.

High-severity fire negatively impacts spotted owls

Across the Sierra Nevada and some areas in Northern California, spotted owls were more likely to abandon previously occupied territories 1–15 years after a fire burned predominantly at high severity. Owl territories with higher proportions of severely burned forests were unlikely to be colonized or recolonized if previously abandoned. These results corroborated prior research showing both immediate (Jones et al. 2016a) and persistent (Jones et al. 2021) territory extinctions following the 2014 King Fire in the central Sierra Nevada. Across the Sierra Nevada, spotted owls were less likely to occur in severely burned territories for up to 2 decades after wildfires based upon passive acoustic surveys (McGinn et al. 2025b). Therefore, we concluded that the loss of old forest to stand-replacing fires increases territory extinction rates, likely owing to a loss of nesting and roosting habitat, which is a primary limiting factor of this species across its range (Ganey et al. 2017). In Southern California, where suitable nesting and roosting habitat is particularly sparse across the landscape (Barry et al. 2025), severe fire explained 10% of occupancy declines over a period of 2 decades (Tempel et al. 2022). Occupancy declines may be also partly attributed to extreme warm summer temperatures and a lack of closed-canopy forest on the landscape (Jones et al. 2016b, McGinn et al. 2023b). In the absence of forest restoration, fires across California are predicted to increase in size and become more homogeneously severe (Jones et al. 2022), which poses concern for this declining species.

We found that spotted owls avoided moving and foraging in areas burned predominantly at high severity. By accounting for individual variation in behavior, we found that owls avoided using forest burned at high severity at all

temporal sampling scales (Figure 7). Previous studies of GPS-marked owls showed significant individual variation in habitat use in burned landscapes. Following the King Fire (2014) that occurred across a patchwork of National Forest System and private lands, individuals selected smaller patches of severely burned forest in their nocturnal movements in home ranges that burned predominately at low to moderate severity (Jones et al. 2020b). On the other hand, where more than 50% of their home range was burned at high severity, individuals avoided severely burned forest (Jones et al. 2020b). In a telemetry study conducted in 3 national parks (Yosemite, Sequoia, and Kings Canyon), where natural fires have been allowed to burn during the past 50 years and prescribed burns have been used to restore natural fire regimes, individuals avoided larger patches of forest burned at high severity (Kramer et al. 2021b). In a subset of sites across California, individuals were unlikely to successfully capture prey in forests burned at moderate to high severity in the decade following wildfires (McGinn et al. 2024). Studies on northern spotted owls have also found that both moderate- and high-severity fire can reduce survival (Rockweit et al. 2017, 2024). Our findings corroborate these previous studies on spotted owl responses to stand-replacing fires and suggest these responses are widespread and ubiquitous.

Positive relationships between pyrodiversity and spotted owls depend on scale

Virtually all research has supported the hypothesis that spotted owls evolved in fire-adapted forests in part because no one has reported a negative effect of low-severity fire (Bond et al. 2002, Lee et al. 2012, Jones et al. 2016a). A number of studies suggest that fires typical of a region's climate can produce landscape configurations that facilitate energetically optimal movement paths and create foraging opportunities for fire-adapted animals (Nimmo et al. 2019). Fire-adapted animals like the spotted owl have specific adaptations that enhance survival and reproduction in landscapes experiencing burn mosaics (Jones et al. 2023). We found that pyrodiversity was positively related to spotted owl occupancy at the territory scale and that occupied territories were more likely to remain occupied following mixed-severity fires than homogeneous high-severity fires.

Mixed-severity fires can create and maintain heterogeneity in forest ecosystems (Collins and Stephens 2007), which in turn may support foraging opportunities for spotted owls to allow them to persist in burned landscapes. A study combining nest cameras, high-resolution GPS tagging, and estimates of energetic expenditure of free-ranging spotted owls in California found that individuals spent less energy foraging and delivered more prey in territories with high pyrodiversity than in territories with low pyrodiversity (McGinn et al. 2024). Another study showed that forest restoration produced patchier pre- and post-fire landscape conditions that yielded greater spatial juxtaposition of nesting and roosting habitat with foraging habitat for spotted owls in the Sierra Nevada (Jones et al. 2025a). Mixed-severity fires at a landscape scale may create hunting opportunities by leaving intact patches of green forest, which function as spotted owl nesting and roosting habitat, near more open patches with regenerating understories, which function as suitable prey cover. Edges between intact patches of green forest and more open patches may thus function as spotted owl foraging habitat.

