# IT'S A TRAP—THE CASE OF THE BUTTE CREEK TERRITORY OF THE NORTHERN SPOTTED OWL

RAYMOND J. DAVIS and NATALIE M. RUGG, U.S. Department of Agriculture, Forest Service, 3200 S.W. Jefferson Way, Corvallis, Oregon 97331; raymond.davis@usda.gov; natalie.rugg@usda.gov

MICHAEL H. HUHNDORF, U.S. Department of Agriculture, Forest Service, 10025 Elk Mountain Rd., Upper Lake, California 95485; Michael.Huhndorf@usda.gov

JOSEPH M. CHOW, U.S. Department of Agriculture, Forest Service, 825 N. Humboldt Ave., Willows, California 95988; joseph.chow@usda.gov

ABSTRACT: In the Pacific Northwest region of the United States, forests within the range of the Northern Spotted Owl (*Strix occidentalis caurina*) have changed dramatically over the last two centuries. It began with the loss of frequent fires that indigenous communities set annually to manage their natural resources. This change was exacerbated a century later with the advent of effective fire suppression by the United States Forest Service. A once diverse forested landscape maintained by frequent fires became more uniform. In recent times, urbanization and widespread timber harvesting largely confined remaining owl habitat to federally managed public forest lands. In some places there was less than historically existed and in other places, more. These changes can create ecological traps—areas of low-quality habitat that are occupied for various reasons—where long-term persistence is not possible. A recent (2024) article in *Western Birds* focused on a Northern Spotted Owl territory that produced three young two years after a large, severe wildfire. Our paper broadens the time perspective for that territory and tells a more holistic story of how the owls occupied it prior to and after the fire. The rapid change in this territory, now unoccupied, is an example of a site-level ecological trap for the Northern Spotted Owl, while the slow forest changes from fire exclusion that preceded the fire exemplify a landscape-scale trap.

Northern Spotted Owls (*Strix occidentalis caurina*) can live up to 21 years in the wild (Davis et al. 2016). They prefer to nest and roost in older Douglas-fir (*Pseudotsuga menziesii*) or mixed-conifer forests with closed canopies for cover and multiple layers of trees for thermoregulation. They nest in tree cavities or structures and forage in the canopy, among fallen trees, and along stands' edges (Forsman et al. 1984, Solis and Gutiérrez 1990, Thomas et al. 1990). In fire-prone areas of the subspecies' range, such as the Klamath Mountains region, the habitat's quality and the owls' fitness benefit from a certain amount of forest heterogeneity caused by frequent fire (Ward et al. 1998, Franklin et al. 2000, Franklin and Gutiérrez 2002). These fires create and maintain other forest cover types intermixed with forest in which the owls nest or roost, allowing them to find food closer to the nest and to spend more energy on successful reproduction than on foraging. In the portions of the Northern Spotted Owl's range where fire is less frequent, forest heterogeneity is less important and the owls prey primarily upon species that inhabit the cover type in which they nest and roost (Forsman et al. 2004).

The forests of the Pacific Northwest that the Northern Spotted Owl inhabits have changed dramatically over the past two centuries and continue to change at an accelerating pace (Hagmann et al. 2017, Halofsky

et al. 2020, Knight et al. 2022, Hoecker et al. 2026). Changes began in the early 19th century when annual fires set by indigenous populations managing their natural resources were ended by expanding western settlements (Huntsinger and McCaffrey 1995, Anderson 1996). The heterogeneous and biodiverse forest landscapes these fires created and maintained (Taylor and Skinner 1998) began to fill in with trees once held at bay by frequent burning. In these previously fire-tended systems, denser forest types in which the Northern Spotted Owl prefers to nest and roost began to slowly spread into and replace other less dense forest types or open areas (Agee and Edmonds 1992, Skinner 1995, Taylor and Skinner 2003). A century later an era of aggressive fire suppression (Loveridge 1944) began exacerbating this process of forest homogenization. Shortly thereafter, an era of industrial timber harvesting reduced remaining Northern Spotted Owl habitat to about half of its former range and largely confined it to federally managed public lands that had been established as forest reserves in the late 19th century (Thomas et al. 1990). Now, we are witnessing an increase in the frequency and extent of large wildfires, causing alarming changes to what habitat remains (Miller et al. 2012, Davis et al. 2017, 2022).

These changes, especially those caused by the logging that sparked the "Timber War" (Petach 2024), which then led to the listing of the Northern Spotted Owl under the Endangered Species Act and the Northwest Forest Plan, left indelible marks and confounding dilemmas. Both the Northwest Forest Plan (USDA and USDI 1994) and the recovery plan for the Northern Spotted Owl (USFWS 2011) recognized that in the portions of the owl's range that formerly burned frequently fires had been excluded for over a century and that active forest management would be required to restore those landscapes. Yet, over three decades later, little has been accomplished and a debate for or against this restoration still rages (Spies et al. 2019, Lindenmayer et al. 2025), a debate fueled by the past and focused on the most obvious change: rapid forest loss. Meanwhile, a slower, less obvious change caused by fire exclusion and spread of forest has garnered little attention. Both, however, can affect the Northern Spotted Owl adversely.

Disturbances responsible for large-scale rapid loss of nesting and roosting forest, whether wildfires, timber harvesting, or other agents, can reduce the owl's populations. In northern California, moderate to severe fires can reduce the owls' survival while having varying effects on recruitment (Rockweit et al. 2017). Persistence in a territory decreases and displacement increases with a fire's severity and extent within a territory (Rockweit et al. 2024). Alternatively, lack of disturbance in historically disturbance-prone forests allows for dense stands to encroach into other forest types and openings that represent good prey habitat, thus lowering the quality of the habitat and the fitness of the owls in it (Franklin et al. 2000). The ability of a territory to support long-term survival and reproduction depends on the proper balance and juxtaposition of both types of forest cover through time. Too much or too little of one or the other can produce an ecological trap and, over time, a population sink.

An ecological trap can be defined as an area that has been altered such that long-term survival and/or reproduction is no longer possible, but the inhabitants remain because some habitat-selection cues persist for a while or because of strong site fidelity (Battin 2004, Merkle et al. 2022). The scale of a

trap can range from a single territory (Gullion 1967) to a landscape (O'Neil et al. 2020). The concept originated over a half-century ago when Gullion (1967), studying the effects of forestry practices on the Ruffed Grouse (*Bonasa umbellus*), found adults' survival was lower at sites of perennial drumming. Dwernychuk and Boag (1972) found that California Gulls (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*) frightened away American Crows (*Corvus brachyrhynchos*), allowing Lesser Scaups (*Aythya affinis*), Mallards *(A. platyrhynchos*), Northern Pintails (*A. acuta*), Gadwalls (*Mareca strepera*), American Wigeons (*M. americana*), and White-winged Scoters (*Melanitta deglandi*) to successfully hatch eggs, but the gulls then consumed all the hatched ducklings! Ganey et al. (1997) speculated that the creation of openings in forest suitable for the Mexican Spotted Owl (*Strix occidentalis lucida*) might attract Great Horned Owls (*Bubo virginianus*), which might prey upon the Spotted Owls. And finally, Comfort et al. (2016) cautioned that intensely burned territories might become ecological traps because they could increase Northern Spotted Owls' exposure to predators or the elements.

