

Dynamic wildlife habitat mapping and attribution analyses reveal that wildfire, not fuels management, drives declines in an old forest species[☆]

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ABSTRACT

Intensifying disturbances such as high-severity wildfire and prolonged drought-related tree mortality – along with forest management activities intended to curb these disturbances – are reshaping wildlife habitat. As a result, older forest-dependent species are being affected in fire-prone forests. Yet, mapping these dynamic processes at fine spatial resolution across broad spatiotemporal scales remains challenging. Using 37 years (1986–2022) of California spotted owl (*Strix occidentalis occidentalis*) detection data from Southern California – the subspecies' southern range limit – we integrated a recently developed statewide fuels management database and remotely-sensed data with random forest models to (1) map annual habitat changes at 30-m resolution, and (2) attribute those changes to major disturbance types. Our analysis revealed that nesting/roosting habitat declined by 54 % since 1986, with 92 % of the remaining habitat concentrated in the San Bernardino National Forest. Prey acquisition habitat decreased by 40 % within this forest. Wildfire primarily drove nesting/roosting habitat loss, explaining 80 % of attributable declines post-2006, followed by drought/other (14 %) and fuels management (6 %). Potential territories with ≥ 48 ha of nesting/roosting habitat declined by 53 %, those with ≥ 48 ha of prey acquisition habitat declined by 47 %, and territories meeting both thresholds declined by 73 %. These results underscore dramatic habitat loss for spotted owls, highlight wildfire's disproportionate impact, and emphasize the San Bernardino National Forest's importance as a refuge. Limited nesting/roosting habitat declines from fuels management highlight its potential to reduce wildfire impacts on older forests. By integrating species distribution models with multi-disturbance mapping, our study offers a regional-scale framework that can be transferred to other species and ecosystems to monitor habitat dynamics and disturbance impacts.

1. Introduction

Forests globally are undergoing rapid structural and compositional changes due to intensifying disturbances, such as wildfires, drought, and insect infestations (McDowell et al., 2020; Fettig et al., 2022; Seidl and Turner, 2022). In many forest ecosystems, interactions between forest management legacies – such as fire suppression and logging – and warming climates intensify these disturbances (Steel et al., 2015). Collectively, these disturbances can result in declines in habitat quality or the complete loss of habitat for older forest-dependent species (Stephens et al., 2018; Fettig et al., 2019; Williams et al., 2019). As a consequence, forest managers in many regions are implementing fuels

reduction practices like tree thinning and prescribed burns to reduce the severity of disturbances (Knapp et al., 2021; Stephens et al., 2023), potentially benefiting many threatened species. However, these management activities also affect habitat quality (Stephens et al., 2009), which may negatively impact vulnerable older forest-dependent species. Thus, understanding spatial and temporal changes in habitat quality and attributing those changes to environmental and anthropogenic drivers has the potential to greatly facilitate the conservation of older forest-dependent species while maintaining forest ecosystem resilience.

Understanding the conservation implications of landscape change is further strengthened by accounting for species-specific use of multiple, spatially distinct habitats that support different life history needs – with

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the spatial juxtaposition of these cover types known as landscape complementation (Dunning et al., 1992). Many predators, for example, likely benefit from landscape complementation by using prey-rich or prey-accessible areas for hunting (Hopcraft et al., 2005; Balme et al., 2007) while selecting separate, secure sites for breeding, nesting, or denning activities. However, in seasonally dry, fuel-limited forests, historical fire regimes created heterogeneous conditions with frequent low-to-moderate severity and mixed-severity fires and few large, high-severity events. The disruption of these regimes, driven by the historical harvest of large, fire-resistant trees and fire suppression, has increasingly homogenized forests and reduced landscape complementation (Steel et al., 2015; Coop et al., 2020). The effects of disturbances like drought, fuels management, and wildfires on landscape complementation depend on their severity, spatial extent, and duration. For example, drought can drive gradual, localized changes in habitat (Bigler et al., 2007), while megafires – though typically exhibiting a mosaic of burn severity – can cause immediate reductions in live canopy cover at broad scales in severely burned areas. Although snags and coarse woody debris often persist and provide habitat for post-fire associated species, the widespread reduction of live canopy cover may diminish habitat quality for older-forest species until forest succession restores sufficient tree growth and canopy cover (Jones et al., 2016; Jones et al., 2021). Similarly, fuels reduction practices can improve complementation in some areas but may simultaneously reduce key habitat elements like canopy cover or downed woody debris (Jones et al., 2024). These potentially interacting disturbances may exacerbate declines in habitat diversity and landscape complementation, posing threats to older forest-dependent species that require multiple habitat types.

Recent advancements in remote sensing and big data enable more robust assessments of the effects of forest disturbance and management on species' habitats (Turner et al., 2015). Large data repositories, such as NASA's Landsat archive, updated daily on Google Earth Engine (GEE; Gorelick et al., 2017), support broad-scale spatial analysis by offering powerful cloud-based processing with over 30 petabytes of remote sensing, climate, and topographic data (Hansen et al., 2013). These tools have been used to model and map changes in habitat quality at a regional scale for several forest-dependent species (Linnell et al., 2023; Shirk et al., 2023). They can also be applied to remotely sensed data to calculate fire severity and estimate the relative impacts of wildfires on changes in forest species' habitats (Jones et al., 2023; Hart et al., 2025). While wildfire impacts on habitat can be straightforward to assess using remotely sensed imagery and field measurements (Morgan et al., 2014), attributing similar changes to drought or forest management remains challenging. The impacts of drought and bark beetles are often more subtle than those of fire, as these stressors cause gradual canopy loss that varies in duration and intensity across space and time (Meigs et al., 2011). In addition, efforts to assess forest management impacts are further complicated by inconsistencies in available data: many forest management databases lack standardization across jurisdictions and show discrepancies between reported field activities and remotely sensed records, which require careful validation to ensure spatiotemporal accuracy (Knight et al., 2022). Reliable, standardized data on forest condition changes are valuable for evaluating how both natural disturbances and fuels management activities influence habitat dynamics, particularly when assessing the varied and sometimes complex habitat requirements of forest-dependent species.

The spotted owl (*Strix occidentalis*) is an older forest-dependent species profoundly impacted by habitat loss and the erosion of landscape complementation due to severe wildfires and historical logging of large trees (Jones et al., 2016). This central-place forager relies on mature forests with dense canopy cover for nesting and neighboring heterogeneous areas rich in prey for hunting (North et al., 2017; Wilkinson et al., 2023; Zulla et al., 2023). Despite its vulnerability, a regional-scale analysis of spotted owl habitat trends that includes both nesting and prey acquisition sites and that attributes changes to the major forest disturbances remains lacking.

However, understanding the impacts of extensive tree mortality in California's forested bioregions – driven by severe bark beetle (*Dendroctonus*) outbreaks, prolonged drought, and atypical wildfires (Westerling et al., 2006; Fettig et al., 2019; Higuera and Abatzoglou, 2021; Robbins et al., 2022) – would inform conservation efforts for the spotted owl and other vulnerable older-forest species by clarifying how these disturbances affect habitat area in space and time. In this study, we focus on California spotted owls in Southern California, where populations at the southern portion of the subspecies' range are exposed to hot, dry climates. Moreover, unlike the productive, mesic forests of the Pacific Northwest, Southern California's fragmented, patchier forests further isolate owl populations, restricting their movement among mountain ranges (LaHaye et al., 1994; LaHaye et al., 2001). These regional pressures call for management strategies tailored to the specific environmental challenges facing spotted owls in Southern California, a need intensified by the recent proposal to list the Coastal-Southern California distinct population as endangered (UNITED STATES FISH AND WILDLIFE SERVICE, 2023).

Here, we modeled nesting/roosting and prey acquisition habitat for spotted owls over 37 years (1986–2022) across Southern California, USA, leveraging recently developed spatial datasets on forest disturbance and management history (Kramer et al., in press). Our objectives were to (i) map spatiotemporal changes in habitat distribution at 30-m resolution, (ii) examine changes in the spatial co-occurrence (landscape complementation) of habitat types, and (iii) quantify the relative impact of wildfire, drought/other, and fuels management on nest/roost habitat change. Understanding how these disturbances and fuels reduction efforts collectively affect habitat is valuable for developing region-specific conservation strategies in ecosystems increasingly prone to transformative disturbances. To our knowledge, this is the first study to assess long-term changes across multiple habitat types while attributing disturbance-driven change using rigorously validated, spatially explicit disturbance data from California forests.