Spotted owls in California primarily eat small mammals like woodrats (*Neotoma* spp.), pocket gophers (*Thomomys* spp.), and flying squirrels (*Glaucomys oregonensis*; Hobart et al. 2021). Dusky-footed woodrats (*Neotoma fuscipes*) are more likely to occur in early-seral forests with nearby mature forest, suggesting that both horizontal and vertical heterogeneity are important for the species (Kuntze et al. 2025). Both northern and California spotted owls at lower and moderate elevations select edge habitat where woodrats are more abundant (Zabel et al. 1995, Ward et al. 1998, Zulla et al. 2023). Mixed-severity fires at lower-to-moderate elevations in California have been shown to balance energetic tradeoffs between foraging and consuming prey for spotted owls (McGinn et al. 2024). Small patches of high-severity fire create ecotones between younger and older forest (Jones et al. 2020b) where suitable woodrat habitat intersects with typical spotted owl habitat (Kuntze et al. 2023, Zulla et al. 2023). At higher elevations, California spotted owls consume relatively more flying squirrels (Hobart et al. 2019). Flying squirrels prefer later seral forests but can occur in burned landscapes if sufficient canopy cover remains following a fire

(Mazzella and Koprowski 2020). Spotted owls consume more flying squirrels in territories with more moderate severity fire (Hobart et al. 2021), so territories with burn mosaics may presumably support both flying squirrel habitat and spotted owl foraging habitat at higher elevations.

Based on the apparent importance of edge habitat for spotted owls and their prey, we expected to find that spotted owls would be more likely to select areas with higher fine-scale pyrodiversity across elevations. Although we found a positive relationship between territory-scale pyrodiversity and persistence on burned landscapes, we did not detect a relationship between fine-scale pyrodiversity and movement or coarse habitat selection. At our intermediate temporal scale, however, we found evidence that individuals selected forest burned at high-severity where fine-scale pyrodiversity was high. This supported our expectation that some individuals may take advantage of edges between differently aged forest stands, created by small patches of high-severity fire, to capture prey (Wilkinson et al. 2022, Zulla et al. 2022, Kuntze et al. 2023).

The effect of fine-scale pyrodiversity on movement and habitat selection varied among territories (Figure 8). Generally, spotted owls that occurred within the boundaries of mixed-severity fires selected for fine-scale pyrodiversity. While spotted owls spend more energy foraging in burned territories than in unburned territories, the foraging opportunities afforded by small patches of high-severity fire and territory-scale pyrodiversity may balance energetic tradeoffs (McGinn et al. 2024). In contrast, we found that owls occurring near large patches of high-severity fire selected against fine-scale pyrodiversity. Large patches of high-severity fire either directly eliminated prey habitat or eliminated vegetation necessary for spotted owls, a sit-and-wait predator, to successfully capture prey. Ecotones at the edges of severely burned forest, where spotted owls presumably hunt, may have been too sparse and inaccessible to offset the energy required to reach those sites. Thus, the energetic benefits of fine-scale pyrodiversity may only outweigh the energetic costs of landscape-scale fire in territories that experience a burn mosaic.

Resolution to lingering controversy

Spotted owls have been at the center of multiple conservation dilemmas for over half a century because they show a strong association with mature, late-successional conifer and mixed conifer-hardwood forests dominated by complex understories and dense overhead canopies (Forsman et al. 1977, Forsman 1980, Carey et al. 1991, Gutiérrez et al. 1995). Spotted owls have also declined in response to a variety of existential threats, including competition with encroaching barred owls (Dark et al. 1998, Gutiérrez et al. 2007, Hamer et al. 2007, Long and Wolfe 2019). The threat of barred owls to California spotted owls has largely been ameliorated (Hofstadter et al. 2022, Kelly et al. 2023), and continued removal of barred owls would likely benefit both California and northern spotted owls (Hobart et al. 2025). Spotted owls in California have also declined in apparent response to the loss of large trees and forests with mature, old-growth characteristics (Jones et al. 2018, Tempel et al. 2022) and large, stand-replacing wildfires (Gutiérrez 2020; Jones et al. 2016a, 2021).