In the summer of 2020, California experienced its largest wildfire on record, the August Complex Fire, which burned about 418,000 ha of forest in the Mendocino, Six Rivers, and Shasta–Trinity national forests (Safford et al. 2022). Chi (2024) reported a pair of Spotted Owls that two years after the fire hatched three young and fledged two. This observation was in the historical Butte Creek territory, which burned intensely. Chi concluded that intensely burned forest may be essential to the Northern Spotted Owl and that high-quality conditions for nesting and roosting persist in a different form after the fire. Here, we offer a longer perspective on the owls' use of this territory before and after the fire by examining forest growth, disturbance, and habitat trends in it. Evidently, the August Complex Fire set an ecological trap in the Butte Creek territory and some (but not all) Northern Spotted Owl territories within its footprint.

## METHODS

### Study Area

The Butte Creek territory lies within the Mendocino National Forest (Figure 1), which was once inhabited by diverse indigenous peoples, including the Yuki, Wailaki, Nomlaki, Patwin, and Pomo (Dugas et al. 2014). The territory, defined by a circle of radius 2092 m (1375 ha) around the 2022 nest, contains a core area defined by a circle of radius 1126 m (398 ha). Aerial imagery from the 1940s shows a road into the territory but no apparent sign of logging. Commercial timber harvesting began in the 1970s and ended by the mid-1980s. At that time, about 13% of the territory and 10% of the core area had been thinned or clearcut. From at least the 1950s to 2020, the territory had largely avoided fire. In 1988 the Butte Fire burned 6.5 ha within a previously harvested area on the northwestern edge of the territory. In 1990 the Carpenter Fire burned 15 ha, also within an area previously harvested on the southern edge of the territory. Then in 2020 the August Complex Fire burned the entire territory, the majority at high severity (Figure 1). Only one small (and ephemeral) patch of interior forest suitable for nesting or roosting (>30 m from the patch's edge) remained

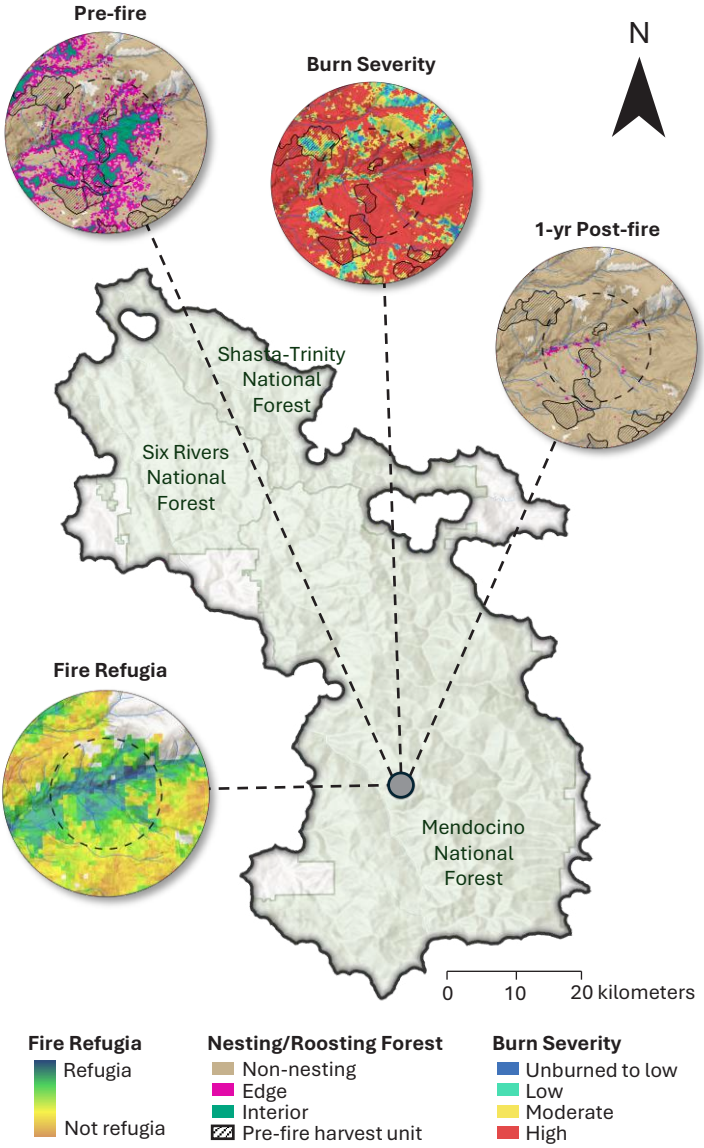



FIGURE 1. Location of the Butte Creek territory (1375 ha) of the Northern Spotted Owl within the perimeter of the August Complex Fire. The dashed circle within the territory indicates the core area (398 ha) within it.

in the core area and within a fire refugium (Krawchuk et al. 2020, Lesmeister et al. 2021: fig. 2). Small nonforested (rock, meadows, etc.) or less densely forested areas burned at low severity, including two areas previously logged (Figure 1).

## Northern Spotted Owl Surveys

Pre-fire surveys of the Butte Creek territory, following the USFWS (1992, 2012) protocol, date back to the 1970s and took place intermittently thereafter. A combination of vocal lure (callback) surveys and passive acoustic-recording surveys has been done every year since the fire (2021–2025). In 2022, over 20 pellets were collected from the fledglings' roost tree and examined for prey content. Within the August Complex Fire's footprint generally, passive acoustic monitoring under the Northwest Forest Plan continued from 2023 to 2025 (Kantor et al. 2022, Lesmeister and Jenkins 2022). Locations for this territory are documented in California's database of Spotted Owl observations (CDFW 2019).

## Forest and Habitat Monitoring

We evaluated changes from 1986 to 2025 on the basis of long-term habitat-monitoring data from throughout the Northern Spotted Owl's range. These data consist of annual time series of Landsat-based forest maps (30-m pixel resolution) and habitat maps (100-m resolution), developed through machine-learning methods trained on locations of Northern Spotted Owl nests and pair roosts (Glenn et al. 2017, Davis et al. 2022). Maps of forest types (suitable for nesting, roosting, or dispersal) are based on stand structure and tree-species composition. Habitat maps are consistent with "high-value habitat" as defined in recovery actions 9 and 10 (USFWS 2011). They are based on the extent and spatial arrangement of nest- or roost-suitable forest at multiple spatial scales, including abiotic factors (e.g., topography and climate). We also examined landscape maps representing large areas (25-km radius, ~1964 $km^2$) covered with enough forest (≥40% cover) to facilitate the owls' movement across the landscape (Davis et al. 2011:40–41).

