

CONTRIBUTED PAPER

Habitat loss and fragmentation for an old-forest species is driven by severe wildfire and drought

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Abstract

Understanding drivers of habitat loss and fragmentation can inform conservation policy and action. However, drivers vary across space and time, and complete datasets of potential drivers that align with time series of species habitat are rare. We developed a 38-year time-series of nesting/roosting habitat for the California spotted owl in the Sierra Nevada, CA, USA, and used a novel disturbance dataset to attribute habitat changes to potential drivers. We found that the total area of high-quality nesting/roosting habitat declined by 43% between 1985 and 2022. Moreover, the average high-quality habitat patch became 68% smaller and 33% more isolated over the study period. During 2002–2022, drought was the most abundant disturbance in spotted owl habitat (49% of habitat affected), followed by high-severity fire (32%) and fuels management (20%). However, the amount of disturbance did not always match impact. Drought, while most common, was responsible for only 20% of estimated habitat losses. High-severity fire was responsible for nearly half (45%) of habitat loss, while fuels management was responsible for only 9% of habitat loss (and 14% of habitat gains). Dominant drivers of habitat loss varied spatially, suggesting the potential to use local information to calibrate conservation action. Previously, the absolute and relative impacts of fuels management, severe wildfires, drought, and other disturbance agents on spotted owl habitat were unknown. Here, we demonstrated that the most influential factor driving losses of high-quality spotted owl habitat was high-severity fire, and that fuels management, while associated with relatively smaller habitat losses, was also associated with habitat gains, suggesting net benefits of fuels management via its effect of reducing high-severity fire. We demonstrate the power of using

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dynamic species distribution models to map and track habitat over time and understand the factors that may be contributing to observed habitat losses and gains.

KEYWORDS

forest restoration, habitat fragmentation, species distribution model, spotted owl, *Strix occidentalis*

1 | INTRODUCTION

There is often enormous variability in ecological relationships, environmental conditions, and agents of change across a given species' geographic range. Local densities of a given species can vary by orders of magnitude across sites within the range (Brown et al., 1996), within-species genetic variation attenuates from the central portion of the range to the margins (Eckert et al., 2008), and populations may respond differently to the same environmental conditions across localities because of local adaptation or other contexts (non-stationarity in habitat selection; Osborne et al., 2007). Some of these population characteristics are driven by spatial and temporal variation in habitat quality, vegetation communities, climate, and other environmental factors (Griffen & Norelli, 2015; Rollinson et al., 2021). Drivers of habitat or population change can also vary spatially: the velocity of climate change and effects to local populations (Loarie et al., 2009) and impacts of fires, droughts, and human land use pressures will differ across geographies (Asner et al., 2015; Newbold et al., 2015) and over time (Hart et al., 2025; Jones et al., 2023). Such variation in agents of change can lead to spatially varying population trends (Bjørnstad et al., 1999; Johnston et al., 2025).

To develop effective approaches for conserving species and local populations, we ideally must fully understand this variation but typically do not. Detailed, long-term ecological studies are often limited to a small number of locales that may have been selected non-randomly, potentially limiting the generalizability of inference (Fournier et al., 2019; Penteriani et al., 2005). The existence of non-stationarity in habitat selection means that a seemingly important species-habitat association derived from one region can weaken or reverse in another region in unpredictable ways (Cushman et al., 2024; Wan et al., 2017). Moreover, the relative threats to species or populations will vary across space (Evans, Watson, et al., 2011), making blanket conservation strategies less effective and highlighting the importance of diagnosing causes of decline and developing appropriate conservation responses locally (Caughley, 1994). In sum, effective conservation planning is challenged by the inherent

variability in ecological relationships, local responses, and threats across a species' range.

Dynamic species distribution models (SDMs; Dobson et al., 2023; Milanese et al., 2020) provide one means to overcome many of these challenges. Dynamic SDMs link time-stamped occurrence data with corresponding time-stamped environmental data and allow predictions of habitat to be made into a spatial time series. Like traditional static SDMs, with sufficient occurrence data one can model habitat quality across an entire species' range at very fine spatial grains (e.g., 10- or 30-m resolution) and often with machine learning algorithms that offer high predictive accuracy (Elith & Leathwick, 2009; Evans, Murphy, et al., 2011; Valavi et al., 2022). But dynamic SDMs also allow researchers to predict habitat at any point in time for which spatial data exist (e.g., Landsat satellite data dating from 1984-present), evaluate spatial and temporal non-stationarity in habitat selection, generate time series of local and range-wide trends of habitat change, and conduct analyses attributing drivers of change (e.g., fire, drought, land use) that may vary across a species' range (Hart et al., 2025; Jones et al., 2023; Shirk et al., 2023). The outcome of applying a dynamic SDM approach is a much more comprehensive spatially and temporally resolved understanding of ecology, environmental conditions, and drivers of change for a species across its range, that can help resolve conservation uncertainties.

Here, we applied a dynamic SDM approach to map the spatial distribution of current habitat, estimate long-term changes to habitat amount and configuration, and attribute habitat change to a range of natural and anthropogenic drivers for the California spotted owl (*Strix occidentalis occidentalis*) in the Sierra Nevada, California, USA. The California spotted owl (hereafter, "spotted owl"), which is traditionally associated with mature and old-growth forests and whose conservation has a substantial impact on timber management practices (Gutiérrez et al., 1995, 2017), is currently proposed for listing under the US Endangered Species Act. A range of threats to spotted owl populations have been identified (Keane, 2017) including large tree logging (Jones et al., 2018), forest fuels management (Hanson, 2021),

post-fire salvage logging (Hanson et al., 2021), large, severe wildfires (Jones et al., 2016, 2021), and recent drought (Steel et al. 2022). However, we do not know how any of these potential drivers have affected long-term habitat changes for spotted owls. Moreover, the influence of these potential agents of habitat change may vary over space and time, and their relative and absolute influences on habitat change are unknown. While several studies have demonstrated how spotted owl individuals, populations, and occupancy respond to fire (Eyes et al., 2017; Jones et al., 2016, 2020; Kramer et al., 2021), management (Gallagher et al., 2018; McGinn et al., 2026; Stephens et al., 2014; Tempel et al., 2014), and, recently, drought (Ng et al., 2026), and previous work has shown how forest conditions associated with spotted owls, such as old-growth or mixed-conifer forests, respond to fire (Weatherspoon et al., 1992), drought (Steel et al., 2023), or fuels management (Tempel et al., 2014), there is no published study to our knowledge that has quantified and mapped California spotted owl habitat in the Sierra Nevada nor evaluated trends in habitat over time. Given that spotted owl habitat conservation and the potential intersection with fuels reduction work is a leading driver of forest management planning in California (Stephens et al., 2019), we sought to answer the questions: “How has California spotted owl habitat in the Sierra Nevada, CA, changed over time, and what has caused these changes?”

2 | METHODS

2.1 | Study area and spotted owl locations

The seasonally dry, mixed-conifer forests of the Sierra Nevada, California, support the majority of California spotted owl populations (Weatherspoon et al., 1992). Prior to Euro-American colonization, frequent low- to moderate-severity fires resulted in heterogeneous forest structures; however, a century of logging practices and fire suppression policies have led to increases in canopy cover, stand density, and surface fuels, shifting the observed fire regime to be less frequent and more severe (Reilly et al., 2026; Weatherspoon et al., 1992).

Our study area encompassed the Sierra Nevada Conservancy (<https://sierranevada.ca.gov/>) bioregional boundary south of the Pit River. This boundary layer excluded lands surrounding Lake Tahoe, so we included these lands using the Sierra Nevada ecoregion boundary (<https://www.usgs.gov/>). The Sierra Nevada Conservancy divides the bioregion boundary into six subregions: North, North Central, Central, South, South Central, and

East Sierra (Figure 1a); however, because our spotted owl dataset did not include locations in the eastern regions of the Sierra Nevada, we excluded the East Sierra subregion from our analysis of habitat. About a third (34%) of the study area was forested (Figure 1), and almost all of this forested area (97%) was federal land, with most of this land managed by the Forest Service (84%), National Park Service (11%), and Bureau of Land Management (4%).

We developed a spatially and temporally comprehensive database of visually confirmed, diurnal, breeding-season California spotted owl nesting and roosting detections ($n = 2445$) across the Sierra Nevada bioregion from several sources. These sources included the California Natural Diversity Database ($n = 1818$), the US Fish and Wildlife Service ($n = 465$), and demographic studies ($n = 162$). Nesting/roosting locations in the database were identified as early as 1985 and as recently as 2022 and occurred in an adequately balanced manner across our subregions: North Sierra, $n = 106$; North Central Sierra, $n = 745$; Central Sierra, $n = 768$; South Central Sierra, $n = 494$; South Sierra, $n = 332$ (Figure 1a). We applied a quality control workflow to ensure that all nesting/roosting locations used in the analysis were accurate, and did not represent other types of non-target behaviors (e.g., nocturnal foraging) or non-breeding season activities (Jones et al., 2023).