Until now, the most comprehensive assessment of fire effects on spotted owls was a meta-analysis conducted by Lee (2018), who concluded that wildfire—regardless of severity—did not negatively impact spotted owls and does not pose a substantial threat to any of the spotted owl subspecies. Lee (2018) also concluded that, given the lack of negative responses of spotted owls to high-severity fire, proposed fuels reduction plans and associated planning documents (Gutiérrez et al. 2017) were unnecessary. Because Lee's (2018) analysis was a synthesis of importance, it generated critical assessment and motivated new research (the work presented herein). In our synthesis, the effect of high-severity fire on spotted owls was clear: we found strong evidence that homogeneous high-severity wildfires pose an existential threat to spotted owls and their habitat. High-severity fire, when it occurs in a patchy configuration with lower severities, has a neutral or beneficial effect on spotted owls. Thus, we believe our analysis provides sufficient evidence to resolve the lingering doubt regarding the effects of high-severity fire on spotted owls in California.

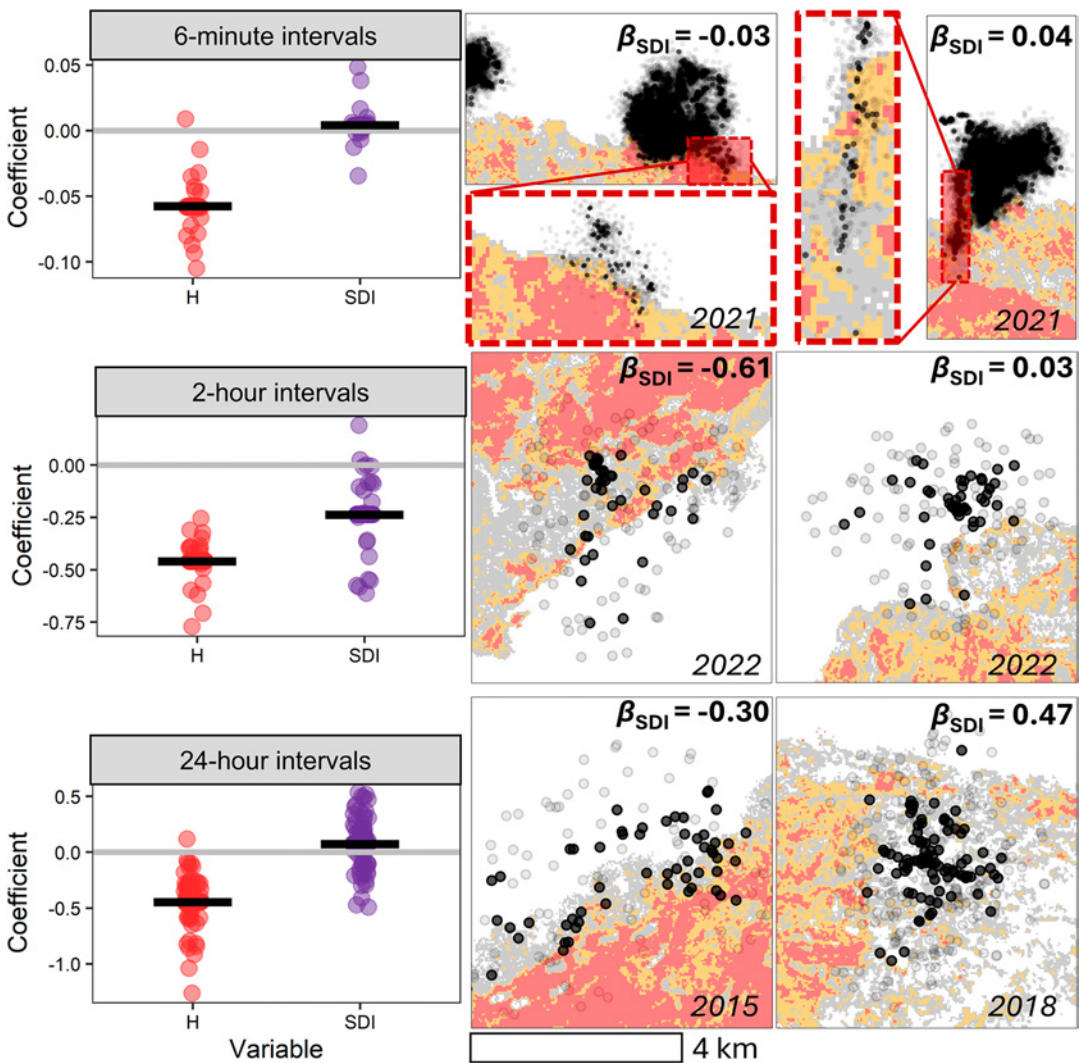


FIGURE 8 Random effects of step and resource selection models for spotted owls in California, USA, 2015–2023. Individuals avoided areas with more high-severity fire (H) at all scales. Pyrodiversity (here defined as Shannon diversity index [SDI]) had a variable effect across scales. On the left panels, dots indicate individual-specific random slopes. Panels show examples of tagged individuals (black dots are used points and grey dots are available points) for which coefficients were positive and negative. High-severity fire is indicated by red, moderate-severity fire is indicated by orange, and low-severity fire is indicated by grey. For the fine-scale step selection analysis using 6-minute intervals between locations, we show movement forays in additional zoomed panels. The year of data collection is included in the bottom right corner of each panel.

Changing climate and existential threats for forest species

Climate change may pose concerns for spotted owls like it does for many species, including higher temperatures (Parmesan and Yohe 2003), increases in atypical disturbance events (Westerling 2006), and loss of habitat (Beyer and Manica 2020). Higher carbon dioxide levels, warmer temperatures, and longer growing seasons may initially increase primary productivity in forests (Lu et al. 2024), creating more habitat for forest species like spotted owls. However, higher primary productivity in forests, in addition to more extreme droughts, may