At the finest spatial scale (core area), light detection and ranging (lidar) data (1-m resolution) from 2018 were used to map the crowns of trees >24 m in height, a height that, according to local height-to-diameter relationships, corresponds with nest- or roost-suitable forest (Forest Vegetation Simulator 2026). Maps of the annual normalized burn ratio, produced from Sentinel 2 satellite imagery (20-m pixel resolution), were used to determine whether the trees were alive or dead before and after the fire. This ratio is a multispectral index that ranges from –1 to +1. Values below zero indicate dead vegetation. Values closer to 1 indicate living vegetation (see figure 3 in Miller and Thode (2007), in which the values are expressed on a scale from –1000 to +1000). The relationship between canopy cover of live trees (based on lidar mapping) and the normalized burn ratio showed that when this ratio equals zero, canopy cover is 4–10% (mean 7%), a ratio of 0.4 equates to canopy cover of 36–42% (mean 39%), and a ratio >0.6 represents a mean canopy cover >60% (Lesmeister et al. 2019: fig. 3). Each tree was assigned a mean annual normalized burn ratio, where a value >0.6 represents living trees with canopy cover >60%, values between 0.4 and 0.6 represent 40–60% live tree cover, values between 0.15 and 0.4 represent 15–40% live tree cover, values between 0 and 0.15 represent 0–15% live tree cover, and values <0 represent 100% dead trees.

## RESULTS

### Surveys

This territory was first surveyed in 1975, when one pair of Spotted Owls was noted. A pair with three young was found the following year (1976). Subsequent surveys took place in 1977 (species detected), 1980 (pair with two young), 1982 (species detected), 1990 (pair with one young), 1992 (pair with two young), 2002 (pair with young), 2006 (pair with two young), and 2008 (pair with one young). There are no records of this territory being surveyed again until the first year following the fire (2021), when one adult male was observed. A pair that produced three young and fledged two was documented the following year (Chi 2024). During that same year four-noted hoots from both a male and a female were detected by an autonomous recording unit placed near the historical nest tree and approximately 390 m uphill and south of the new nest tree. Examination of Spotted Owl pellets from the fledglings' roost tree did not reveal an abundance of small mammal bones, and all cranial bones found belonged to the Dusky-footed Woodrat (*Neotoma fuscipes*). All pellets contained insect exoskeletons. In 2023, a single male was detected aurally once during a callback survey. It was never detected during two other night visits, stand searches, or follow-ups. No Spotted Owls were detected by autonomous acoustic recorders placed within 200 m of the nest tree and recording for six weeks during the breeding season in both 2023 and 2024, or during six callback surveys in 2025.

Within the August Complex Fire's footprint, annual rangewide passive acoustic monitoring detected Spotted Owls in 9 of 13 (69%) 5-km$^2$ hexagons in which four autonomous recording units had been deployed. These included a pair about 21 km north-northeast of the Butte Creek territory, in an area that burned with mixed severity (Figure 2). The following year (2024), Spotted Owls were detected in 4 of 9 such hexagons surveyed (44%), including a pair in the same hexagon as in 2023. In 2025, the owls were detected in 2 of 7 hexagons surveyed (29%), including one pair in a hexagon about 20 km to the south that had also burned with mixed severity. The northerly hexagon with two back-to-back years (2023 and 2024) of recording units detecting a pair was surveyed in 2025 by local biologists and the pair was confirmed, marking three consecutive years of pair occupancy. In 2025 this hexagon contained 115 ha of habitat in refugia that survived the fire (Figure 3). In all three of these years this same monitoring also detected Great Horned Owls throughout the fire's footprint. A Barred Owl (*Strix varia*) was detected in 2023 in the northern portion of the fire (Six Rivers National Forest), but no Barred Owls were detected in the vicinity of the Butte Creek territory.

### Forest and Habitat Monitoring

Prior to the August Complex Fire, the extent of forest suitable for Spotted Owl nesting or roosting within the Butte Creek territory was increasing at a rate of 0.13 ± 0.07% (95% confidence interval) per year; within the core area it was increasing by 0.21 ± 0.10% per year (Figure 4a). The immediate effect of the fire was a decrease of 97.7% in such forest at the territory scale and 96.1% within the core area. By the fifth year post-fire (2025), these losses had increased to 99.3% and 98.9%, respectively, owing to trees' delayed mor-

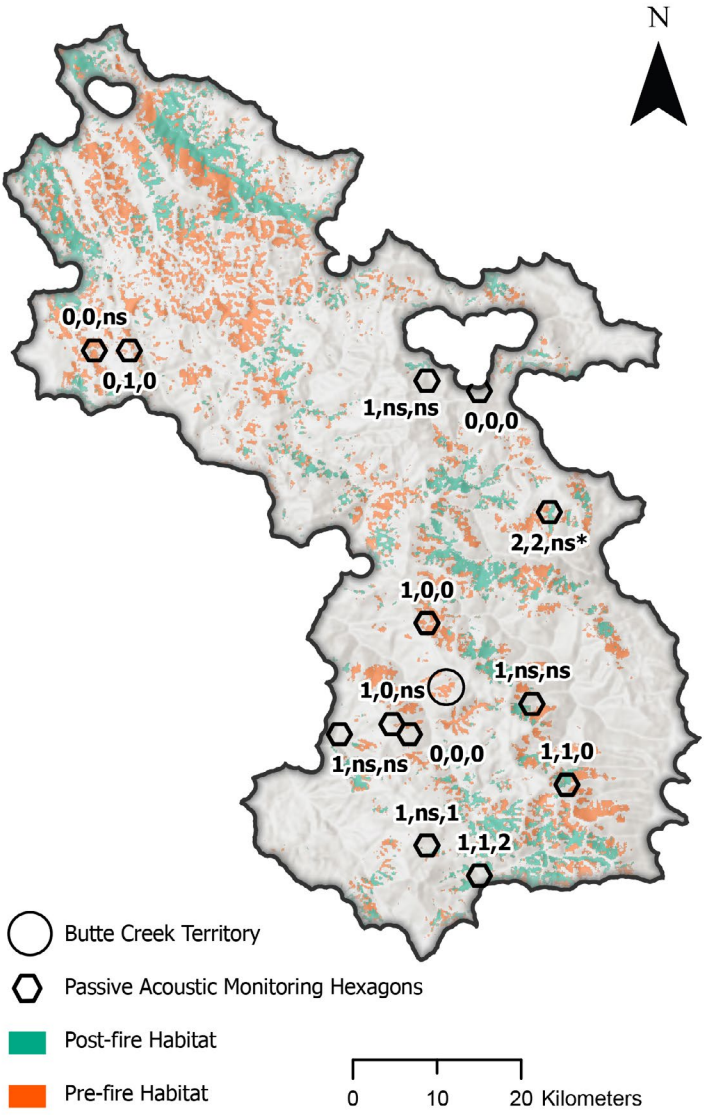



FIGURE 2. Detections of the Northern Spotted Owl within the perimeter of the August Complex Fire by passive acoustic monitoring under the Northwest Forest Plan from 2023 to 2025. The three numbers associated with each hexagon represent the results for each year (2023, 2024, 2025), where 0 = no owls detected, 1 = a single owl detected, 2 = a pair detected, and ns = not surveyed by this technique. The asterisk (*) represents a pair detected through callback surveys in a hexagon unsurveyed that year by an autonomous recording unit. Pre-fire habitat represents habitat lost from the fire; post-fire habitat represents habitat remaining in 2025.