2. Methods

2.1. Study area

Our study area encompassed the Los Padres, Angeles, San Bernardino, and Cleveland National Forests in Southern California, USA (Fig. 1). The area included topographically complex mountain ranges that vary in elevation, vegetation type, and climatic conditions. The climate is Mediterranean, with most precipitation occurring from December–February (winter) as rain or snow. The vegetation in the region varies with altitude and topography, ranging from woody shrubland, chaparral, deserts, and savannahs at lower elevations, to conifer woodlands at mid-to-high elevations. The forests on high slopes are typically dominated by pine and fir species, such as lodgepole (*Pinus contorta*), ponderosa (*P. ponderosa*), Jeffrey (*P. jeffreyi*), and sugar pines (*P. lambertiana*), bigcone Douglas-fir (*Pseudotsuga macrocarpa*), as well as canyon live oak (*Quercus chrysolepis*). Within this region, the San Bernardino mountains harbor the largest spotted owl population near the species' southern distributional range (Fig. 1b; Gutiérrez et al., 2017). During the 20th century, these forests were fire-suppressed, and large, old trees were selectively harvested, resulting in increased stand densities, decreased old-growth forests, and more fire-sensitive, shade-tolerant trees (Minnich et al., 1995).

2.2. Data sources

2.2.1. Nest/roost data compilation

We compiled a database of known spotted owl nest/roost locations from 1986 to 2022, recorded on national forests in Southern California. This database included nest/roost sites from US Forest Service project-level surveys, previous demographic studies (LaHaye et al., 2004; Tempel et al., 2022), and opportunistic nest/roost observations reported

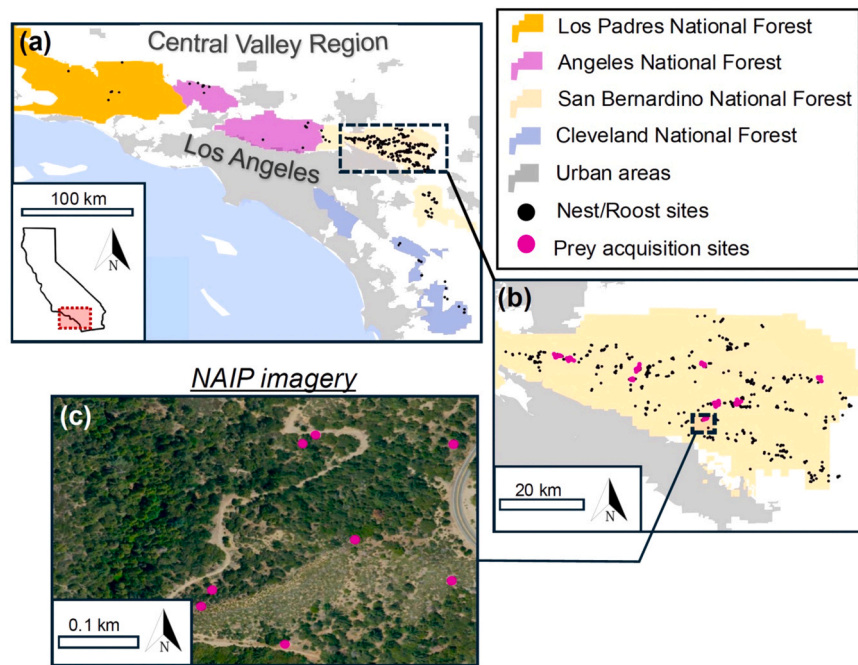


Fig. 1. Study area with nest/roost and prey acquisition locations. (a) Spotted owl nest/roost locations ($n = 474$) documented from 1986 to 2022 in the Los Padres, Angeles, San Bernardino, and Cleveland National Forests of Southern California, USA. The San Bernardino Mountains harbor (b) the largest number of previously documented nest/roost sites and (c) include all prey acquisition locations ($n = 131$ centroids) from 2021.

by cooperating observers. We began with a database of nest/roost locations ($n = 876$) but, following established methods (Jones et al., 2023), applied decision rules for quality control to yield a standardized database of high-quality locations. Here, we applied seven decision rules for quality control to maximize data quality, minimize potential spatial autocorrelation, and reduce the likelihood that observations might represent behaviors other than nesting or roosting.

First, we eliminated roost location(s) when surveyors detected a nest location during the same survey. We considered nest locations to contain more biologically important information than roost locations because they directly indicate reproductive habitat, represent sites of strong fidelity across years, and provide less ambiguous information than roost locations, which may shift frequently or represent temporary behaviors. Second, we randomly selected one roost location when two were recorded for a pair at the same location (e.g., pair roost). Third, we selected only observations during the breeding season from March 1st to July 31st. Observations after this period are less likely to represent breeding habitats, as owl ranges are wider in the late summer (Carey et al., 1990, Ganey et al., 1999). Fourth, we selected only one nest site in the same territory per year. Fifth, we eliminated any detections recorded as roosts that occurred during twilight or nocturnal hours because owls may have already moved from their day roost for nocturnal hunting activities. Sixth, we eliminated roost locations that were inferred from audible detections but were not visually confirmed. Seventh, to avoid pseudo-replication while retaining a sufficient sample size, we excluded a roost site if it was within 150 m of a nest site, regardless of the year of detection, reflecting the tendency of spotted owls to reuse nearby structures. We then performed visual inspections of all locations to ensure that locations were not mapped incorrectly (e.g., urban areas, lakes) due to data recording errors. Our sample size was reduced ($n = 474$) following these decision rules (Figure A.1).

2.2.2. Prey acquisition data from GPS tags

Next, we created a prey acquisition database to determine potential differences in prey acquisition habitat compared to nest/roost habitat. In 2021, Wilkinson et al. (2023) used owl vocalizations to locate territorial pairs based on historical locations in the San Bernardino National Forest.

Upon discovering the nests and confirming nesting status, Wilkinson et al. (2023) captured the males ($n = 10$) to attach tail-mounted GPS tags (Alle-300, Ecotone, Poland). This tracking method provides owl locations during their nocturnal movements and hunting bouts. The GPS-tags recorded owl locations every two minutes for ten hours each night until the batteries expired (4–12 nights). The authors defined prey acquisition clusters (i.e., putative prey kill sites) containing at least 10 GPS points within a 20-minute window, with points no more than 250 m apart from the most distant points and followed by a direct flight back to the nest. Moreover, Wilkinson et al. (2023) placed infrared cameras (AXIS Q1786 – LE, 4 megapixel) near nest trees to confirm prey delivery events. In this study, we identified the centroid ($n = 131$) of each prey acquisition cluster as the prey acquisition location used to model prey acquisition use locations.

2.3. Goal 1: mapping spatiotemporal changes in habitat distribution

2.3.1. Selecting habitat covariates influencing habitat quality

To understand how spotted owl habitat quality varies with vegetation, climate, and topography, we used 140 covariates to produce a spotted owl species distribution model (e.g., Jones et al., 2023, Shirk et al., 2023), which included 118 covariates derived from Landsat multispectral satellite imagery and 12 climatic and 10 topographic indices (Table A.1). While the Landsat and climate variables changed annually and required temporal matching, topographic variables were considered static over the study period. We based our covariate selection on previous research on spotted owl habitat selection (e.g., Bond et al., 2009, Jones et al., 2020, Kramer et al., 2021, Wilkinson et al., 2023) and the expertise of our research team in owl ecology and remote sensing, ensuring that the predictors were both biologically meaningful and consistent with established methods. Our primary objective was to create a model with high local spatial accuracy (i.e., an accurate map) (Tredennick et al., 2021). Moreover, we were unconcerned with potential multicollinearity, which affects inference about variable importance but not predictive performance. Due to correlations among individual predictors, we avoided direct comparisons of their relative importance and focused our interpretation on pooled variable types. We

included all remotely-sensed variables deemed potentially useful for predicting owl habitat. We were not concerned with model overfitting given the robustness of random forest models to overfitting and the evidence from out-of-bag error rates indicating good model fit (see Results Section below).