increase available fuels and contribute to increasing fire activity (Ellis et al. 2022). In addition to limiting the availability of nesting habitat, reducing opportunities for movement within forest cover, and reducing foraging opportunities, large stand-replacing fires also threaten important climate refugia for spotted owls. Typical older forest characteristics like closed canopies and taller trees comprise spotted owl roosting habitat (Forsman 1980, Barrows 1981, Weathers et al. 2001, McGinn et al. 2023a). These vegetation structures stabilize microclimates around roosts when ambient temperatures approach and exceed the species' physiological limits (McGinn et al. 2023a) and allow individuals to avoid increased energetic expenditure associated with heat stress (McGinn et al. 2023b).

As temperatures rise and heat waves become more frequent and extreme, these refugia will likely become increasingly important to climate-vulnerable species (Morelli et al. 2020). In Southern California, historical spotted owl territories at lower elevations have been completely vacated where temperatures are above the species' upper critical threshold (Weathers et al. 2001) and where taller forests are absent (Tempel et al. 2022, McGinn et al. 2023b). Indeed, spotted owls are sparse across their range in Southern California (Barry et al. 2025). Uncharacteristically severe fires are projected to eliminate much of the remaining older forest in California (Steel et al. 2023), which may amplify the negative consequences of heat waves for spotted owls and exacerbate the challenge of conserving the species.

MANAGEMENT IMPLICATIONS

As uncharacteristically large and severe fires become more common in seasonally dry forests in the western United States, fuels reduction forest restoration activities have become a priority for land managers and policy makers. One approach for managing forests is restoring landscapes to more resilient conditions (Hessburg et al. 2021), which may be complementary to management that references the occurrence of spotted owls. If the goal of land managers is to conserve spotted owls as climate and forest conditions continue to change, then forest restoration and management strategies that create resilient forests and reduce the extent and severity of wildfires are necessary. Based on the results of our analysis and our synthesis of the literature, we have developed recommendations in support of spotted owl conservation in fire-prone forests in California:

1. Retain and promote older forests in currently occupied and historically occupied suitable spotted owl nesting and roosting habitat (Figure 9). Spotted owls in California require large trees for nesting and roosting (Barrows 1981, North et al. 2017), and the importance of these structural features for spotted owls will likely increase as global temperatures rise (Jones et al. 2016b, McGinn et al. 2023a, b). Large trees provide stable microclimates during both times of extreme cold and extreme heat, which are conditions that have been shown to coincide with reduced reproductive success and local territory extinctions, respectively (Franklin et al. 2000, McGinn et al. 2023b). In dry montane forests in western North America, spotted owls may nest and roost in fire refugia that remain persistently unburned across multiple fire events (Stephens et al. 2016). Such stands are protected by topographic features and can remain unburned through multiple fire events (Downing et al. 2021), and they can reach later successional stages dominated by shade-tolerant species (Krawchuk et al. 2020). Thinning projects could attempt to retain dense stands of mixed conifer forests on north-facing slopes and in drainages (Hessburg et al. 2015), which historically burned less frequently than south-facing slopes and ridgetops (North et al. 2009, Hessburg et al. 2016). In areas that historically experienced more frequent and severe fire (e.g., south-facing slopes and ridgetops), the removal of species that are not fire resistant (e.g., white fir) may facilitate growth and resilience of other large trees that are fire resistant (Binkley et al. 2007, Hessburg et al. 2015).
2. Employ moderate-intensity fuels reduction treatments in spotted owl foraging and transit habitat in known territories and retain or promote woodrat habitat at lower elevations (Figure 9). Treatments that increase canopy