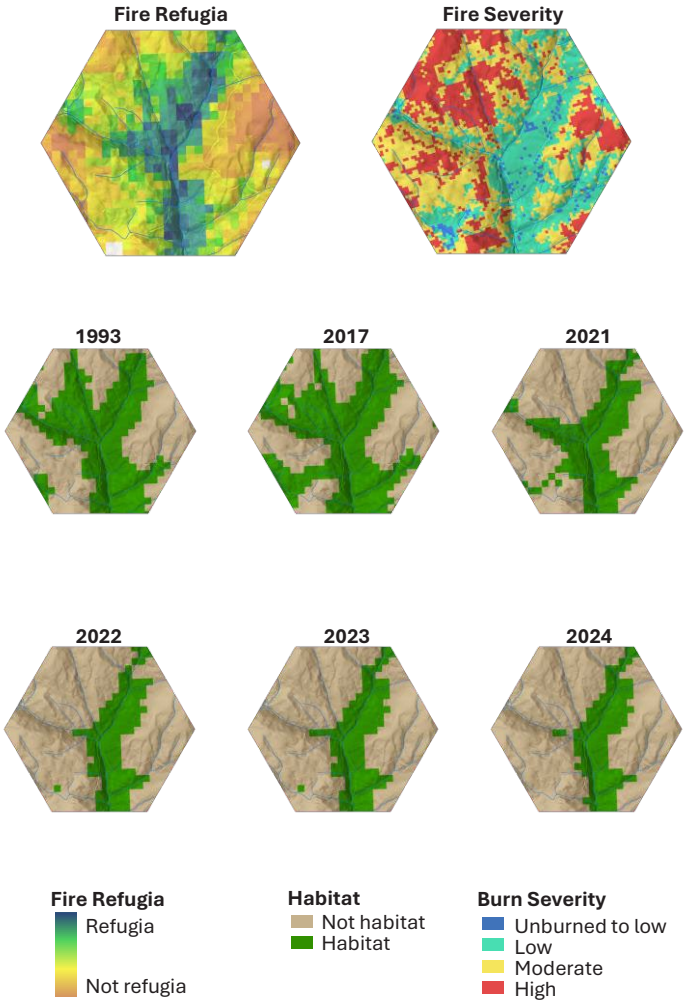



FIGURE 3. Distribution of habitat suitable for the Spotted Owl in a 500-ha hexagon monitored by passive acoustic recording 3 to 5 years after the August Complex Fire. Over time, the habitat conformed to topo-climatic fire refugia and, without disturbances, expanded outward into nonrefugial areas (1993 to 2017). The post-fire maps (2021–2024) show the effect of trees' delayed mortality from the fire and how wildfires can realign Spotted Owl habitat with fire refugia.

tality. In 1993 (the first year of habitat mapping) the forest in this territory contributed to 245 ha of habitat suitable for long-term occupancy by a pair (Glenn et al. 2017). From 1993 to 2020, suitable habitat within the territory increased by 24%, but it was completely removed by the fire. At the landscape scale (the footprint of the August Complex Fire) habitat had increased, over

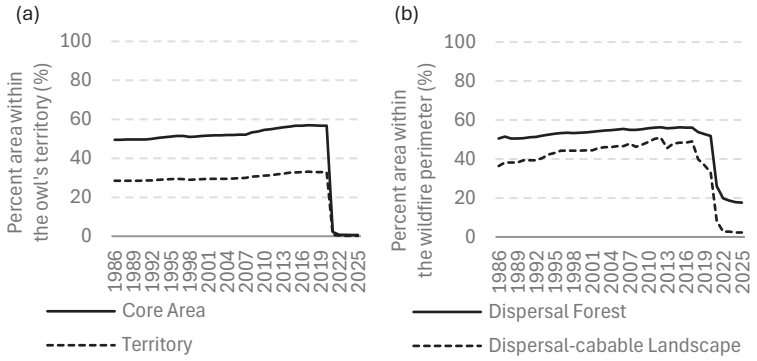



FIGURE 4. (a) Trends in the extent of forest suitable for Spotted Owl nesting or roosting within the Butte Creek territory. (b) Trends in the extent of forest and of landscape suitable for Spotted Owl dispersal in the August Complex Fire's footprint.

this same interval, by 27.7% and the carrying capacity for Spotted Owl pairs had increased by 4.2%, on the basis of Glenn et al. (2017). The notable difference between the gains in habitat and carrying capacity has to do with the spatial pattern of the gains, which essentially expanded from source patches within fire refugia. This expansion offered only more space use for existing territories, not an equivalent percentage of new territories. The effect of the fire, after 5 years, was a 54.3% loss of habitat, but a 30.4% reduction in carrying capacity. Before the fire, the area of suitable habitat nearest the Butte Creek territory's activity center was slightly over 2 km away (Pinto Creek). After the fire, the distance increased to 3 km in 2021 and 4 km by 2025.

Also, we analyzed forest suitable for Spotted Owl dispersal at the scale of the August Complex Fire. Prior to the listing of the Northern Spotted Owl as threatened in 1990, it covered slightly over half of this future fire's footprint. Post-listing, it began increasing at an average rate of 0.29 ± 0.10% per year until 2005, when damage from insects began increasing above background levels (Figure 4b). From 2006 to 2017 such forest increased at an average rate of 0.07 ± 0.17% per year, essentially remaining stable as recruitment was balanced with losses from disturbances. A notable decrease from 2017 to 2020 coincided with a significant increase in tree mortality related to insects (CFPC 2018). The immediate effect of the August Complex Fire was a decrease of 49.7%, and by the fifth year the loss had reached 66.1%. The landscape suitable for dispersal generally followed the same trend as forest suitable for dispersal. It increased monotonically from 1986 to 2007, followed by a period of instability until 2017, when it began to decrease rapidly. This decrease was initially related to insects and drought, then followed by the August Complex Fire. The area suitable for dispersal within the fire's footprint had increased from 36% in 1986 to 51% by 2017 but was slightly over 2% in 2025.

Within the core area of the Butte Creek territory, approximately 12,000 large live trees, median height 41 m, constituted the forest suitable for the owl's nesting or roosting (Figure 5). The largest trees (99$^{th}$ percentile) occurred within fire refugia. Before the fire, 95% of trees had mean normalized burn

ratios above 0.6. In the first-year post-fire, no trees with a ratio >0.6 remained. About 3.7% had ratios >0.4. This proportion declined to 1.2% in the second year post-fire and to 0.6% by the third, where it remained until 2025. The tree in which the owls nested in 2022 was in an area where the normalized burn ratio was 0.15–0.4 in 2021, 0–0.15 in 2022, then <0 subsequently. The nearest distance from the nest tree of 2022 to trees with ratios >0.4 in 2021 was about 40 m. This distance increased to about 200 m in the following years.

