Science of the Total Environment 890 (2023) 163414

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Northern spotted owl nesting habitat under high potential wildfire threats along the California Coastal Redwood Forest

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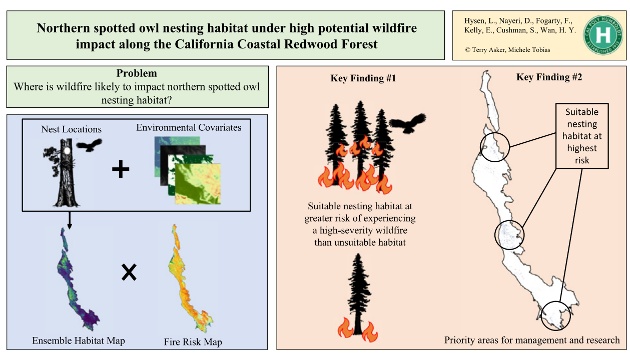
HIGHLIGHTS

- Severe wildfire risk is increasing in the western USA, threatens to impact habitat.
- Managers require spatially-explicit information to prioritize wildfire mitigation.
- Northern spotted owl nesting habitat is at a high risk of high-severity wildfire.
- Identified habitat at risk of severe wildfire could benefit from management action.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo Soria

Keywords:
Disturbance ecology
Ecological niche model
Ensemble learning
Fire ecology
Multi-scale
Species distribution model

ABSTRACT

Large and severe wildfires, exacerbated by climate change and human behavior, are occurring more frequently in many forests across the western United States. While wildfire is a natural part of most terrestrial ecosystems, rapidly changing fire regimes have the potential to alter habitat beyond the adaptive capabilities of species. Spatial assessments of wildfire risks to species habitat may allow managers to pinpoint locations for management activities. To illustrate this, we spatially assessed wildfire risk within habitat that supports the nesting activity of the federally threatened northern spotted owl (*Strix occidentalis caurina*) in the California redwood coast ecoregion. To accomplish this, we built a scale-optimized ensemble nesting habitat suitability model and identified habitat with the highest wildfire hazard potential. Percent canopy cover at 100-m scale, slope at 400-m scale, and January precipitation at 800-m scale were the most influential environmental covariates for predicting northern spotted owl nesting habitat. Nearly 60% of nesting habitat was predicted to be at high or very high (>1986 index value) wildfire risks. We identified three areas in the Maple Creek Area of Humboldt County, Jackson State Demonstration Forest in Mendocino County, and Point Reyes National Seashore in Marin County, California with a high concentration of nesting habitat that are at a very high risk of experiencing high severity wildfires. We recommend these areas be targeted for future research to understand the impact of wildfire on northern spotted owl as well as management attention.

1. Introduction

Wildfire is an integral part of many ecosystems (Agee, 1996; Bond and Keeley, 2005). In the high latitude regions of the western United States, wildfires are projected to continue becoming larger, more frequent, and more severe under climate change (Kasischke and Turetsky, 2006;

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http://dx.doi.org/10.1016/j.scitotenv.2023.163414
Received 2 January 2023; Received in revised form 5 April 2023; Accepted 6 April 2023
Available online 21 April 2023

Abatzoglou and Williams, 2016; McKenzie and Littell, 2017). In addition, increased vegetation density and connectivity brought about by a century of fire suppression further exacerbates the risk of high-severity wildfire (Miller and Safford, 2012; Parks et al., 2018; Parks and Abatzoglou, 2020). Many ecosystems, such as many temperate high-latitude regions in the western United States, did not historically evolve with frequent high-severity wildfire (Kelly et al., 2013). Predicting where wildfire is likely to impact ecosystems and species is of prime interest to both conservationists and managers (Bowman and Johnston, 2014).

The diverse ecosystems of California have been at the forefront of wildfire management in recent decades because few North American regions are more ecologically and economically affected by growing threat of larger and more severe wildfires (Hagmann et al., 2017; Steel et al., 2018). In 2020 alone, over 4 million acres of land burned in California, impacting human communities and ecosystems alike (California Department of Forestry and Fire Protection, 2022). The area burned by fire in California is projected to increase in the coming years (Littell et al., 2018; Wan et al., 2019), and a greater proportion of wildfires will likely burn at a high severity (Parks et al., 2018). The increasing risk of more frequent high-severity wildfires has the potential to impact many species' habitat, especially those that depend on old-growth forests, which is a primary management concern in the northwestern California region (USDA & USDI, 1994; USFWS, 2011; CALFIRE, 2021a).