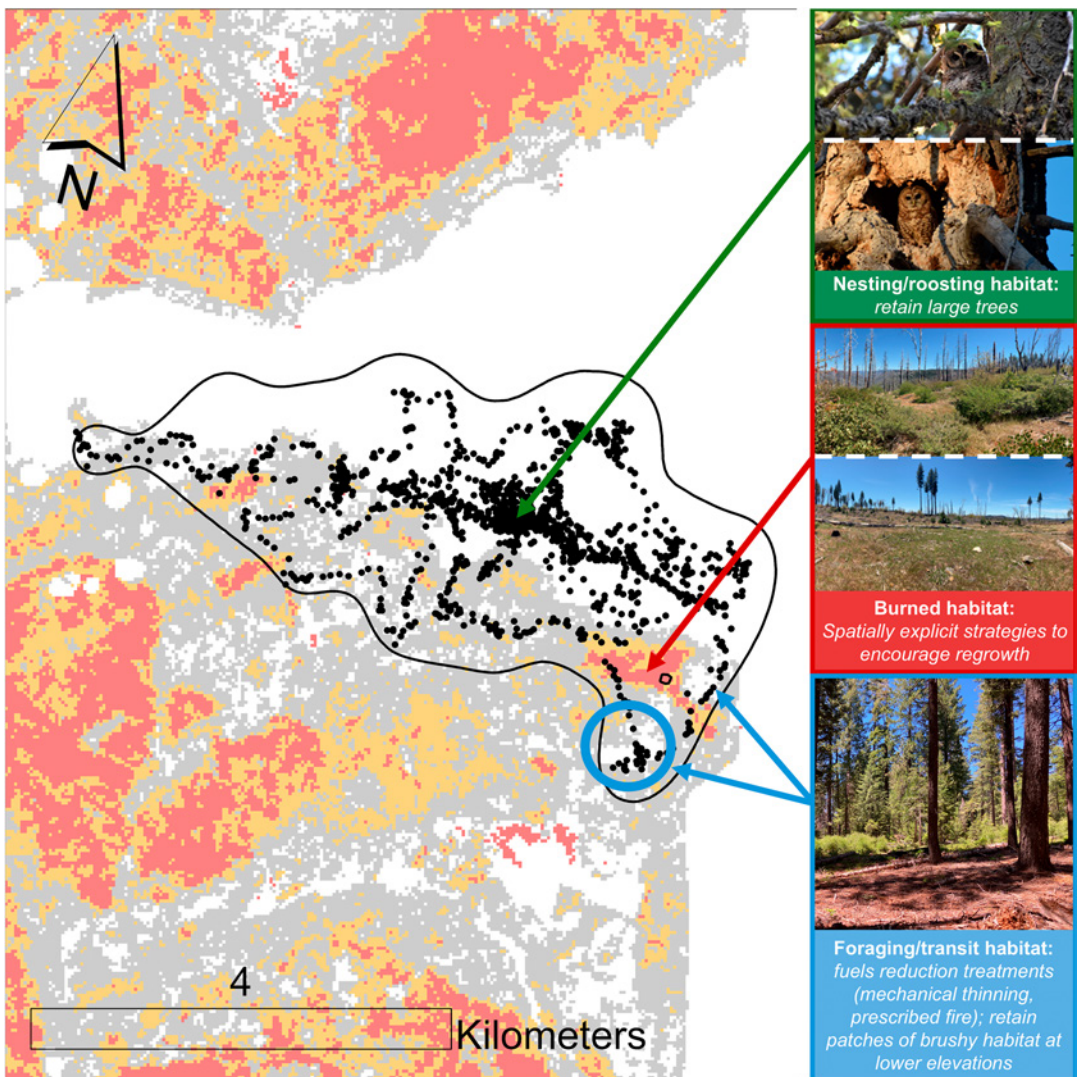


FIGURE 9 Recommendations for forest management based on the conclusion that severe fire negatively affects spotted owls in California, USA. Tagging data obtained in 2022 from an individual occurring near the perimeter of a fire are shown as black points. The green arrow points to the tagged individual's known nesting location. The 95% kernel home range is shown by the solid black line. The blue circle indicates a presumed foraging location based on a previous study (McGinn et al. 2024).

base height, reduce ladder fuels, and reduce canopy bulk density may not only mitigate severe fire but also promote spotted owl foraging and transit habitat (Wright et al. 2023). Spotted owls appear to be resilient to high-intensity fuels management when it is implemented across limited extents (e.g., <30% of a territory) and directly benefit from low-intensity management (McGinn et al. 2025a). A combination of high- and low-intensity treatments that preserve sufficient nesting and roosting habitat may ultimately increase spotted owl occupancy (McGinn et al. 2025a). Heterogeneity has been shown to benefit both spotted owls and one of their main prey species, the dusky-footed woodrat (Zulla et al. 2022, 2023; Kuntze et al. 2023). On south-facing slopes where early seral forests were historically more prevalent (Hessburg et al. 2016) and at lower elevations where woodrats dominate spotted owl diets (Hobart et al. 2019), fuels reduction treatments to create patches of

younger forest may mediate predator-prey interactions. Because dense woodrat habitat may be more susceptible to high-severity fire, these patches of younger forest should be small enough to limit the spread of intense wildfire but big enough to provide a source population for woodrats to disperse into resilient forests (Kuntze et al. 2023).

3. Employ high-intensity fuels reduction treatments in unoccupied habitat, habitat less suitable for spotted owls, or in occupied habitat adjacent to nesting areas to generate forest heterogeneity, resilience, and resource complementarity (Figure 9). Wildfire is a contagious process; the area of forest that has the potential to burn at high severity depends on the availability and configuration of fuels across landscapes at multiple scales (Parks et al. 2015). Forest area burned at high severity can increase with forest fuel availability and connectivity (Francis et al. 2023). Reducing fire risk by reducing fuel loads across the broader landscape may reduce the likelihood that extensive severe fires burn into occupied spotted owl habitat (Tempel et al. 2015, Jones et al. 2022), and doing so may also produce important spatial juxtaposition of nesting and foraging habitat (Hobart et al. 2019, Wright et al. 2023, Jones et al. 2025a). In fire-suppressed forests, the implementation of fuels treatments can reintroduce landscape heterogeneity, which is important for spotted owl foraging (North 2012, Zulla et al. 2022, Wright et al. 2023). Managers could consider implementing higher-intensity management in areas where early seral vegetation is more common (e.g., south-facing slopes, upper slopes, and ridgetops; Hessburg et al. 2015). Landscapes where earlier seral vegetation communities occur in proximity to late-successional forests in drainages and on north-facing slopes may ultimately improve spotted owl fitness by juxtaposing foraging and nesting habitat (North 2012, Wright et al. 2023). Finally, leveraging wildfire's natural treatment of landscapes—specifically in areas that burn at lower severities—may restore ecosystem resilience to uncharacteristically severe fires (Stephens et al. 2012, Parks et al. 2015, North et al. 2021). Implementing treatments following low- to moderate-severity fires, identifying managed wildfire zones, and implementing prescribed fire in conjunction with thinning treatments may support landscape heterogeneity and shift future disturbance events into manageable burns (North et al. 2012, 2021).