## DISCUSSION

Almost two-thirds of the August Complex Fire's 4180-km² footprint had not experienced a wildfire since 1878 (Safford et al. 2022, CALFIRE 2025). Prior to the 2020 fire, forest suitable for the Northern Spotted Owl's nesting

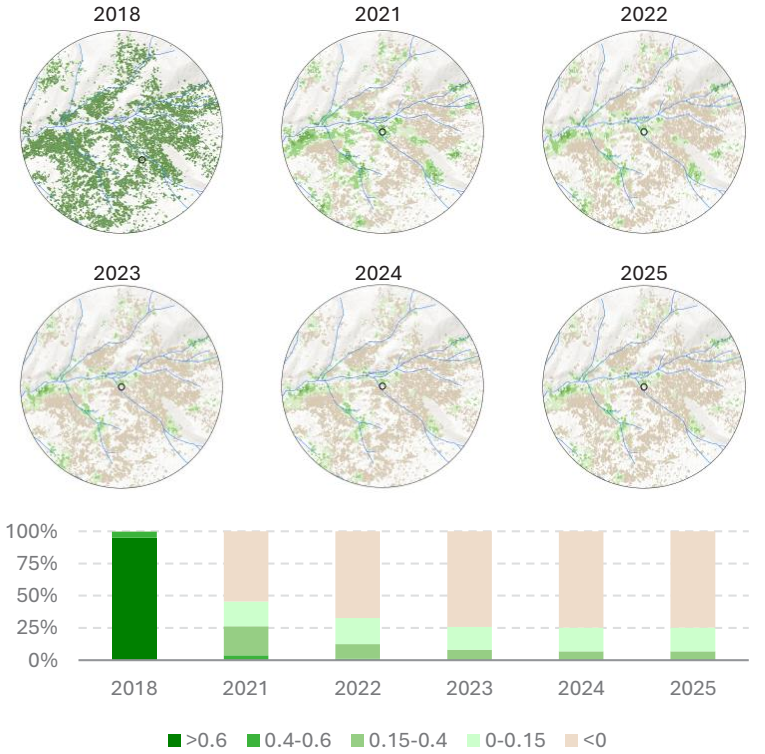



FIGURE 5. Changes in the coverage of live and dead large tree crowns within the Butte Creek core area before and after the August Complex Fire. The black hollow dots represent nest trees' locations before (2018) and after the fire. Nesting was observed in 2022 but not in the years following. Values are the mean normalized burn ratio of tree crowns, representing the percentage of live tree cover, shown in shades of green to tan (live to dead).

or roosting was expanding steadily. Additional forest suitable for dispersal was displacing other cover types (Figure 4). Prolonged exclusion of fire from this landscape, formerly burned annually by indigenous peoples, set a "slow" landscape-scale ecological trap (Figure 6). Over time, this trap likely lowered the owls' fitness in several territories. Not only does fire exclusion have the potential to lower their fitness, it also increases the risk of severe fire and large-scale loss of habitat (Safford and Stevens 2017), setting the stage for "fast" site-level ecological traps (Figure 6).

Five years after the August Complex Fire, it appeared that Spotted Owls no longer occupied the Butte Creek territory. We contend that the August Complex Fire set a "fast" ecological trap by rapidly reducing the amount of forest that provided the owls cover from predators and the elements. The Butte Creek pair, remaining in their territory, were able to find temporary refuge in a small ephemeral patch of interior forest with a suitable nesting cavity nearby. A diffuse edge of the forest suitable for nesting and roosting (Comfort et al. 2016) and the increase in prey that normally follows a forest disturbance (Carey et al. 1992, Culhane et al. 2022) likely created conditions conducive for foraging and reproduction. The lack of sufficient closed-canopy forest, however, likely increased the owls' vulnerability to predation, and at least one of their offspring was preyed on by a mammal (Chi 2022).

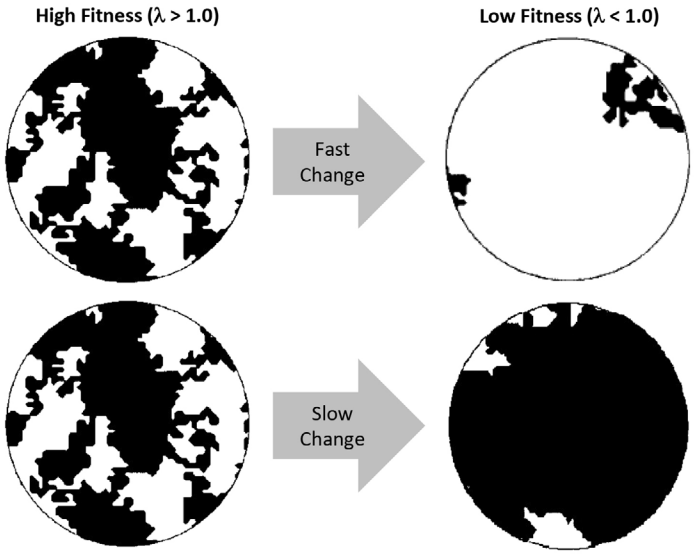



FIGURE 6. Spotted Owl territories (circles of radii 0.71 km) from Franklin et al. (2000: fig. 10), illustrating two types of ecological traps. The top circles illustrate a rapid loss of nesting/roosting forest resulting in a territory in which survival is low (< 1.0). The bottom circles illustrate how slow gains in nesting/roosting forest, owing to prolonged periods of fire exclusion, may also result in low fitness because of a low rate of reproduction. Black areas, nesting/roosting forest; white areas, other vegetation types. Graphics used with permission from A. Franklin.

With every passing year, accumulating tree mortality tightened the "noose." Favorable habitat disappeared, and the Spotted Owls were no longer able to find adequate cover and shelter. Eventually, they likely succumbed to these pressures or moved elsewhere.

Documentation of the Pacific Fisher (*Pekania pennanti*) near the nest (Chi 2022) hints that it may have been responsible for predation of one of the three hatchlings. While the fisher is an opportunistic forager and doesn't specifically target the Spotted Owl, the remains of birds and eggshell fragments have been found in its scat (Zielinski et al. 1999). In California, Pilgrim et al. (2023) found DNA of raptors and cavity-nesting birds in fisher scat, but it was unknown if it was from eggs, nestlings, or adults. While there are no published accounts of a fisher preying on a Northern Spotted Owl, during a nearby long-term study of the owl's demography, one was observed entering a nest—being defended by the male owl—that subsequently failed (Mark Higley pers. comm.). The female owl was not seen again after this encounter. Also, in 2022, automated recording units detected a Great Horned Owl, known to prey on juvenile Spotted Owls (Forsman 1976, Marcot and Gardetto 1980), and in 2024 they detected a pair within the core area.

In addition to exposure to predators, the combination of climate and extent of suitable forest, rather than these factors individually, is an important factor explaining variation in the Spotted Owl's survival (Franklin et al. 2000). The species is less heat tolerant than many birds (Weathers et al. 2001). Ganey et al. (1993) found that Great Horned Owls were better at thermoregulation than Mexican Spotted Owls. Ting (1998) found that Northern Spotted Owls appear heat intolerant and select forest with a multilayered structure that provides stable, cooler microclimates. Therefore the loss of such forest where owls can thermoregulate may also depress their survival (Barrows and Barrows 1978), even without an increase in predation.