We generated the Landsat-derived covariates using the Continuous Change Detection and Classification (CCDC) algorithm (Zhu and Woodcock, 2014), applied through GEE to a 37-year time series of surface reflectance data from Landsat satellites (1986–2022). The CCDC algorithm fits a harmonic regression model to each pixel's time series and detects breakpoints, which indicate disturbances. From the harmonic regression outputs, we created annual synthetic images for two key dates – March 1 and June 1 – representing early and peak vegetation phases. First, we included six spectral bands (blue, green, red, near-infrared, shortwave infrared 1, and shortwave infrared 2) extracted at both dates, resulting in 12 raw band values per year. Second, we calculated four spectral indices at both dates representing 1) vegetation quality (normalized difference vegetation index, NDVI; Tucker, 1979), 2) moisture content of leafy vegetation (normalized difference wetness index, NDWI; Gao, 1996), and 3–4) vegetation disturbance from fire, timber harvest, tree pathogens, and other agents of forest loss (normalized burn ratio, NBR and NBR2; Key and Benson, 1999). This yielded 8 index values per year (4 indices $\times$ 2 dates). Last, we also included the CCDC model coefficients themselves as predictors, namely the slope coefficient and the 1st/2nd/3rd-degree cosine and sine coefficients for each of the six bands and the NDVI index at these two dates, yielding 98 harmonic metrics. Including the CCDC model coefficients as predictors in the random forest model aids in minimizing the false signal of habitat recruitment following fire or other disturbance events that is produced by rapid vegetation green-up (Witt et al., 2022). Together, the raw band values ($n = 12$), indices ($n = 8$), and harmonic terms ($n = 98$) totaled 118 reflectance-based covariates (Table A.1).

We produced the climate covariates using ClimateNA version 7.42 (Wang et al., 2016), a software package that downscales PRISM climate data (Daly et al., 2008) – spatially gridded historical climate observations interpolated with topographic adjustments – to finer resolutions using a digital elevation model (DEM). Here we used a 30-m resolution DEM from NASA's Shuttle Radar Topography Mission (SRTM; Farr et al., 2007). This created a gridded dataset at 30-m resolution, which includes 30-year average monthly values for minimum temperature, mean temperature, maximum temperature, precipitation, and growing degree days before each year. From these monthly climate variables, we calculated twelve derived climate covariates including 1) summer mean temperature (May–August average of the daily mean temperature), 2) summer mean maximum temperature (May–August average of the daily maximum temperature), 3) mean temperature during the warmest month, 4) late winter mean minimum temperature (January–February average of the daily minimum temperature), 5) mean minimum temperature during nesting season (May–June average of the daily minimum temperature), 6) annual precipitation, 7) late winter precipitation (January–February total precipitation), 8) summer precipitation (May–August total precipitation), 9) nesting season precipitation (May–June total precipitation), 10) precipitation as snow (November–January total precipitation), 11) annual growing degree days (degree days above 5 °C), and 12) Hargreaves climatic moisture deficit (mm).

We derived 10 topographic covariates from the same 30-m DEM as above, primarily using algorithms in GEE. These covariates included 1) slope, 2) elevation, 3) distance to coast (kilometers from the Pacific ocean), 4) heat load index (a measure of incident radiation), 5–9) five topographic position indices (TPI), which quantified the elevation of a focal pixel relative to its neighbors within a specified radius (90 m, 180 m, 360 m, 720 m, and 1440 m), and 10) a topographic ruggedness index (TRI), which measured topographic heterogeneity from the same DEM using algorithms implemented in SAGA GIS software (Conrad et al., 2015).

2.3.2. Developing a species distribution model

We applied a use-availability study design (Johnson et al., 2006) to fit models of spotted owl habitat distribution within the study area, where 'used' locations are the known locations occupied by owls and the 'available' locations are locations an owl could have potentially used or not used. Since nest/roost sites were widely dispersed throughout the study area (Fig. 1a), we randomly generated available locations across the entire study area, constrained to forested areas using a forest mask. We created this forest mask by classifying a pixel as 'forest' if it had been classified as deciduous, coniferous, or mixed forest by the National Land Cover Database classification in any period or if the Hansen Global Change Model (Hansen et al., 2013) predicted forest canopy cover $\geq 20\%$. We used this conservative forest mask to avoid projecting habitat models into areas that were unsuitable for spotted owl nesting/roosting sites (e.g., open fields or bare ground) and to ensure the inclusion of forests that experienced type conversion to non-forest during our study period from factors including wildfire, drought, timber harvest, bark beetle infestation, etc. We visually confirmed with satellite imagery that the $\geq 20\%$ canopy cover threshold effectively excluded non-forested areas while still capturing edge habitats that owls may use (Hart et al., 2025), offering a more inclusive boundary than the $\geq 40\%$ cover typically associated with nesting habitat (Tempel et al., 2016, North et al., 2017). Prey acquisition sites, on the other hand, were more localized (Fig. 1b), so we distributed available locations for these models within a maximum convex polygon (MCP) surrounding each individual owl-year location. For each survey year with spotted owl detections, we generated ten available locations for every spotted owl nest/roost ($n = 474$) and prey acquisition site ($n = 131$). We then extracted covariate values for both used locations and the corresponding available locations for each year.

To estimate the likelihood of spotted owl nest/roost and prey acquisition site occurrence, we employed a random forest classifier using GEE (Breiman, 2001). Random forest, a robust machine learning algorithm, is particularly effective in modeling ecological relationships due to its capacity to handle correlated, nonlinear, and interacting factors (Evans et al., 2011). This algorithm constructs multiple decision trees by bootstrapping samples and randomly selecting predictor subsets at each node. The combination of these trees improves the model's ability to generalize predictions (Strobl et al., 2009). The optimal random forest hyperparameters included 50 decision trees, 6 variables per split, and a bag fraction of 0.5. We applied 10-fold cross-validation, where ten models (one for each fold) were trained using 90 % of the data, while 10 % was withheld for validation. From these ten model runs, we calculated the mean and standard deviation of the relative importance of each variable. To assess model goodness of fit, we assessed the mean out-of-bag error, area under the receiver operator curve (AUC; Hanley and McNeil, 1982), sensitivity, specificity, and the true skills statistic. We then projected these ten models onto each year's suite of environmental covariates and calculated the mean and standard deviation across the ten projections to create a continuous layer at 30-m of average habitat probability ranging from zero to one, with higher values indicating higher quality, across the study region for each year (1986–2022). Last, we overlaid spotted owl habitat quality maps with detection locations and NAIP imagery (1-meter aerial photographs captured during the growing season) to visually assess whether areas predicted as high-quality habitat aligned with expected forest structure and composition. This modeling workflow was repeated for both the nest/roost and prey acquisition sets of used and available locations.

2.3.3. Mapping habitat quality and spatiotemporal trends

To address Goal 1, we used our projected annual layers of nest/roost and prey acquisition habitats to quantify trends in habitat area. First, to exclude widespread habitats of the lowest quality that spotted owls would likely consider unsuitable, we converted values below the "classification threshold" to zero (Allouche et al., 2006). The "classification threshold" corresponded to the point where the false positive rate

equaled the false negative rate and where specificity equaled sensitivity. At this threshold, prey acquisition habitat models had a cutoff of 0.31 and roost/nest habitat models had a cutoff of 0.29. Pixels with values above this classification threshold were more likely to represent suitable owl habitat, while those below were considered non-habitat. Next, to quantify temporal trends in habitat area across each national forest, we summed the cell probability values annually and multiplied these sums by the area of each cell (900 m²). This calculation provided the total area of suitable habitat, weighted by quality. We assessed habitat trends and their slope/direction by fitting a linear model with year as the predictor and area of suitable habitat as the response across the entire study period and for each decadal period.