2.2 | Habitat covariates

We developed a suite of 142 environmental covariates that we thought would contribute to a strong predictive model of spotted owl habitat. Covariates (m) fell into three broad categories: topography ($m = 10$), climate ($m = 12$), and reflectance ($m = 120$). In most SDM applications, the primary objective is to develop a model that can produce very good spatial predictions (i.e., an accurate map). This objective is different from studies that focus on inference or exploration, where the goal is to test or generate hypotheses about system behavior (Evans, Murphy, et al., 2011; Tredennick et al., 2021). In many predictive modeling applications, especially when using machine learning algorithms like random forest (Breiman, 2001) as the predictive engine, multicollinearity of predictors is not as concerning as they are in inferential or exploratory analyses. This is because the focus is not on interpreting coefficients (“how does rainfall relate to habitat quality?”), but instead the focus is on interpreting the predicted outcome (“where is habitat quality highest?”). It is for this reason we have included a large number of predictors in our model, so that we can produce highly accurate local spatial interpolation of spotted owl habitat across our modeling region.

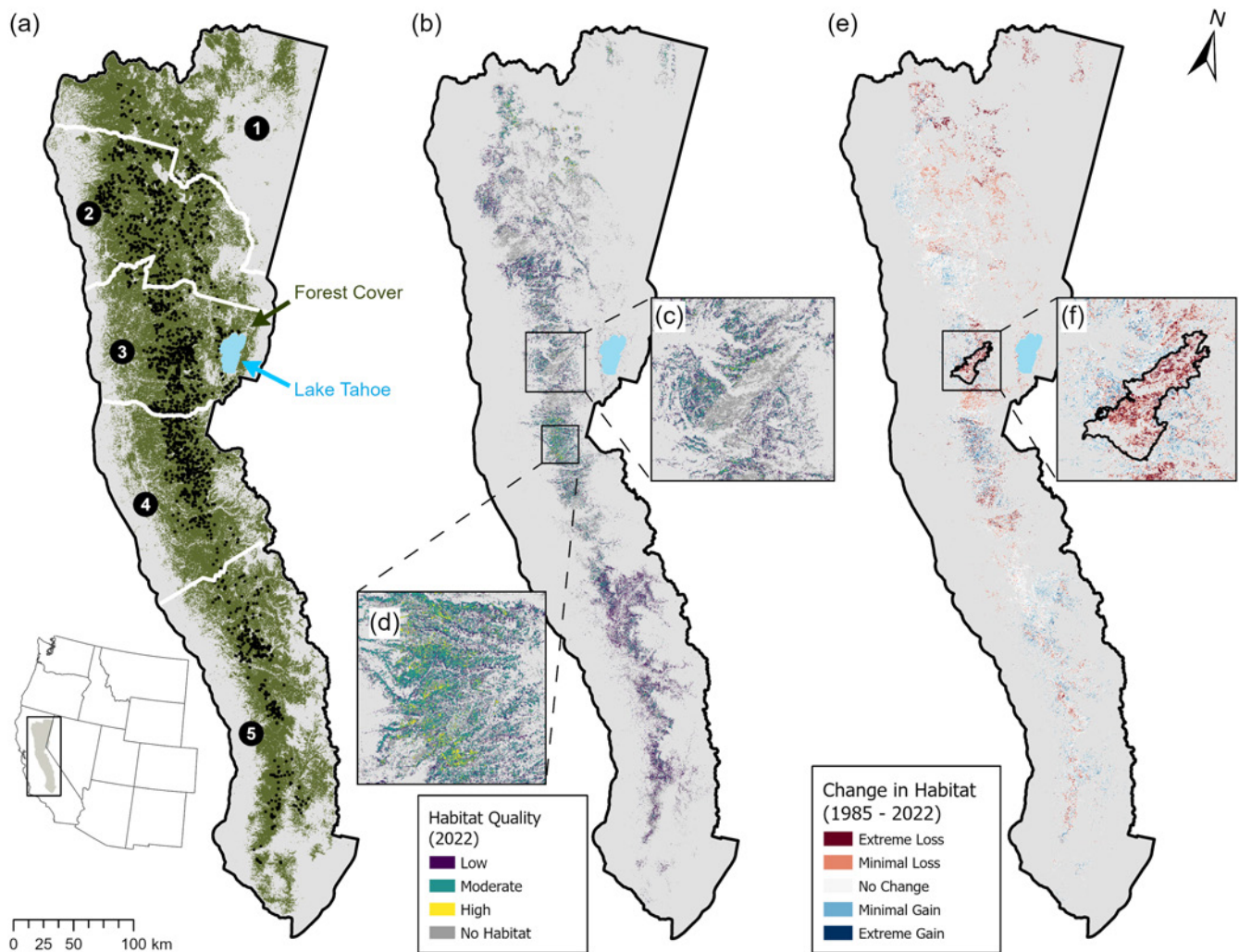


FIGURE 1 (a) Study area map of California spotted owl roosting and nesting locations (dark points) within forested areas (green) within the subregions (1) North Sierra, (2) North Central Sierra, (3) Central Sierra, (4) South Central Sierra, and (5) South Sierra. (b) Spotted owl roosting/nesting habitat quality in 2022 with two insets (c and d) to demonstrate habitat quality (gray cells indicating “No Habitat” show cells that were habitat in previous years but not the current year). (e) Change in habitat quality from 1985 to 2022 with an inset (f) of the 2014 King Fire (same extent as (c)).

We derived topographic variables using a 30-m resolution digital elevation model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM; Farr et al., 2007). Variables included elevation, slope, heat load index (HLI; characterizes incident radiation), topographic wetness index (TWI; characterizes potential soil moisture), topographic ruggedness index (TRI; characterizes topographic relief), and topographic position index (TPI; characterizes ridge versus valley locations by comparing the elevation of each pixel to that of its neighbors). For slope, HLI, TWI, and TRI, we extracted covariate values at 30-m scale. For TPI, we extracted covariate values across five scales, as the size of the neighborhood can significantly change TPI results (Salinas-Melgoza et al., 2018), representing the radii of circles centered on the focal point: 90, 180, 360, 720, and 1440-m. Slope, HLI, TPI, and TRI

were derived within the Google Earth Engine (GEE) environment (Gorelick et al., 2017), and TWI was derived using ESRI's ArcPro version 2.9.5 (Environmental Systems Research Institute, Redlands, CA).

We derived climate variables using the software ClimateNA, version 7.42 (Wang et al., 2016). The outputs of this software include a variety of climate variables for the 30-year normal historical periods in 10-year increments: 1951–1980, 1961–1990, 1971–2000, 1981–2010, and 1991–2020 and the projected climate for 2011–2040. The 30-year normals describe climate for the final year in the period based on data from the previous 30 years (e.g., the climate described in 2010 is based on historical climate data starting in 1981). So, to avoid an assumption of constant climate within each 30-year period and to avoid abrupt modeled change artifacts at each decade, we

linearly interpolated annual climate values for covariate attribution and also prediction (Hart et al., 2025; Shirk et al., 2023). ClimateNA is unique compared to other climate datasets in that it spatially interpolates climate based on the resolution of a DEM provided by the user. Thus, we provided the same 30-m resolution SRTM DEM that we used to compute topographic variables to the ClimateNA algorithm. We averaged select monthly variables to derive seasonal climate variables that were relevant to spotted owl nesting and roosting habitat (Jones et al., 2023; Peery et al., 2012; USFWS, 2012): mean minimum temperature and mean precipitation for the late-winter (January and February) and nesting seasons (April and May); mean maximum and mean temperature and mean precipitation for the summer season (July–September); mean temperature for the warmest month (July); mean precipitation as snow for the winter season (November–February); and mean annual precipitation, annual growing degree days, and annual climatic moisture deficit.

We used reflectance variables (representing vegetation conditions) rather than using classified and derived metrics, such as forest cover or landcover type, because raw reflectance values contain more information (as information is lost in the classification process), and previous studies have found that using these variables produces more accurate predictive models (Jones et al., 2023; Shirk et al., 2023; Zhu & Woodcock, 2014). We derived reflectance variables (representing vegetation conditions) by applying the Continuous Change Detection and Classification algorithm (CCDC; Zhu & Woodcock, 2014) to a 38-year (1985–2022), 30-m resolution Landsat 5/7/8 Tier 1 surface reflectance time series within the GEE data repository and workspace. Briefly, CCDC is a change detection algorithm that uses a combination of linear and harmonic models to create robust temporal trend estimation and reliable change detection in remotely sensed data. The CCDC coefficients are then used to generate smoothed annual synthetic Landsat images. We derived a total of 120 covariates for each year from 1985 to 2022 from six synthetic Landsat bands (Blue, Green, Red, NIR, SWIR-1, SWIR-2) and five derived indices (normalized difference vegetation index, NDVI; normalized difference wetness index, NDWI; normalized difference snow index, NDSI, and normalized burn ratio, NBR and NBR-2) at two dates (May 1 and August 1 to account for the start of the green-up and the peak of vegetation, respectively). Finally, we used the CCDC model coefficients themselves as predictors, namely the slope coefficient and the first/second/third-degree cosine and sine coefficients for each of the bands and indices at the two dates. Including the CCDC model coefficients as predictors in the random forest model minimizes the false signal of habitat

recruitment following fire events that is produced by rapid vegetation green-up (Witt et al., 2022). See Table S1 for a list of all covariates.