Our recommendations for the management of montane forests in California center on spotted owls and their occurrence. Alternatively, managers may consider other strategies that restore historical conditions on the landscape to support natural disturbance processes without consideration for spotted owl occurrence. Regardless, our data synthesis provides evidence that some form of forest management aimed at modifying fire behavior is a necessary component to spotted owl conservation in California (Steel et al. 2023, Jones et al. 2025b).

Areas for future research

We did not explicitly examine the impact of pre- or post-fire forest management on spotted owl occupancy or behavior. Based on simulated projections of future fire behavior, pre-fire fuels reduction treatments may reduce the loss of typical spotted owl habitat to severe fire (Tempel et al. 2015, Jones et al. 2022). However, we require more empirical studies that examine the regional impacts of fuels treatments on spotted owls. Recent work suggests that spotted owls are resilient to fuels treatments, either directly or indirectly benefiting from fuels management following fires depending on intensity of the treatments (McGinn et al. 2025a). As the strategies listed above are implemented across California, studying wildlife responses will resolve lingering uncertainty regarding the relative impacts of fuels treatments and fires on vulnerable wildlife (Figure 1A,B).

Post-fire treatments may also affect wildlife responses to fire, though more research is needed to not only quantify the magnitude of these effects but also the direction. Following fires, salvage logging is often implemented on the landscape followed by reforestation efforts. There is evidence that salvage logging may exacerbate the negative consequences of high-severity fire on spotted owls (Clark et al. 2011, Lee et al. 2013, Jones et al. 2020b, Rockweit et al. 2024). On the other hand, substantial evidence suggests that California spotted owls preferentially

forage in ecotones between older and younger forest (Wilkinson et al. 2022, Kuntze et al. 2023, Zulla et al. 2023), and replanting forests post-fire may create foraging opportunities for spotted owls in the peripheries of burn scars and help re-establish forest conditions conducive to nesting and roosting more quickly. Recent work suggests that post-fire salvage logging does not affect spotted owl occurrence (McGinn et al. 2025a). Studies that examine the relative impacts of pre-fire treatments and post-fire treatments on spotted owls across spatial and ecological scales are necessary to design more effective conservation approaches for spotted owls in California.

ACKNOWLEDGMENTS

This synthesis effort was made possible because of decades of challenging field work by individuals dedicated to the conservation of the spotted owl. We thank T. Munton, S. Whitmore, W. Berigan, P. Shaklee, and L. Gallagher for managing field crews and compiling survey data. We thank the many wildlife technicians and graduate students who assisted with data collection. We especially thank C. Zulla, B. DeYampert, Z. Wilkinson, D. Reid, N. Holmes, J. Barry, M. McDonald, and the wildlife biology staff of Sierra Pacific Industries and Tanner Environmental Services for their support in locating, surveying, capturing, and tagging owls in this study.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ETHICS STATEMENT

All birds in this study were handled with appropriate state and federal permits and study protocols were approved by the University of Wisconsin-Madison Institutional Animal Care and Use Committee (IACUC).

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Associate Editor: David Koons.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: McGinn, K., M. Z. Peery, J. Keane, K. Roberts, B. Dotters, S. A. Whitmore, W. J. Berigan, L. R. Gallagher, P. A. Shaklee, T. E. Munton, et al. 2026. Impacts of wildfire on spotted owls in California: a bioregional-scale data synthesis. *Wildlife Monographs* 224:e70014.
<https://doi.org/10.1002/wmon.70014>