Finally, the type of forest disturbance matters less than what remains and where it remains after the disturbance. In the case of the Butte Creek territory, Spotted Owls persisted and reproduced years after the territory and core area were disturbed by pre-fire timber harvesting. This harvesting changed only a small portion of the territory and left enough suitable forest to support survival. Intermixed with this forest accommodating nesting and roosting were other types of forest that supported prey populations. Nesting/roosting forests were concentrated within fire refugia, which support their development and maintenance, and where they are naturally more resilient to fires. What little forest suitable for nesting and roosting that remained in the territory following the fire, remained in fire refugia.

## SUMMARY

In July 2023, three years after a fire had killed 99% of the forest suitable for nesting and roosting, the last detection of a Spotted Owl within the Butte Creek territory was recorded. A male at the territory's southeastern edge, it had presumably dispersed from an active territory about 5 km to the northeast (see Figure 2). Chi's (2024:300) statement, "It appears that the high-quality conditions for nesting and roosting observed at this site in 2002 (unmanaged from 2002 to 2022) persisted in a different form after the territory burned in 2020"

was perhaps premature. Contrary to the perspective that this territory was "unmanaged" for two decades before the fire, the management decisions to actively suppress fires and limit the amount of active forest management allowed under the Northwest Forest Plan (USDA and USDI 1994) may have contributed to the loss of habitat in this territory, which burned with such high intensity.

Chi (2024:300) also suggested an unrecognized benefit of fire-killed forest is that it may be essential to the Spotted Owl after a wildfire, stating that it is "regularly undervalued, overlooked, and routinely removed." However, burned forest's potential benefits to the Spotted Owl have been recognized since the early 1990s (Carey et al. 1992) and are a focus of active research. On federally managed forests, only a small fraction (4.9%) of burned forest has been removed (Zuspan et al. 2024). Forest managers are beginning to better understand the important role of burned forest, not only for the Spotted Owl but for biodiversity in general (Spies et al. 2012). Additionally, as wildfires burn ever more frequently, more extensively, and more severely, as has been predicted (Davis et al. 2017) and observed (Cova et al. 2025), forest managers are realizing the consequences of excluding fires from landscapes that once burned regularly. While new knowledge is being incorporated into how burned landscapes are managed, adoption of indigenous peoples' knowledge and practices can help restore a balance (Charnley et al. 2007).

The Butte Creek territory provides an example of a site-level ecological trap set by a rapid change in habitat conditions caused by a large wildfire. The slow (at least over a century) increase of dense forests regionally represents a landscape-scale ecological trap. The focus on the adverse effects of forest change on the Northern Spotted Owl has mostly been on the former and has ignored the latter. Active forest management that aims to restore the former balance of forest suitable for nesting and roosting (within fire refugia) and other forest types (outside of such refugia) can defuse existing traps and may be beneficial to the Northern Spotted Owl, or at least neutral (Franklin et al. 2000, Halofsky et al. 2024, Lesmeister et al. 2025).

## ACKNOWLEDGMENTS

We acknowledge Tonja Chi for documenting and highlighting the Northern Spotted Owl's use of burned forest. It was the catalyst needed to elicit the broader story of a century or more of fire exclusion and its effect on the once diverse forests inhabited by this bird and hosts of other species. Long-term monitoring and research for the Northwest Forest Plan made telling that story possible. We also thank Jeremy Rockweit, Alan Franklin, and Brandon Collins for improving this paper through their helpful reviews.

## LITERATURE CITED

Agee, J. K., and Edmonds, R. L. 1992. Appendix F: Forest protection guidelines for the Northern Spotted Owl, *in* Recovery plan for the Northern Spotted Owl—draft. U.S. Fish and Wildlife Service, Washington, DC; https://archive.org/details/recoveryplanforn00unse_0.

Anderson, M. K. 1996. Tending the wilderness. Restoration and Mgmt. Notes 14(2):154–166; doi.org/10.3368/er.14.2.154.

Barrows, C., and Barrows, K. 1978. Roost characteristics and behavioral thermoregulation in the Spotted Owl. W. Birds 9:1–8.

Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. Cons. Biol. 18(6):1482–1491; doi.org/10.1111/j.1523-1739.2004.00417.x.

California Department of Fish and Wildlife [CDFW]. 2019. Spotted Owl observations database management framework. Calif. Dept. Fish and Wildlife, Sacramento; https://wildlife.ca.gov/Data/CNDDB/Spotted-Owl-Info.

California Department of Forestry and Fire Protection [CALFIRE]. 2025. California fire perimeters—all; https://gis.data.cnra.ca.gov/datasets/CALFIRE-Forestry::california-fire-perimeters-all/about.

California Forest Pest Council [CFPC]. 2018. California forest pest conditions. Calif. Pest Council, Sacramento; https://www.caforestpestcouncil.org/forest-pest-conditions-reports.

Carey, A. B., Horton, S. P., and Biswell, B. L. 1992. Northern Spotted Owls: Influence of prey base and landscape character. Ecol. Monogr. 62(2):223–250; doi.org/10.2307/2937094.

Charnley, S., Fischer, A. P., and Jones, E. T. 2007. Integrating traditional and local ecological knowledge into forest biodiversity conservation in the Pacific Northwest. Forest Ecol. and Mgmt. 246(1):14–28; doi.org/10.1016/j.foreco.2007.03.047.

Chi, T. Y. 2022. Preliminary evaluation of Northern Spotted Owl: Plaskett–Keller August Complex Phase I Project Area. Report on file with Mendocino National Forest, 825 North Humboldt Ave., Willows, CA 95988.

Chi, T. Y. 2024. First record of the Northern Spotted Owl nesting in forest burned at the highest level of severity. W. Birds 55:293–303; doi 10.21199/WB55.4.4.

Comfort, E. J., Clark, D. A., Anthony, R. G., Bailey, J., and Betts, M. G. 2016. Quantifying edges as gradients at multiple scales improves habitat selection models for Northern Spotted Owl. Landscape Ecol. 31:1227–1240; doi.org/10.1007/s10980-015-0330-1.

Cova, G. R., Prichard, S. J., Zald, H. S., Gaines, W. L., and Kane, V. R. 2025. Implications of recent wildfires for forest management on federal lands in the Pacific Northwest, USA. Forest Ecol. and Mgmt. 598:123262; doi.org/10.1016/j.foreco.2025.123262.

Culhane, K., Sollmann, R., White, A. M., Tarbill, G. L., Cooper, S. D., and Young, H. S. 2022. Small mammal responses to fire severity mediated by vegetation characteristics and species traits. Ecol. and Evol. 12:e8918; doi.org/10.1002/ece3.8918.

Davis, R. J., Dugger, K. M., Mohoric, S., Evers, L., and Aney, W. C. 2011. Northwest Forest Plan—the first 15 years (1994–2008): Status and trends of Northern Spotted Owl populations and habitats. Gen. Tech. Rep. PNW-GTR-850. U.S. Forest Service, Pac. Northwest Res. Sta., Portland, OR; doi.org/10.2737/PNW-GTR-850.

Davis, R. J., Hollen, B., Hobson, J., Gower, J. E., and Keenum, D. 2016. Northwest Forest Plan—the first 20 years (1994–2013): Status and trends of Northern Spotted Owl habitats. Gen. Tech. Rep. PNW-GTR-929. U.S. Forest Service, Pac. Northwest Res. Sta., Portland, OR; doi.org/10.2737/PNW-GTR-929.