2.3 | Species distribution modeling

We modeled the probability of spotted owl nesting/roosting habitat using random forest classifiers (Breiman, 2001; Cutler et al., 2007; Evans, Murphy, et al., 2011), following similar methods to Shirk et al. (2023) and Hart et al. (2025). We applied a used-available modeling framework (Elith & Leathwick, 2009), where we randomly generated 10 available locations for every used location in each subregion-year combination. We limited available points to a forest mask, where we labeled a pixel as “forest” if it had been classified as deciduous, coniferous, or mixed forest by the National Land Cover Database (NLCD) classification in any period or if the Hansen Global Change Model (Hansen et al., 2013) predicted forest canopy cover $\geq 20\%$. While spotted owl nesting habitat is typically found in forests with 40% canopy cover or more (Tempel et al., 2016), we wanted to allow some flexibility in generating available points in potential edge cases. We used this inclusive forest mask to avoid projecting nest/roost habitat models into areas that were obviously unsuitable for spotted owls nesting sites (e.g., bare ground, meadows) while also ensuring 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. For each used and available location, we extracted all covariate values (see above section) at the pixel level (30-m cell resolution) by matching the year of covariate data to the year of detection. For instance, a nest/roost location from 1990 would be matched with climate and Landsat data from 1990, and so on. We assumed topographic variables were static during the study period.

We developed an SDM within the GEE environment for each subregion, trained on used-available data from the corresponding subregion (Figure 1) to allow for spatial non-stationarity in habitat selection (Hart et al., 2025; Jones et al., 2023; Rollinson et al., 2021). Employing k -fold cross-validation with $k = 10$, we trained 10 distinct random forest classifiers for each subregion. These classifiers were structured with 50 trees, using 12 variables per split, with a bag fraction of 0.5. Data partitioning allocated 90% for model training, reserving the remaining 10% for model validation. We then projected subregion-fold models onto annual environmental data ranging from 1985 to 2022, capturing the evolving characteristics of each subregion, and calculated the mean probability of

habitat suitability per subregion across the 10 folds. To evaluate the accuracy of our SDMs, we computed the mean and standard deviation of the out-of-bag (OOB) error and the area under the curve (AUC) across 10 model runs for each subregion. For our final spotted owl nesting and roosting habitat maps, we projected models onto the region where they were trained, but we also explored the degree to which models were transferable across regions by projecting subregional models onto annual environmental data from each other subregion and calculated the AUC.

2.4 | Classifying habitat

We classified our maps into “non-habitat” as well as three ordinal categories of habitat quality: low quality, moderate quality, and high quality. Classification allowed us to track changes in different tiers of habitat as well as explicit transitions among habitat quality classes and facilitated our ability to compute landscape metrics like patch size and configuration (see Section 2.5). To determine the cut-offs for these categories, we first calculated a threshold that would balance the false positive and false negative error rates, that is, a threshold where the false positive rate (type I error) equals the false negative rate (type II error) (Allouche et al., 2006). We considered all cells below this threshold to be non-habitat and all cells above this threshold to be habitat, as a threshold that balances the false positive and negative rates heuristically described areas that were more likely than not to contain elements known to be associated with spotted owl roosting and nesting habitat. We then categorized the remaining cells above the threshold into three levels of quality. We determined these thresholds by finding the 50th and 95th quantile of all cell values across all years and categorized all cells for each subregion-year into low quality ($\text{threshold}_{\text{subregion}} \leq \text{cell value} < 50\text{th quantile}$), moderate quality ($50\text{th quantile} \leq \text{cell value} < 95\text{th quantile}$), and high quality ($95\text{th quantile} \leq \text{cell value}$). This process was repeated for each subregion. We chose the 95th percentile as the cutoff for high-quality habitat because, heuristically, this corresponds with rare phenomenon in any statistical distribution, and we wanted to capture the elements that constitute the most limiting of owl habitat: nesting and/or roosting structures.

2.5 | Habitat trends, configuration, and summaries

To calculate the total area of spotted owl nesting/roosting habitat for each year and habitat quality class, we

summed the number of cells per class and multiplied by the cell area (900-m^2 , 0.09-ha). We then measured how habitat changed each year by tracking how much habitat for each class transitioned to each other class or remained in the same class. This tracking allowed us to avoid the problem of measuring change in categorical habitat, where a loss from one class may actually mean a gain in another class (as it transitions between classes) rather than absolute habitat loss. By capturing how categorical habitat transitioned into other classes, we can fully understand how much habitat is truly being lost or gained.

In addition to tracking changes in habitat area, we also wanted to understand changes in habitat configuration over time. We converted each subregion-year-class into patches, where each patch was composed of at least four connected cells (0.36-ha) (Turner et al., 2001). We then calculated patch-level characteristics of area, Euclidean nearest neighbor, and fractal dimension index using the R package “*landscapemetrics*” (v. 2.2.1) (Hesselbarth et al., 2019). We chose to focus on these three metrics because they each represent a unique facet of landscape configuration: patch area, patch aggregation or isolation, and patch shape or complexity, respectively (McGarigal et al., 2002). The fractal dimension index ranges between 1 and 2, where indices closer to 1 indicate shapes with simple perimeters, such as squares and circles, while indices closer to 2 indicate more complex shapes (McGarigal et al., 2002). We then calculated the area-weighted mean (McGarigal et al., 2002), coefficient of variation, and standard deviation of each metric for each year to obtain an annual summary of each metric for each class.

2.6 | Understanding potential drivers of habitat change

We overlaid our annual habitat maps with a database of change agents within US Forest Service (USFS) land and covering the period 2002–2022 (Kramer et al., 2026) to attribute habitat changes to a suite of disturbances. This change agent database classified each 30-m cell in each year into 1 of 16 categories: high-severity fire (year-of and 1–3 years post-fire), moderate-severity fire (year-of and 1–3 years post-fire), low-severity fire (year-of and 1–3 years post-fire), post-fire salvage (high-, moderate-, and low-severity), post-fire fuel management (high-, moderate-, and low-severity), drought/other/unknown sources of canopy loss, fuel management, salvage with no fire, and no disturbance. Hereafter, we refer to the disturbance class that Kramer et al. labeled as “drought/other/unknown sources of canopy loss” simply as “drought.” However, it is more accurate to consider it to be “drought-related change”; this category also contains

some amount of non-drought and unknown drivers of canopy loss and change, (e.g., insect damage, disease, windthrow, and landslides), but for ease and clarity we will simply refer to it as “drought” as most change could in this category could be attributed to drought directly (Kramer et al., 2026). Furthermore, for our analysis, we combined year-of and 1–3 years post-fire effects for all fire severity classes into simply “high severity fire,” and so on for the other two severity classes. We combined the two temporal classes to maintain the potential post-fire effects on the landscape in our analysis while also simplifying the number of disturbance classifications for clarity. Kramer et al. (2026) note that the drought, fuel management, and salvage categories have a temporal element, wherein a cell will remain classified as that disturbance for up to 3 years after the initial disturbance, unless a higher-ranking disturbance occurs before then; and so combining the year-of and 1–3 years post-fire categories together results in a similar temporal buffer as the other disturbance classes. We also combined the post-fire fuel management categories with the fuel management without fire category, and we combined the post-fire salvage categories with the salvage with no fire category. Kramer and her team separated fuel management and salvage activity by using the USFS Forest Activity Tracking System (FACTS) database, where some areas had been labeled as “fuels over the 38-year study period management” and some as “salvage.” Briefly, “fuels management” could cover a variety of activities with the purpose of reducing fire ignition, spread, and severity (Husari et al., 2006), such as prescribed and managed fire, fuel piling, pruning and thinning, and mastication, while “salvage” specifically refers to the removal of damaged or dead timber (Leverkus et al., 2018; Thorn et al., 2018). While these two categories could be combined, we left them separate due to interest in the effects of spotted owl habitat post-salvage (Hanson et al., 2021). Thus, in our final analysis, we focused on the following six disturbance classes (in addition to undisturbed area): high-severity fire, moderate-severity fire, low-severity fire, salvage, fuel management, and drought. Disturbance classifications were computed only within USFS land, as we only had data of fuel management and salvage within these boundaries. Because drought data in the database only range from 2002 to 2022 due to data availability, we limited the temporal window of the following attribution analyses to only this period. Notably, this period covers the extreme drought during 2012–2016 that particularly affected the South Sierra region (Asner et al., 2015; Fettig et al., 2019; Steel et al., 2023).

We measured how area in each habitat quality class changed within each disturbance category annually, differentiating between areas that decreased in habitat

quality and those that increased in quality. For example, to quantify the extent to which drought increased habitat quality in 2005, we calculated the area where drought in 2005 co-occurred with areas that increased in habitat quality from 2005 to 2006. We repeated this method for all years, all disturbance types, and for both increases and decreases in habitat quality. We then used binomial tests (Sokal & Rohlf, 1995) to examine whether spotted owl habitat in particular was disproportionately affected by different disturbances compared to the study area as a whole and whether disturbances resulted in transitions among habitat classes that were different from background habitat change in areas that were not affected by a known disturbance driver.

Finally, we measured how habitat loss due to disturbance varied spatially. We used watersheds (hydrologic unit code 12, i.e., HUC12) (Seaber et al., 2007) to visualize these spatial disturbances. For each year since 2002, we determined where habitat loss occurred and what disturbance class occurred that year that could be attributed to that loss. Across all years, we summed the number of times each disturbance class could be attributed to habitat loss for each cell. We then determined which disturbance contributed the most to habitat loss in each watershed boundary.