We assessed habitat trends for both nest/roost and prey acquisition habitats. For the prey acquisition habitat, we excluded areas located within the interiors of severe wildfires because spotted owls are unlikely to access these areas for hunting until sufficient forest regeneration occurs (Jones et al., 2020), which may take decades in Southern California. We obtained fire severity data using the methods of Cova et al. (2023) and Parks et al. (2019) to estimate the composite burn index (CBI) for all 30-m pixels that burned in fires larger than four ha from 1984 to 2022. The CBI appears to provide a more direct measure of ecological effects and aligns better with actual ground conditions compared to other commonly used spectral indices, such as the Relativized Burn Ratio (Picotte et al., 2021). We classified pixels with CBI > 2.25 – indicative of vegetation with high to complete mortality (Miller and Thode, 2007) – as severely burned and identified high-severity patches as clusters of orthogonally contiguous pixels. We defined interiors as areas more than 100 m away from the nearest unburned or lower severity (low or moderate) burned forest. Additionally, we also considered small patches of unburned or lower severity burned areas ≤ 0.36 ha (four connected pixels) part of the surrounding interior, consistent with the methods of Kramer et al. (2021), because spotted owls are unlikely to travel deep into severely burned forests to access small, less burned patches (Jones et al., 2020). For example, if a fire occurred in 2003, all severely burned prey acquisition habitat > 100 m from the patch edge was excluded from analysis in all subsequent years.

We analyzed trends in prey acquisition habitat using two approaches: one where we assessed trends across the entire study area without a buffer, and another where we applied a buffer around prey acquisition areas relative to nest/roost habitat for the same year. The buffer was necessary to account for prey acquisition habitat inaccessible to owls. To establish the buffer, we first determined the minimum patch size for the nest/roost habitat at known nest/roost sites. We did this by converting the continuous nest/roost habitat quality maps into binary rasters of habitat/non-habitat (using the classification threshold of 0.29 from the nest/roost models, where values above this cutoff were considered suitable). We then measured the size of the contiguous suitable nest/roost habitat patch overlapping each known nest/roost site in each year from 1986 to 2022. We delineated patches independently for each year and matched them only to nest/roost sites from the corresponding year, ensuring that spatial boundaries remained discrete and did not merge across years. Separate sites could share the same patch, in which case they were assigned the same patch area. We used the 95th percentile of these values, which yielded a minimum suitable nest/roost habitat patch size of 1.19 ha. Next, we modified our habitat maps to exclude any patches smaller than 1.19 ha and applied a 1000-meter buffer around the remaining patches (the approximate radius of a spotted owl's home range). This buffer represented potentially accessible prey acquisition habitat for that year. We then clipped the prey acquisition habitat map to these buffers and set all values outside the buffer to zero, enabling us to calculate trends in accessible prey acquisition habitat over time.

2.4. Goal 2: quantifying changes in landscape complementation

To address Goal 2, we evaluated how frequently nest/roost and prey

acquisition habitat co-occurred within the same spatial units, serving as a proxy for landscape complementation. Specifically, our measure of landscape complementation was based on the within-territory co-occurrence of both habitat types. We overlaid a continuous grid of 375-hectare hexagons – approximating typical spotted owl territories – across the study area for each year from 1986 to 2022 (Zimmerman et al., 2001, Tempel et al., 2014, 2022). Within each potential territory, we applied binary thresholds to assess the presence of suitable habitat. For nest/roost habitat, we required ≥ 48 ha (12.8 % of the home range area) of habitat above the “classification threshold” of 0.29. We based this criterion on Jones et al. (2018), who found that owl territories in national parks in the southern Sierra Nevada, about 254 ha in size, had 48 ha (or 19 %) of forest with large trees and dense canopy cover, associated with high-quality habitat characterized by lower predicted extinction rates and stable occupancy. For the prey acquisition habitat, we applied the same 48-hectare threshold, using the “classification threshold” of 0.31. Potential territories meeting both thresholds were considered to support landscape complementation. We used the same 48-hectare threshold to enable consistent comparison between habitat types, while also ensuring biological relevance by reflecting the minimum amount of high-quality habitat typically present in occupied territories (Jones et al., 2018). To evaluate temporal and spatial changes in habitat, we calculated the number of potential territories within each National Forest, for each year, that met the thresholds for nest/roost, prey acquisition, and landscape complementation.

2.5. Goal 3: attributing nest/roost habitat change to major disturbances

To attribute changes in nest/roost habitat to the three disturbance agents, we first separated our yearly weighted habitat area – defined as the total area of pixels exceeding the classification threshold, weighted by their habitat quality values – into negative and positive change categories. We calculated the annual habitat change by subtracting the weighted habitat area in year t from year $t - 1$. For example, the habitat changes for the year 2000 were determined by subtracting the habitat area in 2000 from that in 1999 (i.e., $\text{habitat change}_{2000} = \text{habitat}_{2000} - \text{habitat}_{1999}$). For each year, we overlaid these maps with the corresponding area affected by each disturbance. To focus on ecologically meaningful changes and reduce the influence of noise from satellite imagery artifacts or minor fluctuations, we tested multiple thresholds of annual pixel-level habitat change (i.e., 1 %, 2 %, 5 %, 10 %). Changes below 5 % largely reflected background variability, while higher thresholds reduced the proportion of habitat change attributable to disturbance. We therefore attributed disturbance only where annual pixel-level habitat change exceeded 5 %. We then used an annual disturbance raster developed by Kramer et al., (in press) to attribute these pixel-level changes to the different disturbance types.

Habitat change attributed to wildfire included areas within fire perimeters from the current year, as well as up to three years prior. For example, the year 2000 assessment included all wildfires from 1997 to 2000, and any negative habitat change overlapping these fires was attributed to wildfire. Research suggests that secondary fire effects, such as increased tree mortality due to insect attacks or drought, generally occur within 2–8 years post-fire (Hood et al., 2010, van Mantgem et al., 2015, Miller et al., 2016). We conservatively used a three-year post-fire window to capture most fire-related mortality.

To account for fuels management, Kramer et al., (in press) modified records originating in the U.S. Forest Service's Forest Activity Tracking System (FACTS). These methods filter the spatiotemporal records by fuels management activity types and apply a temporal buffer (spanning four years) that better accounts for the time when active management was taking place and when those changes are reflected in the satellite data. Note that when fuels management overlapped with wildfire (i.e., post-fire treatments), we assumed that the effects of the wildfire would supersede those of the fuels management and attributed all change to wildfire.

Last, to assess the lasting impacts of severe drought-related tree mortality, we examined the annual canopy cover loss in any remaining undisturbed pixels. We estimated canopy cover loss with annual 30 m rasters of the Mortality Magnitude Index (MMI) from the eDaRT system for Landsat processing (Koltunov et al., 2020, Slaton et al., 2024). If the canopy cover loss in a given pixel was greater than 12 % (with no other disturbance in that year), we classified that pixel as having severe drought-related tree mortality or other disturbance agent (though we assumed and visually confirmed in NAIP imagery that most of these pixels were due to drought). To account for other possible causes of canopy cover loss, including unrecorded small-scale fuelwood cutting, salvage logging, localized insect outbreaks, windthrow, and the inherent limitations of satellite detection, we classified these collectively in our results as “drought/other”. The 12 % canopy cover loss threshold was consistent with Ng et al. (in review), who reported that a 12 % canopy loss threshold in the Sierra Nevada closely corresponded with observed drought gradients. However, in Southern California, we observed that some drought-impacted areas identifiable in NAIP imagery were not captured using the 12 % threshold. To address this, we applied a lower 8 % threshold, which we determined through visual inspection of NAIP imagery to more effectively capture areas showing signs of localized drought-related canopy loss that may have otherwise been missed. Importantly, we applied a five-year lag to any pixel classified as drought such that a pixel classified as drought in 2005 would also be considered drought from 2006 to 2010 unless that pixel was disturbed by one of the other disturbance agents (we assumed that both fuels management and wildfire would have a larger impact on the landscape than drought).