Davis, R., Yang, Z., Yost, A., Belongie, C., and Cohen, W. 2017. The normal fire environment—Modeling environmental suitability for large forest wildfires using past, present, and future climate normals. Forest Ecol. and Mgmt. 390:173–186; doi.org/10.1016/j.foreco.2017.01.027.

Davis, R. J., Lesmeister, D. B., Yang, Z., Hollen, B., Tuerler, B., Hobson, J., Guetterman, J., and Stratton, A. 2022. Northwest Forest Plan—the first 25 years (1994–2018): Status and trends of Northern Spotted Owl habitats. Gen. Tech. Rep. PNW-GTR-1003. U.S. Forest Service, Pac. Northwest Res. Sta., Portland, OR; doi.org/10.2737/PNW-GTR-1003.

Dugas, M., Huberland, A., and Weaver, R. 2014. Yuki settlement on the Black Butte River revisited. Proc. Soc. Calif. Archaeol. 28:26–42.

Dwernychuk, L. W., and Boag, D. A. 1972. Ducks nesting in association with gulls—an ecological trap? Can. J. Zool. 50:559–563; doi.org/10.1139/z72-076.

Forest Vegetation Simulator Staff. 2026. Inland California and southern Cascades (CA) variant overview—forest vegetation simulator. U.S. Dept. Agr., Forest Service, Forest Mgmt. Service Center, Fort Collins, CO; https://www.fs.usda.gov/sites/default/files/forest-management/fvs-ca-overview.pdf.

Forsman, E. D. 1976. A preliminary investigation of the Spotted Owl in Oregon. M.S. thesis, Ore. State Univ., Corvallis.

Forsman, E. D., Meslow, E. C., and Wight, H. M. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monogr. 87:3–64.

Forsman, E. D., Anthony, R. G., Meslow, E. C., and Zable, C. J. 2004. Diets and foraging behavior of Northern Spotted Owls in Oregon. J. Raptor Res. 38:214–230.

Franklin, A. B., and Gutiérrez, R. J. 2002. Spotted Owls, forest fragmentation, and forest heterogeneity. Studies Avian Biol. 25:203–220; https://digitalcommons.usf.edu/sab/vol25/iss1/18.

Franklin, A. B., Anderson, D. R., Gutiérrez, R. J., and Burnham, K. P. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecol. Monogr. 70:539–590; doi.org/10.2307/2657186.

Ganey, J. L., Balda, R. P., and King, R. M. 1993. Metabolic rate and evaporative water loss of Mexican Spotted and Great Horned Owls. Wilson Bull. 105:645–656; http://www.jstor.org/stable/4163356.

Ganey, J. L., Block, W. M., Jenness, J. S., and Wilson, R. A. 1997. Comparative habitat use of sympatric Mexican Spotted and Great Horned Owls. J. Wildlife Res. 2:115–123.

Glenn, E. M., Lesmeister, D. B., Davis, R. J., Hollen, B., and Poopatanapong, A. 2017. Estimating density of a territorial species in a dynamic landscape. Landscape Ecol. 32:563–579; doi.org/10.1007/s10980-016-0467-6.

Gullion, G. W. 1967. Selection and use of drumming sites by male Ruffed Grouse. Auk 84:87–112; doi.org/10.2307/4083257.

Hagmann, R. K., Johnson, D. L., and Johnson, K. N. 2017. Historical and current forest conditions in the range of the Northern Spotted Owl in south central Oregon, USA. Forest Ecol. and Mgmt. 389:374–385; doi.org/10.1016/j.foreco.2016.12.029.

Halofsky, J. E., Peterson, D. L., and Harvey, B. J. 2020. Changing wildfire, changing forests: The effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. Fire Ecol. 16(4):1–26; doi.org/10.1186/s42408-019-0062-8.

Halofsky, J. S., Donato, D. C., Singleton, P. H., Churchill, D. J., Meigs, G. W., Gaines, W. L., Kane, J. T., Kane, V. R., Munzing, D., and Hessburg, P. F. 2024. Reconciling species conservation and ecosystem resilience: Northern Spotted Owl habitat sustainability in a fire-dependent forest landscape. Forest Ecol. and Mgmt. 567(122072); doi.org/10.1016/j.foreco.2024.122072.

Hoecker, T. J., Davis, K. T., Littlefield, C., Chandler, J., Parks, S., Maguire, A., Kemp, K., Yegorova, S., and Dobrowski, S. 2026. Alternative future vegetation pathways reveal potential transformations of western U.S. ecosystems. Global Change Biol. 32(3):e70795; doi.org/10.1111/gcb.70795.

Huntsinger, L., and McCaffrey, S. 1995. A forest for the trees: Forest management and the Yurok environment, 1850 to 1994. Am. Indian Culture and Res. J. 19(4):155–192.

Kantor, S., Lesmeister, D., and Davis, R. 2022. Bioacoustics and artificial intelligence: A new chapter for Northern Spotted Owl monitoring and research. Sci. Findings 245:1–6; https://research.fs.usda.gov/download/treesearch/63670.pdf.

Knight, C. A., Anderson, L., Bunting, M. J., Champagne, M., Clayburn, R. M., Crawford, J. N., Klimaszewski-Patterson, A., Knapp, E. E., Lake, F. K., Mensing, S. A., and Wahl, D. 2022. Land management explains major trends in forest structure