The forests of northwestern California are home to some of the largest, most long-lived trees on the planet (Mooney and Zavaleta, 2016). Coastal redwoods (*Sequoia sempervirens*), the world's tallest trees which are found nowhere else on Earth, along with a variety of other large conifer species, provide an important source of timber, erosion control, and carbon sequestration due to their large amount of accumulated biomass (Cooperrider et al., 2000; Busing and Fujimori, 2005; Mooney and Zavaleta, 2016). These forests make up a distinctive part of a biodiversity hotspot known as the California Floristic Province (Mooney and Zavaleta, 2016; CEPF 2022). The forests provide habitat for a variety of endemic plants and epiphytes, which in turn moderate forest microclimates (Mooney and Zavaleta, 2016). The region also supports multiple at-risk wildlife species, including the Humboldt marten (*Martes caurina humboldtensis*), marbled murrelet (*Brachyramphus marmoratus*), and northern spotted owl (*Strix occidentalis caurina*; Mooney and Zavaleta, 2016). Many of these species rely on similar habitat characteristics found in northwestern California, which are now increasingly being transformed by large, severe wildfires.

The federally threatened northern spotted owl (hereafter NSO) relies heavily on forest habitat and has often been used as a proxy to identify forest conditions important to the survival of multiple other species in the region (USDA & USDI, 1994; USFWS, 2011; Lesmeister et al., 2019). Northern spotted owls are one of the world's most well-studied birds and have often been used as an indicator of structurally diverse forest habitat with mature trees, contiguous canopy cover, and variable tree heights, which they use for foraging, roosting, and nesting (USFWS, 2011; Sovern et al., 2019; Franklin et al., 2021). Historically, the primary threat to NSOs was habitat loss due to logging which resulted in population decline (USFWS, 2011). To protect NSO habitat, legislation like the Endangered Species Act and management policies like the Northwest Forest Plan mandate that logging activities be restricted within designated critical habitat (USDA & USDI, 1994; Lesmeister et al., 2019). Plans like the Northwest Forest Plan place a large focus on protecting NSO habitat, which is thought, in turn, to provide umbrella protection for other old growth forest-dependent species (USDA & USDI, 1994; Lesmeister et al., 2019). Despite reduction in habitat loss from logging in the past two decades, habitat loss from wildfires has increased markedly, and is widely regarded as a major current threat driving accelerated habitat loss (Clark et al., 2011; Rockweit et al., 2017; Wan et al., 2019).

The impact of higher-than-usual-severity wildfire on NSO nesting habitat is complex (Ganey et al., 2017). For example, high-severity wildfires, along with post-fire salvage logging, in southwestern Oregon caused a decrease in the amount of suitable NSO habitat (30–41%) below the amount thought to be required for maximizing NSO survival (Clark et al., 2011). Further, following a 2008 fire in northwestern California, the apparent post-fire survival of NSOs decreased and recruitment rates increased, suggesting that the wildfire caused a reduction in habitat quality that was unable to support NSOs over the long-term (Rockweit et al., 2017). However, there is also evidence that high-quality interior NSO nesting habitat can act as fire refugia, mitigating fire severity while nearby edge or non-nesting habitat burn more severely (Lesmeister et al., 2021).

The literature related to wildfire is also mixed when considering all three subspecies of spotted owl in North America, and the California spotted owl has the most wildfire related studies among the three subspecies (Ganey et al., 2017; Wan et al., 2018). Recent empirical studies have shown strong contrasts in the responses of California spotted owls to wildfire, which makes it difficult for managers to prioritize management efforts (Lee and Bond, 2015; Jones et al., 2016, 2020; Wan et al., 2020). For example, in the Sierra Nevada, following the King Fire occupancy of California spotted owls declined sharply at sites that burned with a greater proportion of high-severity wildfire (Jones et al., 2016), while occupancy of California spotted owls changed little following the Rim Fire (Lee and Bond, 2015). In the King fire, areas that burned with high-severity were larger and more contiguous than in the Rim fire, suggesting that the spatial pattern of severely burned areas could play a major role in determining how owls respond to wildfire (Ganey et al., 2017).