This five-year window was applied to reflect the possibility that drought impacts on habitat quality can persist beyond the initial remote sensing detection and due to secondary effects (Bigler et al., 2006, Bigler et al., 2007). We conducted our attribution analysis from 2007 to 2022, the earliest period for which complete data on wildfire, drought-related tree mortality, and fuels management disturbance types were available (e.g. we only had drought data from 2002 to 2022, and to consistently apply the five-year lag period, we only had full data for 2007–2022).

3. Results

3.1. Goal 1: spatiotemporal changes in habitat distribution

Models using the random forest algorithm with temporally matched covariates produced reasonably accurate predictions of spotted owl habitat, as the mean out-of-bag error during the random forest model fitting for nest/roost and prey acquisition was 5.8 % and 8.6 %, respectively. Model fit was also very high, with AUC values above 0.98 in both cases. Model performance was high for both models at the classification threshold. For the roost/nest models (classification threshold of 0.29), the false positive/negative rates were 0.02, specificity/sensitivity were 0.98, and the true skills statistic was 0.96. For the prey acquisition models (classification threshold of 0.31), the false positive/negative rates were 0.06, specificity/sensitivity were 0.94, and the true skills statistic was 0.89. Topographic and climate variables explained more of the total variable importance than a null expectation for both habitat types (Figures A.2 and A.3). In contrast, reflectance-

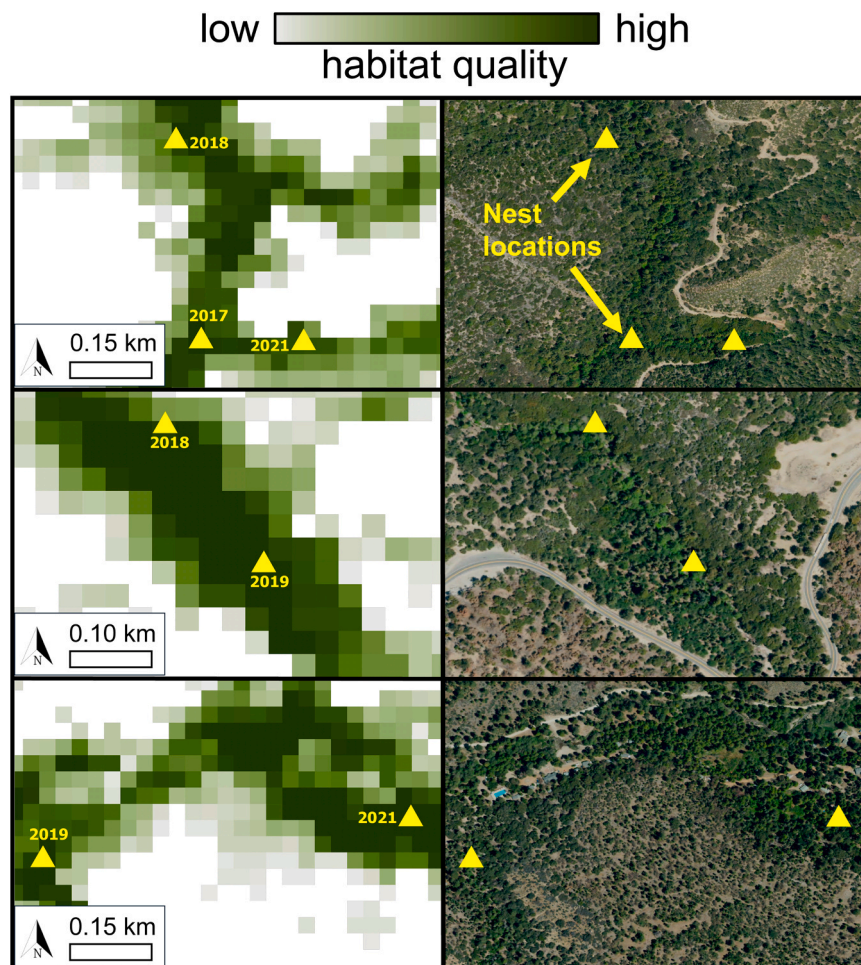


Fig. 2. Probability maps of spotted owl nest/roost habitat in the San Bernardino Mountains, overlaid with random nest tree locations and high-resolution (1-meter) NAIP imagery captured during the 2022 growing season.

based variables explained an average of 72 % and 76 % of total variable importance for nest/roost and prey acquisition habitats, respectively, which was lower than expected given that they constituted 84 % of the predictor variables. Nest/roost habitat probability was relatively higher in low-lying drainages with lower topographic position (Figure A.4). Spotted owl nest/roost habitat quality maps, overlaid with corresponding NAIP imagery and detection locations, showed that our models consistently identified habitat characterized by denser canopy than adjacent open areas (Fig. 2).

According to our most recent 2022 habitat maps, the San Bernardino National Forest harbors 92.1 % of the remaining nest/roost habitat in Southern California (Fig. 3), while the Los Padres, Angeles, and Cleveland National Forests harbor 2 %, 3 %, and 3 %, respectively. Nest/roost habitat for spotted owls declined across our study area (Fig. 3), with the most substantial declines observed from 2001 to 2010 in the San Bernardino National Forest (Table 1). The nest/roost model estimated that in 1986, there were 31,997 ha of spotted owl nest/roost habitat in the San Bernardino National Forest, which declined by 52 % over the study period (1.93 % annual decline) to 15,393 ha by the year 2022 (Fig. 3). The prey acquisition model estimated that in 1986, there were 35,989 ha of spotted owl prey acquisition habitat in the San Bernardino National Forest, which declined by 40 % over the study period (1.33 % annual decline) to 21,669 ha by 2022 (Fig. 3). In the San Bernardino National Forest, both nest/roost and prey acquisition habitat have declined by a rate of 615 ha (95 % CI: -692, -538) and 564 ha (95 % CI: -626, -502) per year, respectively (Table 1).

3.2. Goal 2: changes in landscape complementation

We detected no potential nest/roost territories – defined as 375-hectare hexagons containing ≥ 48 ha of suitable nest/roost habitat – within our continuous hexagonal grids in the Los Padres National Forest during the entire study period, nor in the Angeles or Cleveland National Forests after 1997 and 2002, respectively. In the San Bernardino National Forest, the number of potential territories with suitable nest/roost habitat declined by 47 % (Fig. 4), dropping from 255 nest/roost territories in 1986–119 in 2022. Similarly, potential territories with suitable prey acquisition in the San Bernardino National Forest declined by 53 %, dropping from 323 prey acquisition territories to 171 over the same period, with similar declines observed across the entire national forest and the nesting-available landscape (Figure A.5). Notably, the number of potential territories with both ≥ 48 ha of nest/roost and prey acquisition habitat (i.e., those supporting landscape complementation)

declined by 73 %, dropping from 179 in 1986 to just 48 in 2022. This greater decline indicated that nest/roost and prey acquisition losses often occurred in different territories, resulting in fewer areas where both habitat types coexisted. Of the 48 remaining potential territories with landscape complementation in the San Bernardino National Forest, seven were located in the San Jacinto Mountains, and the remaining 41 were located in the San Geronio Wilderness and Big Bear Lake area of the San Bernardino Mountains (Figure A.6).

3.3. Goal 3: attribution of nest/roost habitat loss

Wildfire contributed to 80 % of the explained declines in nest/roost habitat from 2007 to 2022 in the San Bernardino National Forest, whereas drought/other and fuels management explained only 14 % and 6 %, respectively (Fig. 5). After 2007, when data were available for all three disturbance types, wildfire accounted for the loss of 4798 ha nest/roost habitat based on 5990 ha of attributable nest/roost annual disturbance exceeding 5 % change – a fourteen-fold greater impact than fuels management (339 ha) and more than five times greater than drought/other (853 ha). Before 2007, when drought-related mortality data were unavailable, a total of 13,181 ha of nest/roost habitat was lost (including unattributed loss), with wildfire accounting for 2951 ha, compared to 459 ha from fuels management – over a six-fold difference (Figure A.7). To illustrate the scale of wildfire threats that occurred after our study period, we overlaid 2024 fire perimeters onto 2022 habitat maps and found that the Bridge Fire, which burned 22,675 ha in the San Gabriel Mountains, overlaid approximately half of the remaining nest/roost habitat in the Angeles National Forest – an area already characterized with low owl occurrence (Barry et al., 2025). Also, the Line Fire, which burned 17,797 ha in the San Bernardino Mountains, overlaid about 10 % of the San Bernardino National Forest's remaining nest/roost habitat, where the majority of occupied owl territories persist.