and composition over the last millennium in California's Klamath Mountains. Proc. Natl Acad. Sci. 119(12): e2116264119; doi.org/10.1073/pnas.2116264119.
Krawchuk, M. A., Meigs, G. W., Cartwright, J. M., Coop, J. D., Davis, R., Holz, A., Kolden, C., and Meddens, A. J. 2020. Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. Frontiers Ecol. and Environ. 18(5):235–244; doi.org/10.1002/fee.2190.
Lesmeister, D. B., and Jenkins, J. M. 2022. Integrating new technologies to broaden the scope of Northern Spotted Owl monitoring and linkage with USDA forest inventory data. Frontiers in Forests and Global Change 5:966978; doi.org/10.3389/ffgc.2022.966978.
Lesmeister, D. B., Sovern, S. G., Davis, R. J., Bell, D. M., Gregory, M. J., and Vogeler, J. C. 2019. Mixed–severity wildfire and habitat of an old–forest obligate. Ecosphere 10(4): e02696; doi.org/10.1002/ecs2.2696.
Lesmeister, D. B., Davis, R. J., Sovern, S. G., and Yang, Z. 2021. Northern Spotted Owl nesting forests as fire refugia: A 30-year synthesis of large wildfires. Fire Ecol. 17(32); doi.org/10.1186/s42408-021-00118-z.
Lesmeister, D. B., Davis, R.J., and Rockweit, J. T. 2025. Resolving conservation conflict through fire refugia: Integrating landscape resilience into forest management. J. Environ. Mgmt. 393(126974); doi.org/10.1016/j.jenvman.2025.126974.
Lindenmayer, D., Zylstra, P., Hanson, C. T., Six, D., and DellaSala, D. A. 2025. When active management of high conservation value forests may erode biodiversity and damage ecosystems. Biol. Cons. 305(111071); doi.org/10.1016/j.biocon.2025.111071.
Loveridge, E. W. 1944. The fire suppression policy of the U.S. Forest Service. J. Forestry 42:549–554; doi.org/10.1093/jof/42.8.549.
Marcot, B. G., and Gardetto, J. 1980. Status of the Spotted Owl in Six Rivers National Forest, California. W. Birds 11:79–88.
Merkle, J. A., Abrahms, B., Armstrong, J. B., Sawyer, H., Costa, D. P., and Chalfoun, A. D. 2022. Site fidelity as a maladaptive behavior in the Anthropocene. Frontiers Ecol. and Environ. 20:187–194; doi.org/10.1002/fee.2456.
Miller, J. D., and Thode, A. E. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). Remote Sensing of Environ. 109:66–80; doi.org/10.1016/j.rse.2006.12.006.
Miller, J. D., Skinner, C. N., Safford, H. D., Knapp, E. E., and Ramirez, C. M. 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. Ecol. Appl. 22:184–203; doi.org/10.1890/10-2108.1.
O'Neil, S. T., Coates, P. S., Brussee, B. E., Ricca, M. A., Espinosa, S. P., Gardner, S. C., and Delehanty, D. J. 2020. Wildfire and the ecological niche: Diminishing habitat suitability for an indicator species within semi-arid ecosystems. Global Change Biol. 26:6296–6312; doi.org/10.1111/gcb.15300.
Petach, L. 2024. The timber wars: The Endangered Species Act, the Northwest Forest Plan, and the political economy of timber management in the Pacific Northwest. Public Choice 198:209–226; doi.org/10.1007/s11127-023-01123-3.
Pilgrim, K. L., Green, R. E., Purcell, K. L., Wilcox, T. M., McGregor, E. L., Gleason, L. E., Wasser, S. K., and Schwartz, M. K. 2023. Shifts in Fisher (*Pekania pennanti*) diet in response to climate-induced tree mortality in California assessed with DNA metabarcoding. J. Nat. Cons. 73:126408; doi.org/10.1016/j.jnc.2023.126408.
Rockweit, J. T., Franklin, A. F., and Carlson, P. C. 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. Ecology 98:1574–1582; doi.org/10.1002/ecy.1805.
Rockweit, J. T., Dugger, K. M., Lesmeister, D. B., Davis, R. J., Franklin, A. B., and Higley, J. M. 2024. Changing fire regimes and nuanced impacts on a critically imperiled species. Biol. Cons. 296:110701; doi.org/10.1016/j.biocon.2024.110701.

Safford, H. D., and Stevens, J. T. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. Gen. Tech. Rep. PSW-GTR-256. U.S. Forest Service, Pac. Southwest Res. Sta., Albany, CA; doi.org/10.2737/PSW-GTR-256.

Safford, H. D., Paulson, A. K., Steel, Z. L., Young, D. J., and Wayman, R. B. 2022. The 2020 California fire season: A year like no other, a return to the past or a harbinger of the future? Global Ecol. and Biogeogr. 31:2005–2025; doi.org/10.1111/geb.13498.

Skinner, C. N. 1995. Change in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. Landscape Ecol. 10:219–228; doi.org/10.1007/BF00129256.

Solis, D. M. Jr., and Gutiérrez, R. J. 1990. Summer habitat ecology of Northern Spotted Owls in northwestern California. Condor 92:739–748; doi.org/10.2307/1368693.

Spies, T. A., Lindenmayer, D. B., Gill, A. M., Stephens, S. L., and Agee, J. K. 2012. Challenges and a checklist for biodiversity conservation in fire-prone forests: Perspectives from the Pacific Northwest of USA and southeastern Australia. Biol. Cons. 145:5–14; doi.org/10.1016/j.biocon.2011.09.008.

Spies, T. A., Long, J. W., Charnley, S., Hessburg, P. F., Marcot, B. G., Reeves, G. H., Lesmeister, D. B., Reilly, M. J., Cerveny, L. K., Stine, P. A., and Raphael, M. G. 2019. Twenty-five years of the Northwest Forest Plan: What have we learned? Frontiers in Ecol. and Environ. 17:511–520; doi.org/10.1002/fee.2101.

Taylor, A. H., and Skinner, C. N. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecol. and Mgmt. 111:285–301; doi.org/10.1016/S0378-1127(98)00342-9.

Taylor, A. H., and Skinner, C. N. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecol. Appl. 13:704–719; doi.org/10.1890/1051-0761(2003)013[0704:SPACOH]2.0.CO;2.

Thomas, J. W., Forsman, E. D., Lint, J. B., Meslow, E. C., Noon, B. R., and Verner, J. 1990. A conservation strategy for the Northern Spotted Owl: Report of the Interagency Scientific Committee to address the conservation of the Northern Spotted Owl. U.S. Govt. Printing Office, Washington, DC; doi.org/10.5962/bhl.title.124040.

Ting, T.-F. 1998. The thermal environment of Northern Spotted Owls in northwestern California: Possible explanations for use of interior old growth and coastal early successional stage forest. M.S. thesis, Humboldt State University, Arcata, CA; https://scholarworks.calstate.edu/downloads/xs55mn29q.

U.S.D.A. Forest Service and U.S.D.I. Bureau of Land Management [USDA and USDI]. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. Volumes 1–2 and record of decision. U.S. Forest Service, Portland, OR.

U.S. Fish and Wildlife Service [USFWS]. 1992. Protocol for surveying proposed management activities that may impact Northern Spotted Owls. U.S. Fish and Wildlife Service, Portland, OR.

U.S. Fish and Wildlife Service [USFWS]. 2011. Revised recovery plan for the Northern Spotted Owl (*Strix occidentalis caurina*). U.S. Fish and Wildlife Service, Portland, OR; https://www.fws.gov/sites/default/files/documents/NSO_RevisedRP_2011.pdf.

U.S. Fish and Wildlife Service [USFWS]. 2012. Protocol for surveying proposed management activities that may impact Northern Spotted Owls; https://www.fws.gov/sites/default/files/documents/2012RevisedNSOprotocol.2.15.12.pdf.

Ward Jr., J. P., Gutiérrez, R. J., and Noon, B. R. 1998. Habitat selection by Northern

Spotted Owls: The consequences of prey selection and distribution. Condor 100:79–92; doi.org/10.2307/1369899.
Weathers, W. W., Hodum, P. J., and Blakesley, J. A. 2001. Thermal ecology and ecological energetics of California Spotted Owls. Condor 103:678–690; doi.org/10.1093/condor/103.4.678.
Zielinski, W. J., Duncan, N. P., Farmer, E. C., Truex, R. L., Clevenger, A. P., and Barrett, R. H. 1999. Diet of Fishers (*Martes pennanti*) at the southernmost extent of their range. J Mammal. 80:961–971; doi.org/10.2307/1383266.
Zuspan, A., Reilly, M. J., and Lee, E. H. 2024. Long-term patterns of post-fire harvest diverge among ownerships in the Pacific West, USA. Environ. Res. Lett. 19(12); doi.org/10.1088/1748-9326/ad8e75.

*Accepted 2 June 2026*
*Associate editor: Daniel D. Gibson*