3 | RESULTS

We used fitted random forest models to predict the spatial and temporal distribution of California spotted owl roosting and nesting habitat over a 38-year period from 1985 through 2022 (Figure 1b). While we fit models for each subregion (see Sections 2.1 and 2.3), we mosaicked together all individual models into a full study area raster, and here we will report results for the full study area (see Data S1 for results for each subregion, Figures S4–S14, Tables S3–S11). The mean threshold, 50th quantile, and 95th quantile across all subregion-years were 0.246 (standard deviation: 0.023), 0.324 (SD: 0.0045), and 0.550 (SD: 0.0090), respectively (Figure S1). Our models were highly accurate, with a mean AUC of 0.989 (SD: 0.00347), a mean out-of-bag error of 0.085 (SD: 0.00702), and at the threshold, a mean false positive/negative rate of 0.0398 (SD: 0.00998) across the 10 folds for each subregion (Table S2).

3.1 | Trends in habitat area and configuration

Our models predicted that, in 1985, there were 32,213-ha of high-quality, 305,752-ha of moderate-quality, and

338,752-ha of low-quality spotted owl nesting and roosting habitat. By 2002 (about mid-way through the study period and the beginning of when we began attribution of disturbance effects, see Sections 2.6 and 3.2), there were 27,897-ha of high-quality, 243,446-ha of moderate-quality, and 256,296-ha of low-quality habitat. By 2022, there were 18,447-ha of high-quality, 218,746-ha of moderate-quality, and 334,586-ha of low-quality habitat (Figure 2a). From 1985 to 2002, we thus found net losses of 13.4% of high-quality, 20.4% of moderate-quality, and 24.3% of low-quality; and from 2002 to 2022, we found net losses of 33.9% of high-quality and 10.1% of moderate-quality and a net gain of 30.5% of low-quality habitat. Across the three habitat quality classes, there appeared to be a period of stability or even increase in habitat from the early 2000s to the 2010s. Over the full 38-year study period, we observed net losses of 43% of high-quality, 29% of moderate-quality, and 1% of low-quality habitat. Note that the above percentages reflect net losses and gains in the three habitat quality classes and do not reveal the degree of transition between classes. That is to say, while there were net habitat declines, habitat gains did occur (see Data S1).

From 1985 to 2022, high-quality habitat patches decreased in number and mean patch area, they grew further apart from each other, and they became simpler in shape. Moderate-quality patches decreased in number from 1985 to 2022 and decreased in mean patch size from 1985 to 2002 but then increased in size from 2002 to 2022; the mean distance between patches slightly increased and the mean patch shape tended toward more complex over time, but these changes were relatively small. The number of low-quality patches varied over time but tended to be much higher than the number of high- or moderate-quality patches; the mean patch area

of low-quality patches increased considerably after 2010, as did the mean fractal dimension index, indicating low-quality patches became more complex; the mean distance between low-quality patches varied slightly over time but not by much (Table 1; Figure 2d).

3.2 | Disturbance as a driver of habitat loss and transition

We found that, over the period 2002–2022 on USFS-managed land (the domain of our attribution analysis that makes up 62% of all spotted owl nest/roost habitat), an average of 23.3% (range: 5.8%–47.7%) of spotted owl nest/roost habitat was disturbed each year. Annually, drought disturbed 12.2% (0.30%–27.9%), fuel management disturbed 3.6% (3.0%–4.7%), high severity fire disturbed 2.9% (0.05%–19.0%), moderate severity fire disturbed 2.3% (0.094%–9.8%), low severity fire disturbed 2.0% (0.17%–6.4%), and salvage logging disturbed 0.23% (0.05%–0.44%) of all habitat. Annual disturbance of spotted owl habitat increased substantially after 2012 (a mean of 12.5% habitat disturbed pre-2012, 33.1% post-2012). Most increases in disturbance were driven by drought (7.3% pre-2012, 16.7% post-2012) and all fire—but particularly high severity fire (0.31% pre-2012, 5.3% post-2012) (Figure S2). While an average of 23.3% of spotted owl habitat experienced disturbance each year, a cumulative amount of 86.8% of habitat experienced disturbance at least once over the study period. Cumulatively, 48.8% of habitat was disturbed by drought, 31.7% was disturbed by high severity fire, 20.3% was disturbed by fuel management, 18.2% by moderate severity fire, 12.0% by low severity fire, and 2.6% by salvage at least once. (Note that these percentages exceed 100% because these are not

TABLE 1 The mean (and standard deviation) habitat configuration metrics (patch area, Euclidean nearest neighbor [ENN], and fractal dimension index) for each time step (1985, 2002, 2022) and habitat quality class (high, moderate, and low).

Habitat quality	Year	N patches	Mean patch area (ha) (SD)	Mean ENN (m) (SD)	Mean fractal dimension index (SD)
High	1985	7947	47.0 (10.63)	135.5 (597.2)	1.193 (0.054)
	2002	7916	20.7 (6.34)	152.0 (607.1)	1.176 (0.052)
	2022	5693	15.0 (4.98)	180.1 (716.5)	1.170 (0.051)
Moderate	1985	61,255	99.0 (18.15)	88.4 (302.8)	1.229 (0.059)
	2002	50,153	88.6 (16.99)	91.9 (280.1)	1.224 (0.059)
	2022	45,198	132.8 (20.44)	93.3 (342.5)	1.232 (0.058)
Low	1985	122,751	11.2 (3.89)	94.4 (202.8)	1.199 (0.057)
	2002	97,964	8.5 (3.20)	101.6 (237.7)	1.189 (0.056)
	2022	103,142	67.7 (11.17)	89.3 (268.4)	1.230 (0.059)

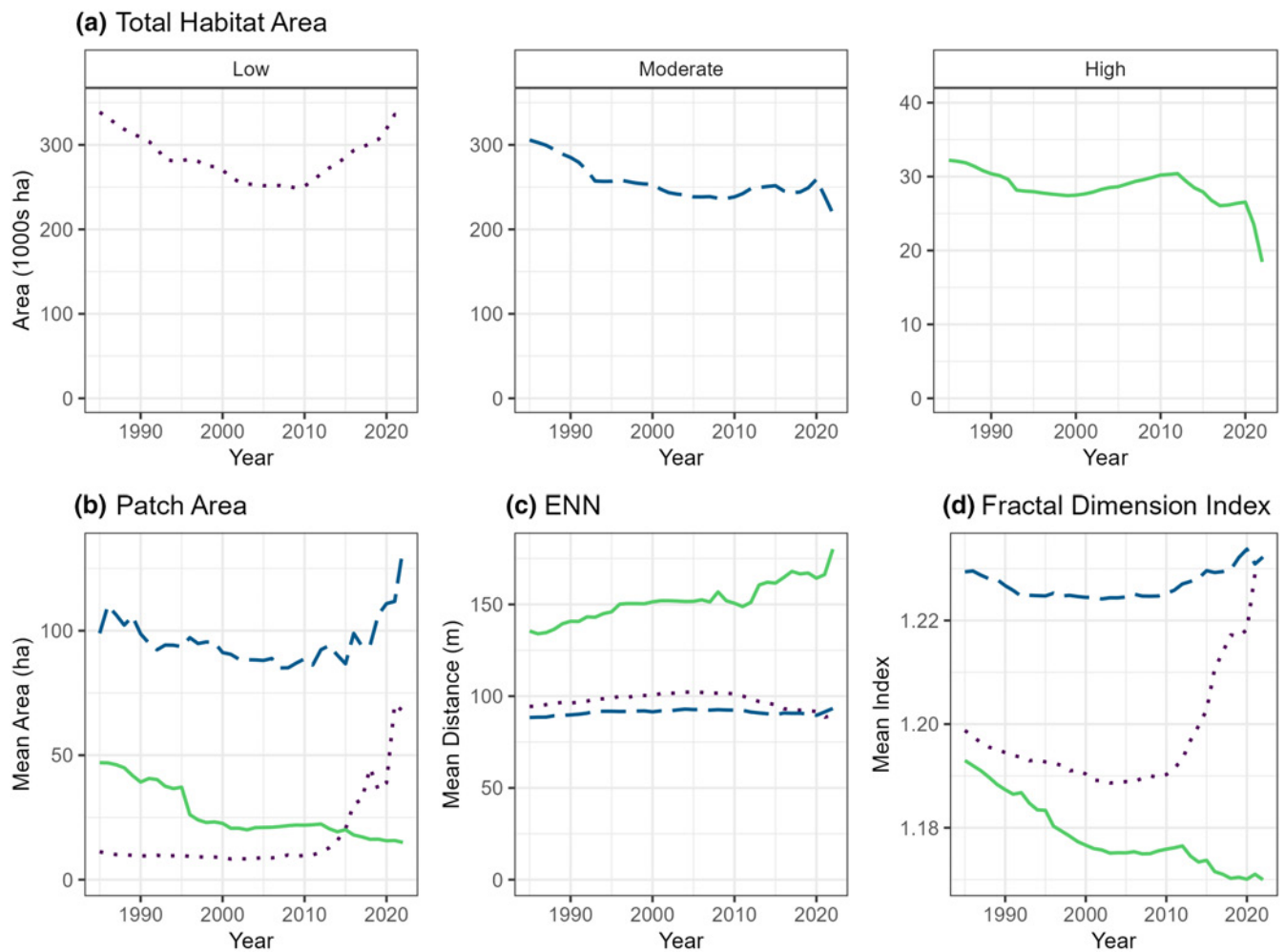


FIGURE 2 Trends in (a) total area, (b) mean patch area, (c) mean Euclidean nearest neighbor (ENN) between patches, and (d) mean patch fractal dimension index for each quality class: low (purple dotted line), moderate (dark blue dashed line), and high (green solid line) across the study period. Note that in (a), each panel shows low-, moderate-, and high-quality habitat in their own panel (left to right respectively) and that the y-axis scale for high-quality (right panel) is different than that for low- and moderate-quality (left and center panels).

mutually exclusive, as cells can experience multiple disturbances over the course of the study period.) For the remainder of this section, we will report results only on high severity fire, drought, and fuel management for clarity, as these were the most common disturbance types. See Table 2 and Figures 3–6 for results on how the remaining disturbances affected spotted owl nest/roost habitat.