4. Discussion

Forests across western North America are transforming rapidly as warming and drying conditions intensify disturbance regimes, including prolonged drought, bark beetle outbreaks, and increasingly large, high-severity wildfires (Westerling, 2016; Fettig et al., 2022). In Southern California – the southern portion of the California spotted owl's range – these changes have accelerated tree mortality and diminished forest resilience in many areas (Jones et al., 2004; Keeley et al., 2009). Our 37-year analysis revealed significant declines in spotted owl nest/roost and prey acquisition habitats, with the most severe losses driven by wildfire. Wildfire alone accounted for approximately 80 % of attributable disturbance-related nest/roost habitat loss, highlighting its dominant role in shaping habitat outcomes for this subspecies. By contrast, fuels management, which contributed just 6 %, had a minimal impact on nest/roost habitat loss during the same period. Our study presents a significant advance in regional-scale habitat monitoring by linking species distribution models with multi-disturbance mapping to identify drivers of change, providing a transferable framework for doing similar analyses in other systems.

4.1. Changes in landscape complementation

Spotted owls rely on the juxtaposition of nesting and foraging habitats to meet life history needs (Zulla et al., 2022; Kuntze et al., 2023; Wilkinson et al., 2023; Zulla et al., 2023). Our results reveal a substantial decline in this landscape complementation, presumably driven mostly by large, high-severity wildfires that reduce nesting structures near key foraging areas like chaparral edges. Moreover, large, severe burns convert structurally diverse forests into expanses of shrubland or nonnative grasslands (Keeley, 2006), reducing both edge density and structural heterogeneity – key elements for prey accessibility. In addition, Wilkinson et al. (2023) found that spotted owls in Southern

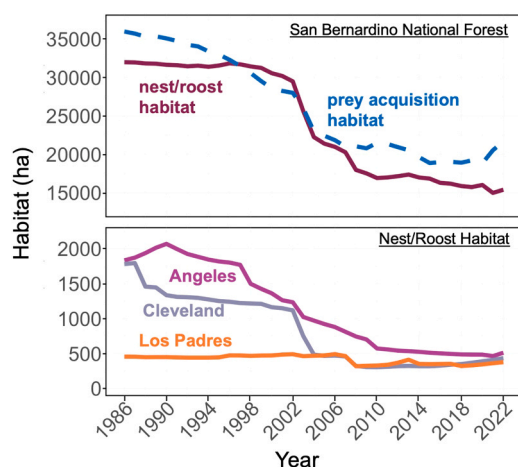


Fig. 3. Changes in the amount of spotted owl prey acquisition and nest/roost habitat in Southern California, USA. Nest/roost habitat is shown for all four National Forests, while prey acquisition habitat is shown only for the San Bernardino National Forest, where the majority of remaining nesting/roosting habitat occurs.

Table 1
Linear model output examining temporal trends in prey acquisition and nest/roost habitat in Southern California from 1986 to 2022. Prey acquisition trends were derived from maps in the San Bernardino National Forest that excluded (i) areas within the interior of severe wildfires (>100 m from unburned or low-severity forest) and (ii) locations more than 1000 m from the nearest nest/roost habitat (patch size > 1.19 ha).

Habitat type	Study Area	Time period	Annual change in habitat (ha)	Standard Error	t-value	R ²	p
Nest/Roost	Southern California	1986 – 2022	-715	42	-17.02	0.89	< 0.01
		1991 – 2000	-141	42	-3.36	0.59	< 0.01
		2001 – 2010	-1689	175	-9.66	0.92	< 0.01
		2011 – 2020	-192	31	-6.15	0.82	< 0.01
		2021 – 2022	-192	31	-6.15	0.82	< 0.01
	San Bernardino National Forest	1986 – 2022	-615	38	-16.28	0.88	< 0.01
		1991 – 2000	-61	35	-1.76	0.28	< 0.01
		2001 – 2010	-1502	156	-9.61	0.92	< 0.01
		2011 – 2020	-177	28	-6.22	0.83	< 0.01
		2021 – 2022	-177	28	-6.22	0.83	< 0.01
Prey acquisition	San Bernardino National Forest	1986 – 2022	-564	30	-18.60	0.91	< 0.01
		1991 – 2000	-680	44	-15.52	0.97	< 0.01
		2001 – 2010	-864	151	-5.72	0.80	< 0.01
		2011 – 2020	-268	57	-4.71	0.73	< 0.01

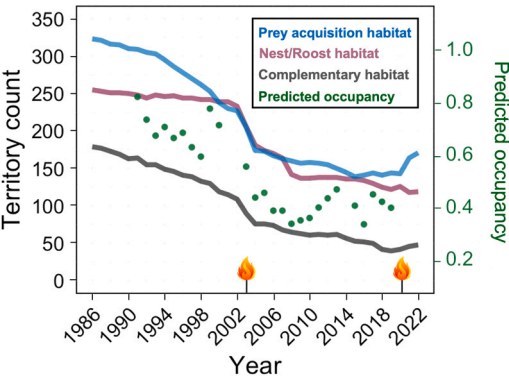


Fig. 4. Changes in the number of potential territories with ≥ 48 ha of nest/roost habitat, ≥ 48 ha of prey acquisition habitat, and ≥ 48 ha of both habitat types in the San Bernardino National Forest, CA. The 2003 and 2020 fire seasons, which burned 11.7 % and 5.8 % of the San Bernardino National Forest, respectively, are indicated by the vertical bars and flame symbols. The predicted spotted owl territory occupancy from Tempel et al. (2022) is represented by green dots and corresponds to the secondary y-axis.

California had higher prey capture success in areas with taller, multi-layered forests, higher heterogeneity in vegetation types, and near forest-chapparral edges. Similarly, Zulla et al. (2023) reported that owls in the Sierra Nevada delivered greater prey biomass to territories with more forest edge, likely due to greater access to large-bodied woodrats (*Neotoma* spp.). Additionally, Zulla et al., 2023 found higher owl reproductive output in heterogeneous territories with a mix of mature and open forests compared to homogenized, fire-suppressed territories dominated by medium-aged trees. Together, these findings underscore the importance of maintaining edge density and structural heterogeneity to support high-quality, juxtaposed habitat conditions. Recent modeling suggests that targeted restoration and fuels reduction can enhance landscape complementation, helping to restore structural conditions that support prey accessibility and owl occupancy (Jones et al., 2024).

The San Bernardino National Forest now holds the only remaining potential territories meeting our ecologically-informed thresholds for both habitat types, yet the number of such territories has declined by 73 % since 1986. In the Angeles, Cleveland, and Los Padres National Forests, no such territories have existed since 2002, signaling a near-total collapse of high-quality habitat in much of the southern range. Spatially extensive surveys in 2022 confirmed very low occupancy in the Angeles and Los Padres National Forests (Barry et al., 2025), with only one occupied territory remaining in the Cleveland National Forest (Tempel et al., 2022). Passive acoustic monitoring in 2024 further corroborated these patterns, detecting low occupancy rates in both the Angeles and Los Padres National Forests (Gustafson et al., 2025).