To assess wildfire risk to that habitat, we must first understand how a species selects habitat, which often varies across spatial scales and necessitates that we explicitly account for that variation in habitat models (Wiens, 1989; Levin, 1992; McGarigal et al., 2016). There have been no habitat suitability studies to date for NSOs that explicitly incorporate scales of effect, although there are studies that investigated scales of effect for other subspecies of spotted owl. For example, Mexican spotted owls (*S. o. lucida*) in southwestern United States forest habitat also exhibit a strong relationship with canopy cover and slope at smaller spatial scales while climatic covariates generally exhibited strong relationships at broader spatial scales (Wan et al., 2017). California spotted owls (*S. o. occidentalis*) also selected for high canopy cover at smaller and intermediate scales (Atuo et al., 2019). Similar research is needed for NSOs to understand the scale depended effects of environmental variation on habitat selection, which would focus targeted management efforts at scales that matter most for the species.

Spatial information regarding potential threats to biodiversity and habitat can facilitate conservation planning (Bowman and Johnston, 2014). As wildfires become a larger threat in many northwestern forests, prioritizing areas for management and conservation efforts can be facilitated by spatial fire risk assessments. By knowing where populations of a particular species are likely to experience a wildfire, managers can prioritize areas such as corridors (Khosravi et al., 2022) and habitat (Kaszta et al., 2020; Wan et al., 2020) that are important to a species' persistence on the landscape. However, to date there have been no landscape-scale fire risk assessments to identify areas of concern for NSOs along the redwood coast of California. Such assessments would be invaluable to managers' efforts to meet the goals of the Northwest Forest Plan more efficiently (USDA & USDI, 1994; Lesmeister et al., 2019).

In this study we investigated (1) where suitable nesting habitat exists for NSOs in northwestern California using a scale-optimization framework and (2) where severe wildfire is most likely to impact suitable NSO nesting habitat. We hypothesized that NSO nesting habitat along the coastal redwood forest is more at-risk of experiencing high-severity wildfire than nonhabitat. To accomplish this, we used scale-optimized habitat suitability ensemble modeling to identify suitable NSO nesting habitat in the redwood coast ecoregion of northwestern California. Then, we quantified the overlap between the predicted suitable nesting habitat and the Wildfire Hazard Potential (WHP) map to identify areas of habitat most at risk of wildfire in the near future (Dillon and Gilbertson-Day, 2020).

2. Methods

2.1. Study area

The study area consists of the Redwood Coast ecoregion (Level III Ecoregion 263a, Fig. 1), an area of approximately 16,500 km^2 dominated