Because spotted owl nest/roost habitat has overall declined over our study period, it is important to understand the main drivers of these losses. While here we will focus on reporting drivers of habitat losses, we also tracked how disturbances resulted in habitat gains; full results for losses and gains can be found in Tables 2–4, Figures 6b and S3. From 2002 to 2022, high-severity fire accounted for, on average across habitat quality class,

45.2% (range: 43.5%–47.3%) of all post-disturbance habitat loss, drought accounted for 19.5% (18.0%–20.8%), and fuel management accounted for 10.9% (9.1%–12.0%) (Table 2; Figure 3). There was a notable increase in post-disturbance habitat losses in the last decade (Figure 3a), where nearly 82% of all habitat loss occurred from 2013 to 2022 compared to 18% over the period 2002–2012. The dominant drivers of habitat loss varied spatially across the study area (Figure 4).

To understand if spotted owl nest/roost habitat was more or less likely to experience a disturbance compared to the study area in general, we used binomial tests to compare disturbance proportions across the whole study area compared to proportions in spotted owl habitat (Table 3; Figure 6a). Compared to non-spotted owl habitat, high-severity fire was less likely to

TABLE 2 Disturbance effects on spotted owl nest/roost habitat.

Disturbance	Habitat quality class	Expected area disturbed (ha)	Observed area disturbed (ha)	% habitat affected (% of disturbed area affected)	Decreases in habitat quality (ha)	% of total observed loss (% of loss in disturbed areas)	Increases in habitat quality (ha)	% of total observed gain (% of gain in disturbed areas)
High-severity fire	High	9121	6386	1.7 (9.6)	6329	28.7 (47.3)	1	0.001 (0.05)
	Moderate	80,093	55,358	1.7 (8.1)	50,541	28.7 (43.5)	5585	3.9 (13.5)
	Low	89,024	128,629	3.5 (14.2)	79,287	28.0 (44.9)	45,226	12.7 (32.3)
Moderate-severity fire	High	8302	3038	0.81 (4.6)	1846	8.4 (13.8)	29	0.20 (1.4)
	Moderate	72,900	44,567	1.4 (6.5)	19,248	10.9 (16.6)	6807	4.8 (16.4)
	Low	81,029	94,533	2.6 (10.5)	31,856	11.2 (18.0)	29,143	8.2 (20.8)
Low-severity fire	High	7483	6277	1.7 (9.5)	1295	5.9 (9.7)	147	1.0 (6.9)
	Moderate	65,713	56,846	1.7 (8.3)	8083	4.6 (7.0)	4289	3.0 (10.4)
	Low	73,041	74,278	2.0 (8.2)	11,172	3.9 (6.3)	11,058	3.1 (7.9)
Salvage	High	1223	7148	0.19 (1.1)	56	0.25 (0.42)	22	0.15 (1.0)
	Moderate	10,742	7323	0.22 (1.1)	774	0.44 (0.67)	456	0.32 (1.1)
	Low	11,939	9118	0.25 (1.0)	1421	0.50 (0.80)	1066	0.30 (0.76)
Fuel management	High	12,901	7964	2.1 (12.0)	1213	5.5 (9.1)	301	2.1 (14.0)
	Moderate	113,288	110,545	3.3 (16.1)	13,298	7.5 (11.5)	5366	3.8 (13.0)
	Low	125,921	140,469	3.8 (15.5)	21,153	7.5 (12.0)	14,440	4.1 (10.3)
Drought	High	25,877	41,934	11.1 (63.2)	2632	11.9 (19.7)	1643	11.5 (76.7)
	Moderate	227,234	412,200	12.4 (60.0)	24,167	13.7 (20.8)	18,881	13.3 (45.6)
	Low	252,575	457,517	12.4 (50.6)	31,766	11.2 (18.0)	39,058	11.0 (27.9)
No disturbance	High	312,132	310,725	82.4 (N/A)	8674	39.3 (N/A)	12,105	85.0 (N/A)
	Moderate	2,740,972	2,624,102	79.3 (N/A)	60,232	34.2 (N/A)	101,078	71.0 (N/A)
	Low	3,046,639	2,775,624	75.4 (N/A)	106,815	37.7 (N/A)	215,001	60.6 (N/A)

Note: Percentages are within each habitat quality class.

occur within high- and moderate-quality habitat (about 1.4 times less for both classes), while it was more likely to occur in low-quality habitat (about 1.5 times more). Drought was 1.73 times more likely to occur within spotted owl habitat regardless of quality compared to the surrounding landscape. Fuel management was less likely to occur in high-quality habitat (1.6 times less) while the likelihood of occurring within moderate- or low-quality habitat was nearly the same compared to non-spotted owl habitat.

We measured post-disturbance habitat class transitions over our study period (Figure 5) and compared these to background habitat transitions in undisturbed areas using binomial tests (Table 4; Figure 6b). When spotted owl habitat experienced high-severity fire, it was about 19 times more likely to decrease in quality compared to the probability of habitat decreasing in quality with no disturbance. Habitat that experienced drought was about two times more likely to decrease in habitat quality, and about four times more likely to decrease in

quality after experiencing fuels management. While these losses are considerable, many of these losses were offset by gains post-disturbance, and habitat often did not transition to another quality class post-disturbance (see Table 4 and Figure 6b).

4 | DISCUSSION

We used a dynamic SDM approach to investigate how the habitat of an old-forest associated species, the California spotted owl, has changed over space and time, and what factors were responsible for those changes. We found that high-quality California spotted owl habitat in the Sierra Nevada, California declined by 43% between 1985 and 2022. Over time, high-quality habitat also occurred in smaller and more isolated patches. In general, the opposite trends were observed for lower-quality habitats, as high-quality habitat was lost and transitioned into lower-quality categories. Our work underscores