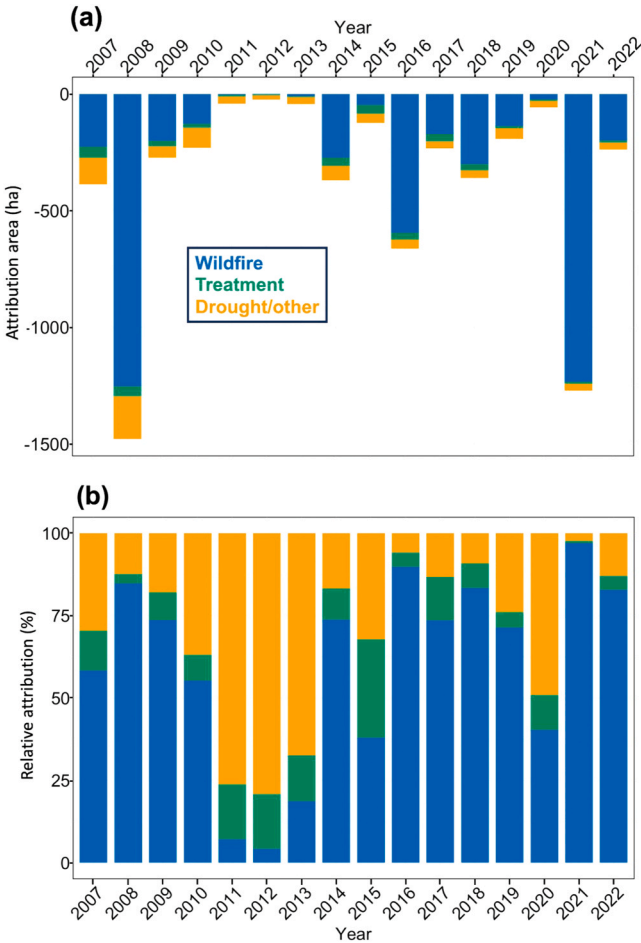


Fig. 5. Disturbance-related loss of nest/roost habitat attributed to wildfire, drought/other, and fuels management in the San Bernardino National Forest from 2007 to 2022, based on areas experiencing more than 5 % habitat loss. Disturbance attribution accounted for 63 % of total observed nesting/roosting habitat loss over this period; the remaining 37 % could not be attributed to a specific disturbance and is not shown in the figure. Unattributed loss may reflect unrecorded small-scale fuelwood cutting or salvage logging, localized insect outbreaks or pathogens, natural processes such as windthrow, or the limits of satellite imagery, including cloud cover or other weather-related interference, that can obscure subtle or fine-scale habitat changes.

Moreover, surveys from 2024 indicated that only 60 owl pairs remain across 129 territories in the San Bernardino Mountains (Tanner Environmental Services (TES), 2024), suggesting that more than half of the

historical territories are currently unoccupied. Additional losses of nest/roost and prey acquisition habitats may further isolate these remaining territories, beyond the effects of urbanization in lowland areas separating populations. While our 375-ha habitat assessment window may slightly underestimate viable territories compared to the potentially smaller home ranges of spotted owls in Southern California (~142 ha on average; McGinn et al., 2024, Gustafson et al., 2025), we nonetheless effectively captured broader-scale trends in habitat loss.

4.2. Drivers of habitat change

4.2.1. Wildfire as the primary driver of habitat loss

Our attribution analysis found wildfire to be the predominant driver of nest/roost habitat loss, consistent with past work showing that large high-severity burns reduce owl occupancy and increase territory abandonment (Lee et al., 2013, Jones et al., 2016, Jones et al., 2020, Jones et al., 2021, McGinn et al., 2025). Ng et al. (in review) similarly found that high-severity fire was the leading cause of spotted owl site loss across the Sierra Nevada, accounting for the loss of approximately 500 sites, sevenfold more than those lost to heavy fuels management. These declines in occupancy are presumably driven by the loss of tall nesting trees (North et al., 2017), dense canopy cover (Tempel et al., 2014), and spatial connectivity to prey acquisition habitat (Wilkinson et al., 2023). As owls typically avoid large, severely burned interiors (Jones et al., 2016, Jones et al., 2020, Kramer et al., 2021, McGinn et al., 2025), their ability to access prey in these areas declines. Though low- to moderate-severity fires with smaller patches of severe fire may preserve key structural features beneficial to owl persistence, contemporary fire regimes increasingly favor large, high-severity events that promote open conditions (Coop et al., 2020), and post-fire salvage logging may further hinder habitat recovery by removing residual structures essential for spotted owls (Lee and Bond, 2015, Jones and Peery, 2019), but see McGinn et al., (in press), who found no effect of post-fire salvage logging on California spotted owl occupancy.

Our estimate that 80 % of attributable nest/roost habitat loss was wildfire-related contrasts with Tempel et al. (2022), who attributed only 10 % of territory occupancy decline to fire. This discrepancy may reflect differences in analytical scope, as our analysis extended through 2022 and included major recent fires – such as the 2020 Apple and El Dorado events – that were not captured in their study, which ended in 2019. Combined, these fires burned approximately 22,700 ha of forest in the San Bernardino Mountains (Fig. 5). Also, some territories in their study remained occupied after fire, suggesting that owls may have persisted in burned conditions (McGinn et al., 2024; Winiarski et al., in press). Notably, their reported 52 % decrease in occupancy closely matches our finding of a 54 % decline in nest/roost habitat and 47 % decline in potential territories meeting ecologically-informed nest/roost habitat thresholds (Tempel et al., 2022). Moreover, Tempel et al. (2022) found that territories burned at ≥ 40 % high severity saw near-zero colonization and increased extinction risk. Combined, these results point to large, severe wildfires as the most pervasive and limiting factor for spotted owl persistence in Southern California. As fire regimes intensify in size and severity, many burned landscapes will lose nesting habitat and remain structurally open, delaying recovery of mature forest conditions for potentially decades. Even after ten years, severely burned stands often remain barren or regenerate as shrublands rather than conifer forests (Collins and Roller, 2013), highlighting the long-term barriers that may impede population recovery.

4.2.2. Limited effect of drought and fuels management on habitat declines

In contrast to wildfire, drought-related tree mortality accounted for just 14 % of attributable nesting/roosting habitat loss, likely due to its more gradual, spatially heterogeneous nature (Bigler et al., 2007) compared to near-complete canopy loss induced by severe wildfires. However, even relatively subtle canopy loss from drought can have important indirect effects of warming temperatures on spotted owls. In

Southern California, McGinn et al. (2023a) found that forests with less dense canopies were significantly warmer than denser forests, often exceeding the thermal neutral zone for spotted owls. Indeed, spotted owls were effectively absent from warmer, lower elevation sites when canopy cover was sparse and large tree density was low (Tempel et al., 2022, McGinn et al., 2023a), and were less likely to occupy cooler high elevation sites when they were characterized by less dense canopies (McGinn et al., 2023a). As extreme heat events become more severe and frequent under a future climate, Southern California will likely experience higher ambient temperatures and increased drought-related tree mortality, compounding the loss of thermally suitable sites. While fuels management can reduce fire severity (McGinn et al., in press) and potentially mitigate drought impacts for some tree species (Restaino et al., 2019, Steel et al., 2021), their limited spatial footprint limits their effectiveness in protecting nesting habitat as disturbance regimes intensify. Thus, while drought-related tree mortality accounted for only a modest proportion of attributable nesting/roosting habitat loss, its impact could increase as the climate warms. Future habitat modeling would therefore benefit from incorporating projected climate scenarios to evaluate how continued warming may interact with drought and disturbance to further constrain suitable habitat for spotted owls.

While we did not model the effects of drought-related tree mortality on prey-acquisition habitat, drought is nevertheless likely to have important impacts on the availability of prey. For example, oaks (*Quercus* spp.) in the Sierra Nevada appear more resilient to drought than pines (*Pinus* spp.), which have suffered extensive mortality in recent years (Paz-Kagan et al., 2017, Fettig et al., 2019, Restaino et al., 2019). Between 2010 and 2017, approximately 129 million trees – primarily large pines – died from either drought stress or bark beetle infestations (California Department of Forestry and Fire Protection, 2018). Species such as ponderosa (*Pinus ponderosa*) and sugar pine (*P. lambertiana*) are particularly vulnerable to drought, mainly due to their taller stature and longer hydraulic pathways, which increase evaporative demand and reduce water-use efficiency (McDowell and Allen, 2015). Moreover, these tree species are often targeted during bark beetle outbreaks – especially in the epidemic phase – when western pine beetles (*D. brevicornis*) and mountain pine beetles (*D. ponderosae*) overwhelm the defenses of large diameter, potentially drought-weakened trees to access their greater carbohydrate stores (Safranyik and Wilson, 2006). Thus, as canopy loss from drought and bark beetle outbreaks opens conifer stands, oak- and mast-producing shrubs may be released from the understory or may expand their range into higher elevations, potentially increasing woodrat abundance in thermally suitable areas. For example, Ng et al. (in review) observed higher owl occupancy in drought-impacted zones in the Sierra Nevada, possibly due to the resilience of oaks, enhanced prey availability, and increased forest heterogeneity in this region. These findings underscore the difficulty of predicting the effects of drought-related tree mortality on prey availability, especially compared to the clear habitat loss induced by wildfire.