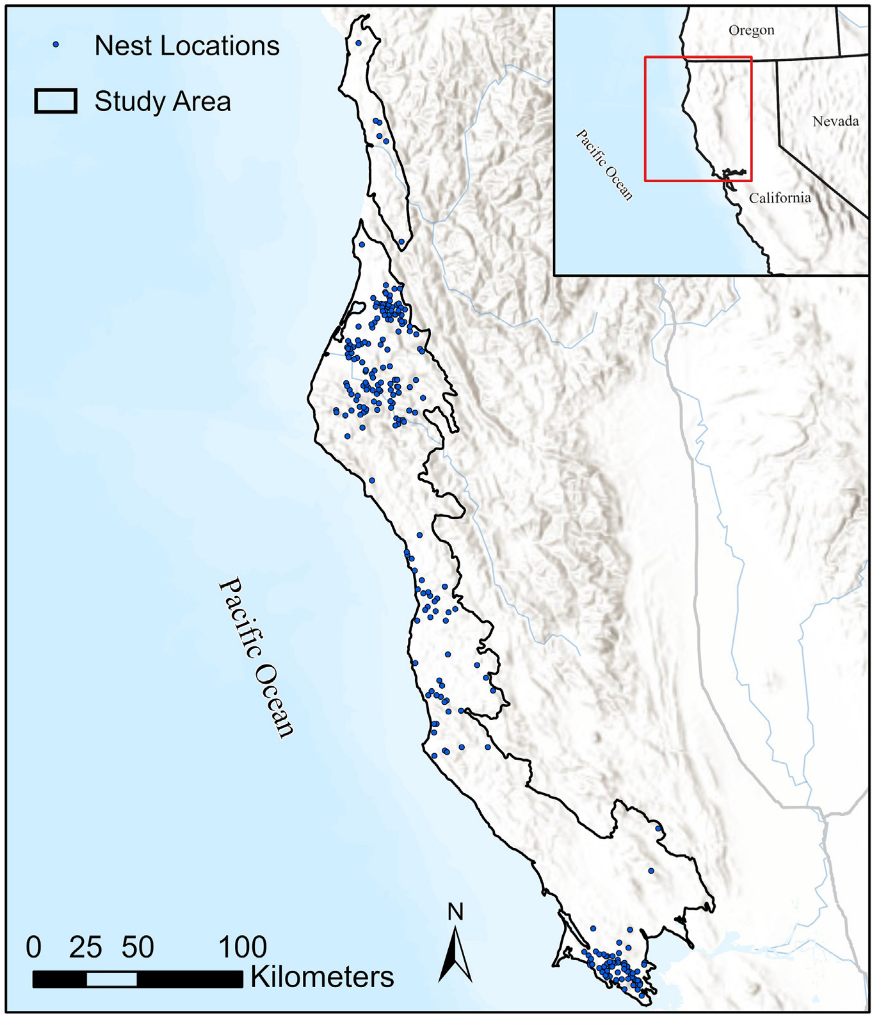

Fig. 1. NSO nest locations (n = 248) used to build the habitat suitability model within the redwood coast ecoregion (263a).
Sources: Esri, USGS, NOAA.

by redwoods and tall evergreen trees, interspersed with patches of broadleaf woodlands and coastal scrubland (USFS, 2017). A large proportion of the region consists of relatively young, second- or third-growth forest resulting from historical and present-day logging activities. Much of the region is also characterized by mild climatic conditions moderated by proximity to the Pacific Ocean, with northern latitudes generally experiencing more rainfall and slightly cooler temperatures than southern latitudes (Rupp et al., 2022). Elevation is also highly variable across the region, ranging from 0 m to 1650 m. Private and tribal ownership makes up 82% (13,413 km^2) of the land holding in the region, with the majority of the remaining land (18%; 2952 km^2) managed by the United States Forest Service, United States Fish and Wildlife Service, Bureau of Land Management, National Parks Service, and other state and local agencies.

2.2. Data collection

We used existing NSO nest data for uniquely identified pairs of owls from the California Department of Fish and Wildlife Spotted Owl Observation Database collected between 2015 and 2020 for our modeling (CNDDB Maps and Data, n.d.). Some owl pairs had multiple known nesting locations due to repeated survey efforts. To avoid pseudoreplication, we filtered the dataset so that we retained only the most recent nest location for each owl pair (n = 248).

We split the dataset into evaluation and training subsets prior to modeling, which is generally preferred when a completely independent dataset is unavailable for evaluation. We used a spatial blocking approach, implemented with the blockCV package in R (Valavi et al., 2019), to set aside 30% of the data (n = 72 presences) for evaluation and used the remaining 70% (n = 176 presences) for training models. We divided the study area into 25 equally sized blocks, each approximately 41 km × 41 km in size. We divided these blocks into five folds, attempting to keep the numbers of presences and background points roughly equal between folds (n = 24–72). Then, to obtain a dataset for the sole purpose of model evaluation, we set aside one fold and used the remaining four folds for cross-validation during model training.

2.3. Background point generation

Random background point generation has been found to produce the most accurate models in regression-based modeling approaches, whereas the generation approach has less of an impact on the accuracy of machine-learning modeling approaches (Barbet-Massin et al., 2012). Following recommendations from VanDerWal et al. (2009), we randomly generated background locations within a region created by subtracting a 1.3 km buffer around all nest locations from a 30 km buffer surrounding all nest locations. We used 30 km for the upper limit based on median dispersal ability for NSOs, which would limit artificial inflation of test statistics (USFWS, 2011), and 1.3 km for the lower limit based on average home range size in the region (Weisel, 2015). This created a set of 20,000 background points we could draw from when training individual models.