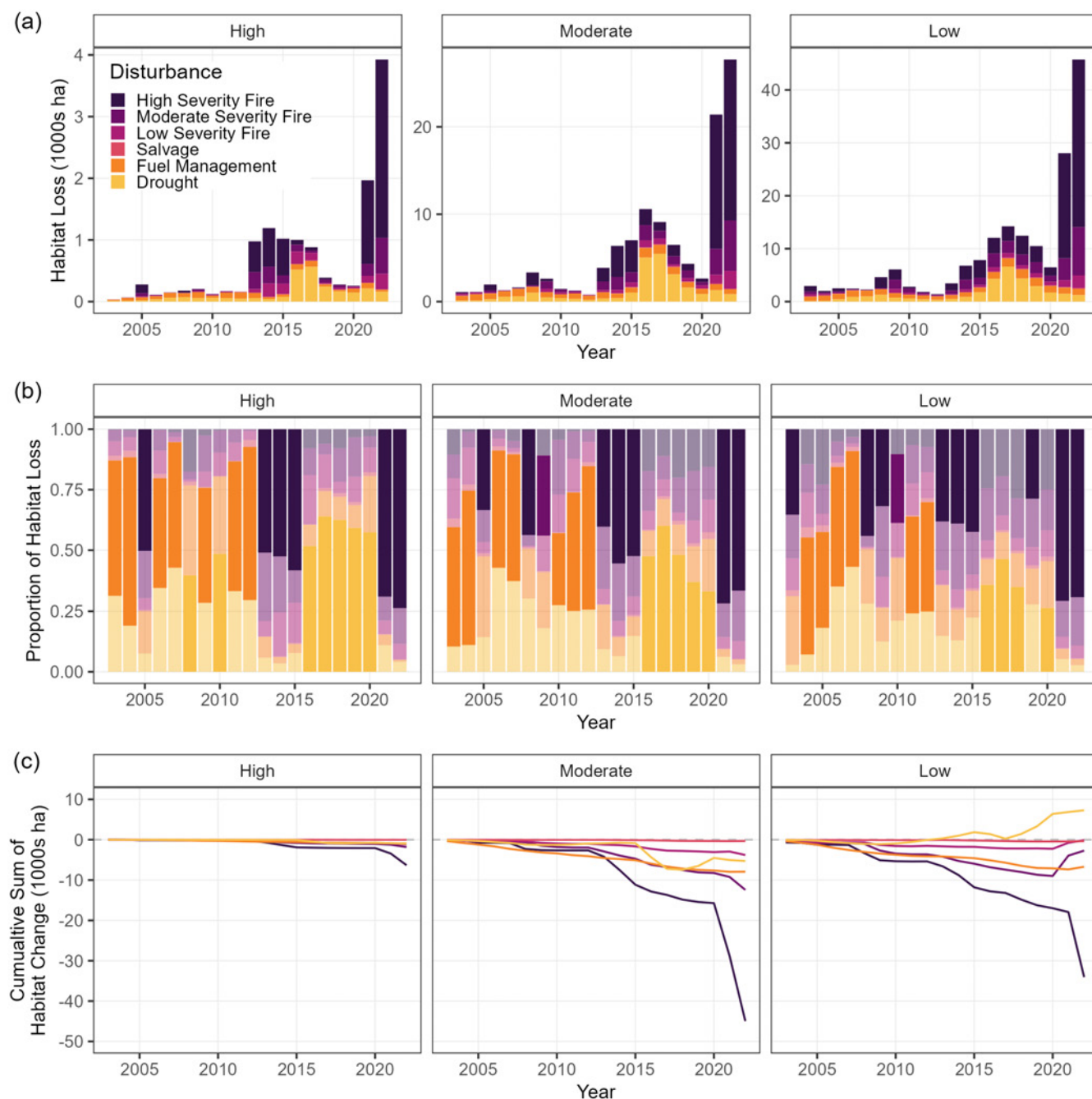


FIGURE 3 Total (a) and proportion (b) of decreases in habitat quality post-disturbance type (bar color) within each habitat quality class (columns) across the limited study period (2002–2012) and area (US Forest Service-managed land); transparency in panel (b) highlights which disturbance could be attributed to the largest proportion of decreases in quality for each year. Panel (c) shows the difference between the cumulative sum of decreases in habitat (from panel a) and the cumulative sum of increases in habitat (from Figure S3a) for each habitat quality class. Note that background decreases (i.e., decreases in habitat quality when there was no attributable disturbance) were not included in this figure, and that the y-axes on panel (a) are different scales for each habitat quality class.

rapid fire- and drought-driven changes to old-forest wildlife habitat and, by comparison, the relatively modest and neutral effects of fuels management. Together, these findings suggest the potential benefits of increasing the pace and scale of fuels management to spotted owls and forest restoration goals in this system.

The spotted owl is one of the most well-studied wildlife species worldwide (Löhmus, 2004). For several years, there has been a considerable effort to study spotted owl demographics, occupancy, and space use and how these life history metrics respond to disturbances, notably fire, fuel management, and drought. As spotted owls are

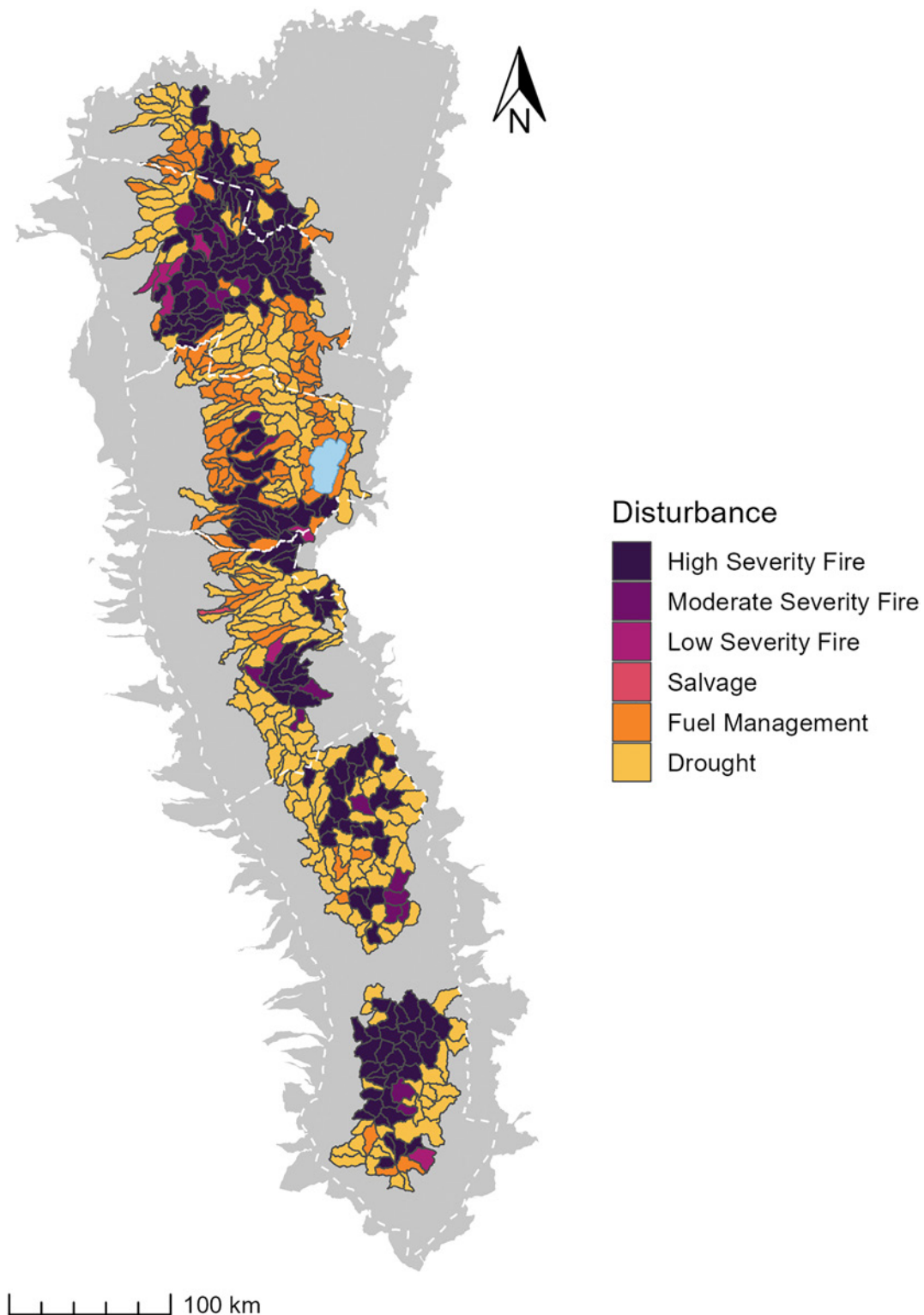


FIGURE 4 Map depicting the cumulative effects of disturbances on habitat loss on spotted owl habitat. To aid in visualization, we used watershed boundaries (hydrologic unit code 12, i.e., HUC12). For each watershed boundary, we counted which disturbance could be attributed to the most habitat loss across the study period (2002–2022) and area (US Forest Service managed land). The gray areas denote watersheds with no spotted owl habitat, exhibiting no habitat loss or attributable disturbance, or lying outside the boundaries of US Forest Service-managed land. The white dotted lines indicate the subregional boundaries.

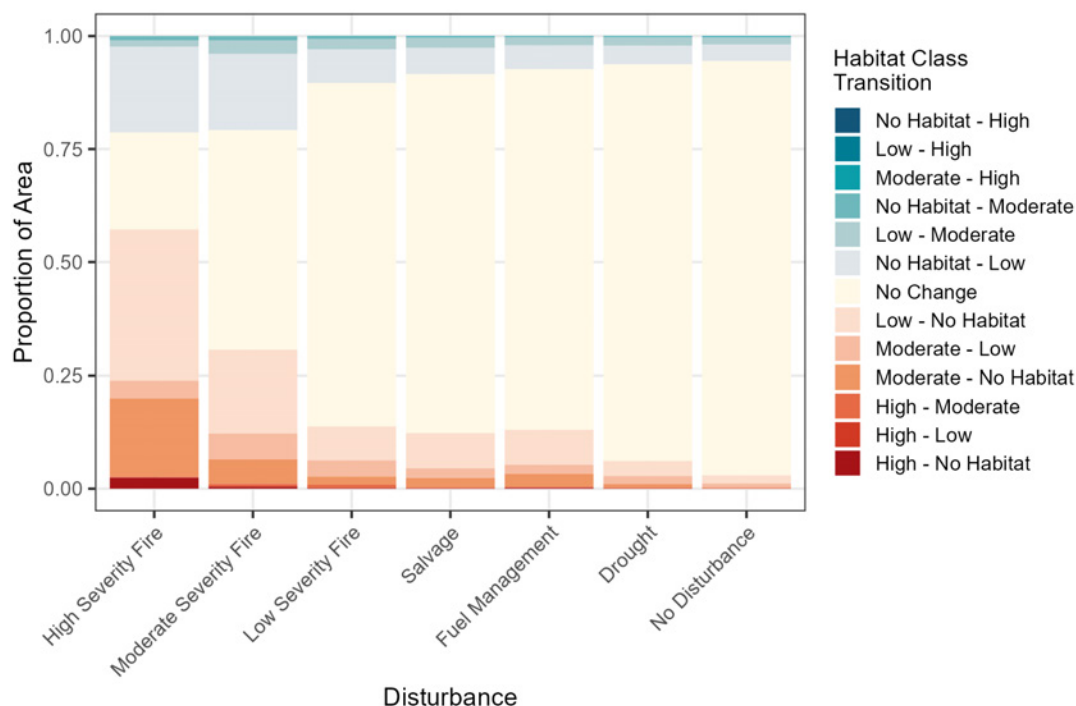


FIGURE 5 Proportion of how much habitat transitioned from one class to another post-disturbance type compared to no disturbance (right-most bar) across the limited study period (2002–2012) and area (US Forest Service-managed land). Blue-green colors indicate that habitat transitioned into a higher class (e.g., low-quality to high-quality), red-orange colors indicate that habitat transitioned into a lower class (e.g., high-quality to low-quality), and yellow indicates habitat remained the same class, or “No Change.” Note that some transition types do not appear in each bar (e.g., “No Habitat–High” does not appear in the High Severity Fire bar) or their proportional affect is so small to be barely visible in this figure.

strongly associated with old-growth and mixed-conifer forests (Jones et al., 2018), many researchers use these forest types as proxies for spotted owl habitat. Our work extends these vegetation-focused efforts to explicitly quantify spotted owl habitat, track its changes over time, and associate drivers of that change. Our results align with other recent studies: Steel et al. (2023) found that a large amount of conifer forests in the southern region of the Sierra Nevada declined during extreme drought from 2012 to 2016, particularly in spotted owl protected activity centers; Ng et al. (2026) and Barry et al. (2026) similarly concluded that high-severity wildfire presents the biggest threat to California spotted owl habitat and occupancy; and Wright et al. (2023) and McGinn et al. (2026), who both conclude that spotted owl habitat gains and reduced fire effects from fuels management far outweigh temporary spotted owl habitat loss post-management.