Our analysis also suggests that fuels management contributed minimally to nesting/roosting habitat declines, accounting for only 6 % of the explained disturbance-related loss. This small change is inevitably the result of the limited spatial extent of treatments in Southern California (5.4 % of the region from 1986 to 2022) and, ultimately, the slow pace and scale of fuels management in California (Forest Management Task Force, 2021). Our attribution framework treated all habitat change in areas where fuels management occurred within three years after wildfire as wildfire-related, a conservative assumption given the dominant effects of high-severity fire. However, this simplification does not capture the potential mitigating influence of prior fuels management on wildfire severity, as treatments can reduce canopy loss during subsequent wildfires and thereby lessen habitat degradation compared to untreated stands (e.g., Jones et al., 2022, McGinn et al., in press). While we did not attempt to quantify this interaction, future work that more explicitly models the interactive effects of fuels management and wildfire would provide greater confidence in estimates of habitat change

associated with each disturbance type.

Even so, evidence from Southern California and the Sierra Nevada mountains suggests that the direct effects of fuels management on spotted owl habitat are generally limited. For example, Tempel et al. (2022) found that fuels treatments had minimal effects on spotted owl occupancy relative to wildfire in Southern California, with treated territories experiencing higher turnover but supporting higher reproductive output than those affected by low- to moderate-severity wildfire. Moreover, in our study, we may have overestimated the impacts of fuels management, as lower-intensity treatments appear to have negligible effects on spotted owl territory occupancy in the Sierra Nevada (Ng et al., in review; McGinn et al., in press). In the Sierra Nevada, McGinn et al. (in press) showed that higher intensity fuels treatments reduced the extent of high-severity fire within megafire footprints, indirectly benefiting spotted owl occupancy despite some short-term habitat loss (Jones et al., 2022).

4.3. Management implications

Wildfires are the primary driver of habitat loss for spotted owls in Southern California, with far greater impacts than drought-related tree mortality and fuels management. Preventing further declines will require balancing the potential negative short-term impacts of fuels management, which we and others (Ng et al., in review) have found to be minimal, with their long-term benefits for mitigating fire risk and improving habitat quality. When implemented judiciously, these treatments can increase forest resilience (Knapp et al., 2021, Low et al., 2021), protect remaining owl habitat (McGinn et al., in press), and enhance prey accessibility (Wright et al., 2023). However, treatments typically reduce vertical structural complexity, particularly in dense, multi-layered forests, and may compromise the microclimatic buffering that spotted owls depend on during extreme heat (McGinn et al., 2023a, McGinn et al., 2023b). Thus, while treatments may promote horizontal heterogeneity and edge conditions beneficial for prey acquisition, they may simultaneously erode key thermal refugia. Acknowledging this tradeoff can help inform fuels management strategies that balance fire risk reduction with the preservation of critical owl habitat features.

Protecting higher-elevation thermal refugia – such as multi-layered forests in riparian corridors, forested northern aspects, and deep forested canyons – will become increasingly important under continued climate warming. These areas can provide essential shelter during extreme heat events and are more likely to persist as viable habitats over time (McGinn et al., 2023a). Moreover, fuels management in these areas that promote deciduous species, such as black oaks (*Quercus velutina*), can help enhance prey abundance and thermal buffering. However, large oaks (*Quercus* spp.) are increasingly threatened by invasive pests and pathogens such as the goldspotted oak borer (*Agrilus auroguttatus*) and *Phytophthora ramorum*, the agent of sudden oak death (Frankel, 2008). In Southern California, infestations by the goldspotted oak borer have already caused significant oak mortality (Coleman and Seybold, 2008), potentially reducing both the thermal buffering capacity of forests used by spotted owls and habitat quality for key prey species like the dusky-footed woodrat (*Neotoma fuscipes*) (Innes et al., 2007). Thus, as insect and disease outbreaks accelerate oak mortality and canopy thinning, heat exposure could rise beyond the owls' physiological limits, leading to both the loss of thermal refugia as well as access to important prey, underscoring the importance of protecting oak-dominated forests in cooler microclimates.

Collectively, our findings and recent research identify five primary threats to the persistence of the Southern California spotted owl: (1) large, high-severity wildfires; (2) oak mortality due to invasive pests and disease; (3) increasing temperatures and physiological stress; (4) landscape homogenization and isolation; and (5) declining genetic diversity (Tempel et al., 2022, Kulzer, 2023, McGinn et al., 2023a, 2023b, Barry et al., 2025). Addressing these interconnected threats will require regionally coordinated, ecologically informed management strategies

that restore natural disturbance processes, protect thermal refugia by retaining vertical forest structure in mature forests, enhancing prey accessibility by promoting horizontal heterogeneity and edge-rich mosaics, and maintaining habitat connectivity to support gene flow. But most importantly, without a rapid and meaningful reduction in high-severity fire activity, Southern California's spotted owl population will remain at high risk of extinction.

4.4. Mapping wildlife habitat in dynamic landscapes

Our study offers several lessons for improving how habitat change is mapped for wildlife in disturbance-prone ecosystems. First, by mapping landscape complementation, we demonstrate the value of considering multiple habitat types for a single species and show how tracking their spatial juxtaposition reveals functional habitat loss that single-habitat approaches may miss. Second, integrating our species distribution models with disturbance maps enabled us to quantify both the extent of habitat change and its underlying causes by attributing changes to fire, drought/other, and forest management. While studies focused on a subset of disturbance types have provided valuable insights into specific drivers of habitat change for fire-sensitive species – such as Mexican spotted owls (Jones et al., 2023), fishers (*Pekania pennanti*) (Hart et al., 2025), and red tree voles (*Arborimus longicaudus*) (Linnell et al., 2023) – a more comprehensive approach can reveal the relative impacts of all major disturbance agents. Our approach parallels previous efforts to map northern spotted owl habitat trends under the Northwest Forest Plan (Davis et al., 2016), but advances this work by incorporating rigorously validated, spatially explicit disturbance layers developed for the California region. As canopy mortality products (e.g., Slaton et al., 2024) expand regionally and accuracy in habitat mapping improves (e.g., Ackers et al., 2015), these tools can be integrated into dynamic modeling frameworks to better monitor habitat change and guide conservation in disturbance-prone landscapes. Finally, by pairing public remote sensing products with cloud-based tools like GEE, we offer a reproducible framework for tracking habitat change over decades at regional scales. This approach enables consistent, high-resolution monitoring across large areas and long time periods, helping to fill data gaps in disturbance-prone ecosystems by leveraging global 30-m satellite coverage (Zhao et al., 2021). In sum, our approach demonstrates the value of combining diverse ecological data with disturbance mapping and cloud-based processing to support conservation in dynamic environments.

CRediT authorship contribution statement

Gavin M Jones: Writing – original draft, Methodology, Conceptualization. **Ronan Hart:** Writing – original draft, Visualization, Methodology, Formal analysis. **McGinn Katherine:** Writing – original draft, Investigation. **Kramer Heather:** Writing – original draft, Methodology. **Peery Marcus Zachariah:** Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Barry Joshua Michael:** Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

I have nothing to declare.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.123386](https://doi.org/10.1016/j.foreco.2025.123386).

Data availability

The data and code supporting the attribution findings of this study are publicly available in the Figshare repository at 10.6084/m9.figshare.30793112. Other data will be made available on request. Geographic locations of spotted owls are sensitive; these data are owned by the Department of Forest and Wildlife Ecology at the University of Wisconsin-Madison and are available to qualified researchers by contacting the principal investigator (M. Zachariah Peery; email: mpeery@wisc.edu)

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