2.4. Environmental covariates

We collected a list of a priori predictor covariates potentially related to NSO habitat selection based on relevant literature, including composition (i.e., forest structure, land cover), topographic, and climatic covariates (USFWS, 2011; Dunk et al., 2019). We chose composition and climatic covariates from 2017 to reduce the risk of mischaracterizing the conditions present at a nest location, which could have resulted from events such as wildfire or logging. We obtained covariates from the Landscape Ecology, Modeling, Mapping, and Analysis Gradient Nearest Neighbor (LEMMA, GNN) project from Oregon State University (Ohmann and Gregory, 2002), Landscape Fire and Resource Management Planning Tools Project (LANDFIRE, 2017), and the Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate group at Oregon State University (Rupp et al., 2022). We calculated an additional three covariates, curvature, slope, and insolation, from a digital elevation model obtained from LANDFIRE using Spatial Analyst Tools in ArcGIS Pro Version 2.5 (Esri Inc, 2020). All covariates were then converted into raster data layers, projected into the NAD 1983/UTM 10N projection, and resampled to 30 m resolution if necessary. Table A1 in the Supplementary Material lists all 24 considered covariates.

2.5. Spatial autocovariate

Since spatial autocorrelation is a potential issue in any spatially explicit regression model, we checked for spatial autocorrelation using Moran's I and included a spatial autocovariate in each regression-based model. The calculation for this spatial autocovariate is given by Eq. (1), where y_i is the response value at j among i's set of k_i neighbors; and w_{ij} is the weight given to j's influence over i (Dormann et al., 2007). We used the “spdep” package (Bivand, 2022) in R (R Core Team, 2022) to perform the calculation.

$$y_i = \Sigma_{j=1}^{k_i} w_{ij} y_j \qquad (1)$$

2.6. Scale optimization and variable selection

We determined the optimal scale for each covariate through univariate testing across a range of biologically meaningful scales for each species (McGarigal et al., 2016). To do this, we conducted focal statistics on each covariate using a circular moving window of six radius scales: 100 m, 200 m, 400 m, 800 m, 1600 m, and 3200 m. We chose the maximum scale of 3200 m as it was approximately two times larger than the average home range size for NSOs in the region. Then, we extracted values from each scale for every covariate to the nest locations and randomly generated non-nest locations (i.e., background points). We performed the scale optimization this way because we were interested in the general pattern of scale-dependent selection (i.e., finer-scale vs broader-scale) rather than identifying specific scales.

To compare values extracted at nesting locations to background locations for each scale, we used two-tailed *t*-tests and selected the optimal scale as the one with a lower *p*-value, indicating a greater difference between nesting locations and background locations (Zeller et al., 2021). We repeated this for each covariate. To protect against multicollinearity in our models, we conducted a pairwise Pearson's correlation among covariates at their optimal scales. For any pair of covariates that had a correlation of $|r| > 0.7$, we chose to retain the covariate that showed a greater contrast between the values at nesting points compared to background points (smaller p-value).

2.7. Training and testing individual models

To identify suitable nesting habitat for NSOs, we built a multi-scale optimized habitat suitability model using an ensemble modeling approach with all covariates at their optimal scale (Mohammadi et al., 2022). The ensemble model was produced by weight-averaging six modeling approaches by their AUC-ROC using the biomod2 package in R (Thuiller et al., 2021). These approaches consist of two categories: regression-based and machine learning approaches. The regression-based approaches used in our modeling consisted of generalized linear models (GLM), generalized additive models (GAM), and multiple adaptive regression splines (MARS). Machine learning approaches used in our modeling consisted of random forest (RF), artificial neural networks (ANN), and Maximum Entropy (MaxEnt).

The number of background points used during model training can have a large impact on the performance of individual modeling methods (Barbet-Massin et al., 2012; Liu et al., 2019). Therefore, we decided to optimize the number of background points for training each individual model before ensembling them (Hysen et al., 2022). Briefly, we tested three different background point subsampling strategies (i.e., 1× presence, 10× presence, and 10k overall) from the total number of random background points generated to train each individual model, which we then evaluated against the evaluation dataset using the Area Under the Receiver Operating Characteristic Curve (AUC-ROC). This produced three models for each modeling method for a total of 18 models. For each modeling method, we compared AUC-ROCs between the three background point selections and selected the model with the highest AUC-ROC, leaving us with one model for each modeling method for a total of six models.