Our work reduces uncertainty regarding the absolute and relative importance of threats to spotted owls and their old-forest habitat in the Sierra Nevada, California. For decades, logging and other timber harvesting was considered the biggest threat to the species, especially because of intensive timber harvesting prior to the 1990s (Gutiérrez et al., 1995; Simberloff, 1987) with persistent

population effects (Jones et al., 2018). Large and severe wildfire has also been long-recognized as a possible threat (Keane, 2017; Weatherspoon et al., 1992), with recent natural experiments suggesting clear negative local population consequences (Jones et al., 2016, 2021). More recently, following extensive drought-related tree mortality in the southern Sierra Nevada, drought, and its intersection with severe wildfire, has been viewed as a considerable driver of mature forest habitat losses (Steel et al., 2023). However, until now, we have not understood which of these threats might be the most important across most of the species' range, or how in certain circumstances these “threats” might potentially provide habitat-related benefits. We have shown that, by a considerable margin, high-severity wildfire has resulted in most of the habitat losses observed since 2002 (see also Barry et al., 2026). Both drought and fuels management have contributed to losses in habitat quality and area, but these disturbance types have also offset their losses with gains (Table 2, Figures 3 and S7–S9). We also were able to spatially and temporally isolate effects of severe fire from post-fire salvage logging and demonstrated severe fire typically had 1–2 orders of magnitude greater negative effects to spotted owl habitat than salvage logging

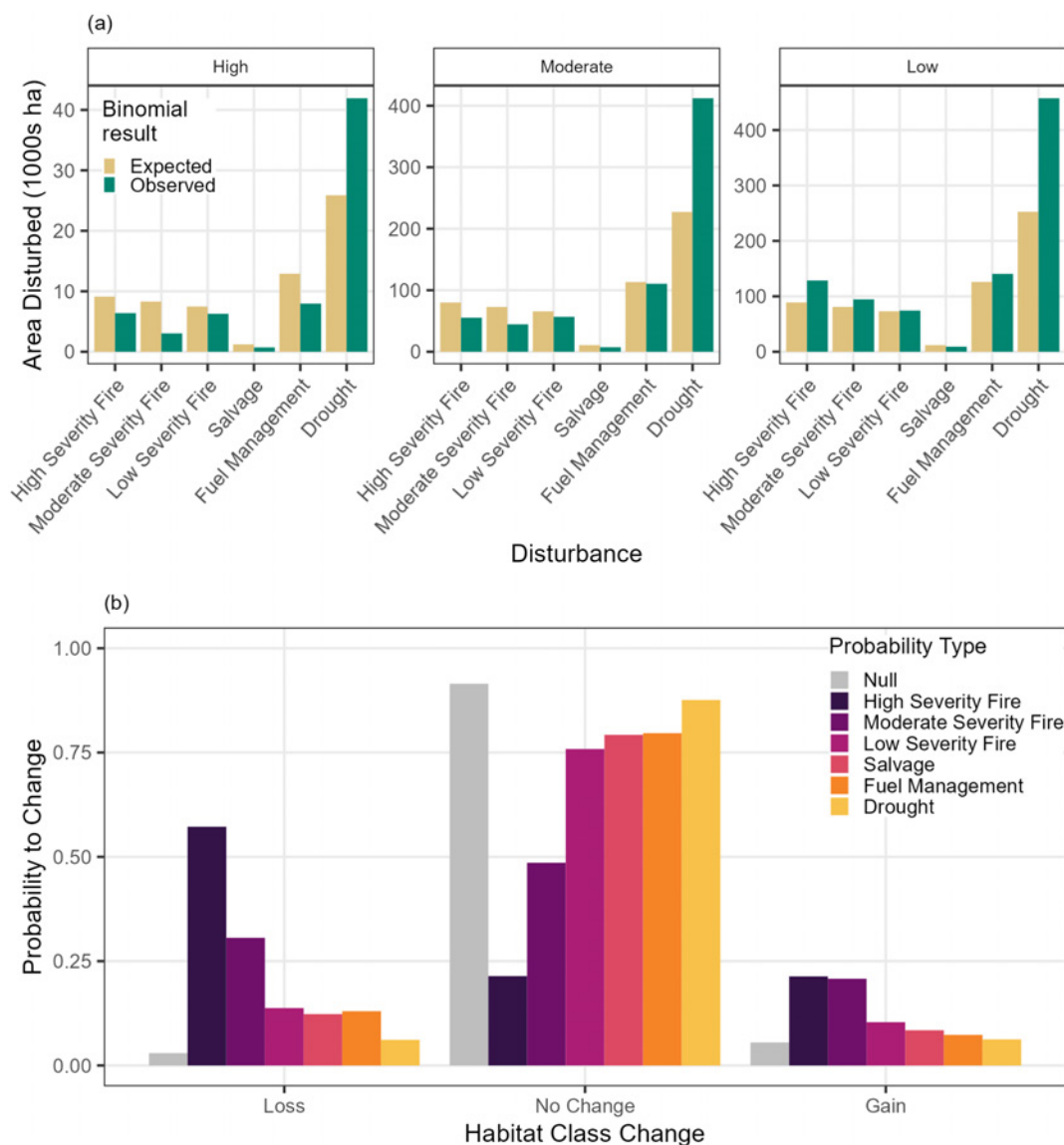


FIGURE 6 (a) Bar graph of how much area was expected to be disturbed (gold bars) based on the proportion of area disturbed in the whole study area compared to the observed area disturbed (green bars) based on the proportion of area disturbed in each spotted owl habitat quality class (facets; note that the y-axis scales differ for each facet). (b) Probability of habitat quality class transitioning into a lower class (loss), remaining the same (no change), or transitioning into a higher class (gain) after experiencing a disturbance (observed probability, colored bars) compared to no disturbance (null/expected probability, gray bars). Note that results for both (a) and (b) are from disturbance affects across the limited study period (2002–2022) and area (US Forest Service-managed land).

(Table 2), supporting findings from previous work (Jones et al., 2016, 2021).

Understanding habitat loss and its drivers is critical for informing conservation action, but so too is understanding changes to habitat fragmentation and connectivity. In real landscapes, habitat loss is nearly inseparable from habitat fragmentation and decreases in connectivity (Fardila et al., 2017; Fletcher et al., 2018). We observed these patterns, where losses in high-quality habitat area corresponded with increased fragmentation and isolation of remnant habitat patches (Figure 2).

Increased isolation (i.e., decreased connectivity) of breeding habitat in a metapopulation can result in reduced gene flow and a higher likelihood of local extirpation (Hanski, 1998; Van Schmidt & Beissinger, 2020). Thus, beyond habitat loss, observed habitat fragmentation and isolation may be expected to result in additional negative consequences to population processes in California spotted owls. At the same time, spotted owls have superb dispersal abilities, with adults often exhibiting dispersal in the range of tens of kilometers and juveniles sometimes dispersing much longer distances such as 50 to 100-km

TABLE 3 The probability of spotted owl habitat (broken down by quality class) experiencing a disturbance (regardless of post-disturbance effects) compared to the probability of surrounding non-spotted owl habitat experiencing that same disturbance.

Disturbance	Probability of occurring in non-spotted owl habitat	Habitat quality class	Probability of occurring within quality class
High-severity fire	0.024	High	$0.017 \pm 1e-4$
		Moderate	$0.017 \pm 4e-5$
		Low	$0.035 \pm 6e-5$
Moderate-severity fire	0.022	High	$0.008 \pm 9e-5$
		Moderate	$0.014 \pm 4e-5$
		Low	$0.026 \pm 5e-5$
Low-severity fire	0.020	High	$0.017 \pm 1e-4$
		Moderate	$0.017 \pm 4e-5$
		Low	$0.020 \pm 4e-5$
Salvage	0.003	High	$0.002 \pm 4e-5$
		Moderate	$0.002 \pm 2e-5$
		Low	$0.003 \pm 2e-5$
Fuel management	0.034	High	$0.021 \pm 1e-4$
		Moderate	$0.033 \pm 6e-5$
		Low	$0.038 \pm 6e-5$
Drought	0.069	High	$0.110 \pm 3e-4$
		Moderate	$0.125 \pm 3e-4$
		Low	$0.124 \pm 1e-4$
No disturbance	0.8279	High	$0.824 \pm 4e-4$
		Moderate	$0.793 \pm 1e-4$
		Low	$0.754 \pm 1e-4$

(Blakesley et al., 2006; Forsman et al., 2002). Moreover, the high connectivity of fire-prone forests in this region is considered unnatural because of fire suppression and results in higher likelihood of mass fire (Francis et al., 2023; Stephens et al., 2022). More research is needed to understand the implications of changed nesting/roosting habitat connectivity for spotted owls in this region.

With our study having identified fire as a key driver of loss and fragmentation of California spotted owl nesting/roosting habitat, what are the implications for species conservation? Can the potential future impacts of fire and drought be mitigated? Fuels reduction and forest restoration activities in seasonally dry forests, when they act to increase the multi-scaled heterogeneity of forest structure and decrease fuel continuity, can increase resilience of forest ecosystems to both drought and fire (Koontz et al., 2020; McGinn et al., 2026; Young et al., 2017). Historically, forests of the Sierra Nevada were substantially less dense than they are today, suggesting that decreased tree competition supported their resilience to many stressors and disturbances (North et al., 2022).

Disturbances were much more frequent and covered larger portions of the landscape historically than they do even today (Parks et al., 2025), generating strong multi-scaled heterogeneity of vegetation age. When present, such heterogeneity in forest structure has been shown to benefit spotted owls by promoting the juxtaposition of nesting/roosting habitat with prey habitat that facilitates prey capture and supports fitness in private timberlands (Kuntze et al., 2023; Zulla et al., 2022; Zulla et al., 2023). While our analysis suggested that some spotted owl nesting/roosting habitat loss was associated with fuels management (Figure 3), the absolute losses were relatively small, and associated habitat increases were also observed. Increases in foraging habitat quality for California spotted owls have been shown to be associated with fuels management; such actions decrease canopy bulk density, decrease ladder fuels, and increase canopy base height (Wright et al., 2023), can increase overall territory quality (Jones, Stanley, et al., 2025), and is consistent with recent science on the benefits of multi-scale heterogeneity (above). Thus, increases in the pace and scale of fuels reduction in the Sierra Nevada have the potential to

TABLE 4 The probability of habitat transitioning to a lower quality class (i.e., a loss in habitat quality), higher quality class (i.e., a gain in habitat quality), or not transitioning (i.e., remaining the same habitat quality) after no disturbance compared to after a disturbance.

Transition type	Probability of habitat transitioning, no disturbance	Disturbance	Probability of habitat transitioning, post-disturbance
Loss	0.0296	High-severity fire	$0.572 \pm 6e-4$
		Moderate-severity fire	$0.306 \pm 7e-4$
		Low-severity fire	$0.138 \pm 5e-4$
		Salvage	$0.123 \pm 1e-3$
		Fuel management	$0.130 \pm 4e-4$
		Drought	$0.062 \pm 1e-4$
No change	0.915	High-severity fire	$0.214 \pm 5e-4$
		Moderate-severity fire	$0.486 \pm 7e-4$
		Low-severity fire	$0.759 \pm 7e-4$
		Salvage	$0.792 \pm 2e-3$
		Fuel management	$0.796 \pm 5e-4$
		Drought	$0.876 \pm 2e-4$
Gain	0.0553	High-severity fire	$0.214 \pm 5e-4$
		Moderate-severity fire	$0.208 \pm 7e-4$
		Low-severity fire	$0.104 \pm 5e-4$
		Salvage	$0.084 \pm 1e-3$
		Fuel management	$0.073 \pm 3e-4$
		Drought	$0.063 \pm 1e-4$

benefit both forest ecosystems, spotted owls, and biodiversity more broadly (Hurteau et al., 2025; North et al., 2021).

Importantly, threats to species are not uniform across space and over time. During a ~10 year period of apparent stability (and even slight increase) in high-quality habitat from 2002 to 2012 (Figure 2a), fuels management was the most significant driver of annual losses (Figure 3b)—even though these losses were balanced by habitat recruitment. Since the early 2010s, however, fire resulted in losses orders of magnitude greater than cumulative losses from fuels management over the entire study period. It is important to note that habitat trends were not consistent throughout the study period, with varying periods of decrease, increase, and stability. These alternating periods lend support to hypotheses that historical logging (i.e., pre- to mid-1900s logging and clear-cutting) caused contemporary habitat losses (Jones et al., 2018). Moreover, the changes to conservation and environmental regulations that happened in the late 1990s (Gutiérrez et al., 2017; Verner et al., 1992) seemed to be having the intended effect by the early 2000s, with leveling off of declines in low and moderate quality habitat, and a reversal of declines in high-quality habitat (Figure 2). Yet these changes appear to have come at a cost: the legacy effect of that historical logging, when combined with decreases in active

management due to changes in regulations, increased the risk of those forests to disturbance. These logging and management legacies, combined with warming and drying conditions that have accelerated in recent decades, appear to be responsible for a disturbance regime shift responsible for recent habitat losses (Hart et al., 2025; Jones, Collins, et al., 2025; Steel et al., 2023).

Just as threats changed over time, they varied across space. While many regions in the Sierra Nevada showed habitat losses primarily due to drought and high-severity fire, other regions showed that local losses could be mostly attributed to fuels management, and some regions to low- or moderate-severity fire (Figure 6). Thus, it is important to recognize that broader-scale drivers may not always play out at local levels, and such understanding is critical for spatially optimized threat management. Spatially varying threats can also lead to spatially varying habitat and population trends; we saw highly divergent patterns of habitat change across modeling subregions, which corresponded with spatially varying threats (Data S1). While broader-scale efforts to quantify habitat and population trends and associated threats can act to raise awareness of key issues (Rosenberg et al., 2019), modeling that permits both large-extent and fine-grained habitat and population assessments are critical for informing on-the-ground conservation action (Johnston et al., 2025; Stillman et al., 2025).

While we feel the lessons learned in our study are robust, readers should consider several important caveats and limitations regarding our results. First, our maps, trends, and inferences about agents of change all relate to spotted owl habitat—and specifically owl nesting and roosting habitat—not spotted owl populations or realized occupancy. In areas where habitat is predicted to occur, individuals or populations of spotted owls may not necessarily be present because of other factors (e.g., population dynamics, lag effects, competition, etc.), and estimated habitat quality may not correlate with population density (see Ng et al., 2026). Furthermore, these maps and results are of spotted owl nesting/roosting habitat, rather than a general habitat or hunting habitat, for example (see Barry et al., 2026). Second, for simplicity and because we had temporally unbalanced nest/roost data, we assumed that species-environment relationships were stable over time (temporal stationarity). If spotted owls adapt their habitat selection to changing landscape conditions over time, habitat mapping and trend estimation could be biased. Third, we did not account for the ways in which multiple disturbance types might interact in space and time to influence spotted owl habitat. For example, drought-induced habitat losses (or gains) followed by high-severity fire might have unique and unknown effects to owl habitat that each factor alone might not fully capture. Fourth, while our analysis encompassed most of the potential range of the California spotted owl in the Sierra Nevada, we excluded the East Sierra region from our analysis because we did not have nest/roost data from this area, meaning we do not currently know the status or trends of habitat in this portion of the range. Moreover, we excluded non-USFS lands (e.g., private timberland, national parks) from our attribution analysis; future work could reveal differing drivers of change in these landscapes. Finally, we did not explore how spotted owl habitat might recover following disturbances, and how different types of disturbances might lead to different recovery pathways, such as how habitat would respond to fuel management followed by fire. Such an exploration is possible given the data we have but was beyond the scope of our study and should be explored in subsequent analyses.

5 | CONCLUSION

We have shown that severe wildfire and drought-related mortality have resulted in considerable losses (43%) to high-quality nesting and roosting habitat of California spotted owls in the Sierra Nevada since 1985, with most losses occurring in the past decade. As the US Fish and Wildlife Service considers finalizing a proposal to list the subpopulation of spotted owls in the Sierra Nevada as a

Distinct Population Segment under the US Endangered Species Act, understanding the relative influence of different drivers of habitat declines will be critical in helping inform future species recovery. California spotted owls are also a species of management concern in many USFS land management plans (e.g., Regional Forester Sensitive species or species of conservation concern), and better understanding the tradeoffs between direct habitat loss and potential indirect benefits can help guide management planning in a rapidly changing environment. Also critical for species recovery is a means to monitor conservation progress; our development of a dynamic SDM for California spotted owls in the Sierra Nevada provides an automated system for monitoring this species habitat into the future. Our work demonstrates how dynamic species distribution models can be used to understand spatially and temporally complex changes to species habitat and inform conservation action.

AUTHOR CONTRIBUTIONS

Ronan Hart: methodology, software, validation, formal analysis, data curation, writing – original draft, writing – review & editing, visualization. **H. Anu Kramer:** methodology, software, validation, formal analysis, data curation, writing – review & editing. **Josh Barry:** data curation, writing – review & editing. **M. Zachariah Peery:** writing – review & editing, funding acquisition. **Stephanie Eyes:** conceptualization, resources, writing – review & editing, funding acquisition. **Craig Thompson:** conceptualization, resources, writing – review & editing, funding acquisition. **Sarah Sawyer:** conceptualization, resources, writing – review & editing, funding acquisition. **Gavin M. Jones:** conceptualization, methodology, software, validation, resources, writing – original draft, writing – review & editing, visualization, supervision, project administration, funding acquisition.

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CONFLICT OF INTEREST STATEMENT

None declared.

DATA AVAILABILITY STATEMENT

Data publicly archived.

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SUPPORTING INFORMATION

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

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