2.8. Ensemble modeling

We built the ensemble model by weight-averaging the six individual models, weighting each model by its AUC-ROC using biomod2 (Thuiller et al., 2021). We evaluated model performance using AUC-ROC and True Skill Statistic (TSS; Allouche et al., 2006). We chose a threshold for TSS that maximized the sum of sensitivity and specificity for all the component models and the ensemble model (Liu et al., 2013; Liu et al., 2016). Because we used presence-only data to train and evaluate our model, we also chose to evaluate the ensemble model with the Continuous Boyce Index, which is an evaluation metric suitable for use with presence-only data (Hirzel et al., 2006). To calculate the Continuous Boyce Index we split the predicted habitat suitability values into 50 overlapping bins and calculated the ratio of number of predicted presences in a bin to the number of presences that would be expected in a bin using the enmSdmX package in R (Smith, 2023). The Continuous Boyce Index returns values from negative one to one. Negative values indicate that the model predictions are not consistent with the true probability of presences, positive values indicate that the model predictions are consistent with the true probability of presences, and values near zero indicate the model does not perform any differently from random chance. We also evaluated covariate contribution to both the individual models and the ensemble model by making predictions where one variable was randomly permuted and comparing those predictions to predictions made where all variables were unchanged using Pearson's correlation coefficient, ρ (Thuiller et al., 2009). We then subtracted ρ from one. A higher relative value of 1-ρ indicates that the variable had a larger contribution than other variables to the model while a lower value indicates that the variable had less contribution to the model (Thuiller et al., 2009). In addition, we calculated and visually assessed response curves using the evaluation strip method outlined in Elith et al. (2005).

The ensemble habitat suitability model produced by this process is intended to provide a highly predictive but parsimonious scale-optimized model of nest site selection of NSOs that reduces biases inherent to the individual modeling methods it combines. We predicted the model spatially to create a map of baseline habitat suitability across the study area, with a value of 0 suggesting low habitat suitability and a value of 1 suggesting high habitat suitability.

2.9. Fire risk assessment and prioritization

We used the Wildfire Hazard Potential (WHP) map from the U.S. Forest Service's Rocky Mountain Research Station Fire, Fuel, and Smoke Science (FFS) Program to identify areas of potential wildfire impact risk to NSO habitat (Wan et al., 2019; Dillon and Gilbertson-Day, 2020). The WHP layer expresses the risk that a fire will occur in an area, and the risk that a given wildfire could exhibit fire behavior (e.g., torching, crowning) that would be difficult to contain with available suppression resources (Dillon and Gilbertson-Day, 2020). In addition to identifying areas that could exhibit extreme behavior, the WHP can also provide an indication of areas in need of fuels treatments (Dillon and Gilbertson-Day, 2020) and possibly indicate areas where fires exhibiting these behaviors could substantially affect NSO habitat. The WHP is expressed as an index with values ranging from 0 to 100,000, with higher values indicating greater risk of severe wildfire (Dillon and Gilbertson-Day, 2020). We used a discretized version of the WHP, with classes "very low" (0–61), "low" (62–178), "moderate" (179–489), "high" (490–1985), and "very high" (1986–100,000; Dillon and Gilbertson-Day, 2020). Hereafter, we will refer to these index ranges by their classifications defined above.

We binarized the habitat suitability map into "suitable nesting habitat" and "nonhabitat" using a threshold selected by maximizing the sum of sensitivity and specificity (Liu et al., 2013, 2016). Then, we quantified the amount of suitable nesting habitat and nonhabitat under low, very low, moderate, high, and very high risk of experiencing a difficult-to-contain wildfire should one occur (Dillon and Gilbertson-Day, 2020). Finally, to identify the areas of highest-quality nesting habitat at most at risk of experiencing a severe wildfire, we multiplied the discretized WHP layer with the ensemble habitat suitability map and standardized the output into z-scores. In effect, this assigned heavier weights to highly suitable habitat at a high/very high risk, while assigning lower weights to less-suitable habitat at a low/very low risk. We selected three z-score thresholds (i.e., 2, 2.5, and 3) to explore high-quality nesting habitat at a high risk of experiencing severe wildfire.

3. Results

Twelve environmental covariates were retained, in addition to the spatial autocovariate (Table 1). The scales of effect for each environmental covariate varied; compositional variables, like canopy cover, generally had finer scales of effect (≤800 m), climatic covariates, like average January precipitation, had coarser scales of effect (≥800 m), and topographic covariates generally had finer scales of effect (≤400 m; Table 1).

3.1. Northern spotted owl habitat

The predictive performances of the six component modeling approaches and the ensemble model were generally considered good or excellent when evaluated using AUC-ROC, with values ranging from 0.786 to 0.855 (Table 2). When evaluated using TSS, the predictive performance was generally considered moderate, with values ranging from 0.361 to 0.533 (Table 2). Some models showed consistently moderate-high nesting habitat suitability across the study area (e.g., ANN), while others showed more of a contrast between low and highly suitable habitat (e.g., MaxEnt; Fig. 2).

While the ensemble model did not have the highest performance metrics (random forest did), we chose to use it for further analysis because of its ability to correct for biases present in each of the component models (Araújo and New, 2007). In addition, ensemble models are generally less sensitive to the background sample used to train component models (Hysen et al., 2022). We used the ensemble model to spatially predict suitable nesting habitat for NSOs in the redwood coast ecoregion (Fig. 3). The ensemble model had a Continuous Boyce Index value of 0.85, indicating that the model predictions were consistent with the true probability of presences (see also Fig. A2 in Appendix A; Hirzel et al., 2006, Smith, 2023). The AUC-ROC and TSS of the ensemble model were 0.834 and 0.361, respectively (Table 2). Across the ecoregion, suitable nesting habitat largely follows valleys and is concentrated in the northern two-thirds of the study area, with some habitat in the southern region, the majority of which is concentrated in Marin County, California.

Table 1
Covariates kept for modeling after checking for correlation, including the scale of effect, covariate contribution to the ensemble model, the class (e.g., composition, topographic, climatic) and the data source for each covariate. Bold values indicate covariates that had an importance >0.05. Chosen covariates were originally used in USFWS (2011) and Dunk et al. (2019).

Covariate	Class	Scale (m)	Importance (1-ρ)	Source
Curvature	Topographic	400	0.0164	LANDFIRE
Elevation	Topographic	100	0.0288	LANDFIRE
Insolation	Topographic	400	0.0188	LANDFIRE
Slope	Topographic	400	**0.0919**	LANDFIRE
Canopy	Composition	100	**0.1141**	LEMMA GNN
Northern hardwoods	Composition	800	0.0037	LEMMA GNN
Oak woodland	Composition	200	0.0151	LEMMA GNN
Pine	Composition	800	0.0012	LEMMA GNN
January precipitation	Climatic	800	**0.0834**	PRISM
January temperature	Climatic	3200	0.0090	PRISM
July precipitation	Climatic	3200	0.0131	PRISM
July temperature	Climatic	3200	0.0142	PRISM
Auto covariate	–	–	**0.0523**	–

Table 2
The AUC-ROC and TSS for each individual model and the ensemble of models.

	GLM	GAM	MARS	MaxEnt	RF	ANN	Ensemble
AUC-ROC	0.793	0.786	0.819	0.799	0.855	0.808	0.834
TSS	0.424	0.464	0.470	0.533	0.499	0.405	0.361

3.2. Variable importance and responses

Three environmental covariates had a larger contribution to the ensemble model than other covariates (1-ρ > 0.05): canopy cover, slope, and average January precipitation (Table 1). Basal area of pine trees ("pine"), basal area of northern hardwoods ("northern hardwoods"), and mean January temperature ("January temperature") had low (1-ρ < 0.01) contributions (Table 1). No single covariate had a 1-ρ value >0.1141 (Table 1). Canopy cover was the most important environmental covariate for NSO nesting habitat selection (Table 1) and exhibited a positive relationship with nesting habitat suitability (Fig. 4). Slope was the second most important environmental covariate (Table 1), and exhibited a positive relationship with nesting habitat suitability, leveling off at a slope of approximately 15 degrees (Fig. 4). The third most important covariate was average January precipitation (Table 1), which showed a unimodal response to habitat suitability (Fig. 4). The remaining covariates had a mixture of positive, negative, and unimodal relationships with nesting habitat suitability (Fig. 3).

3.3. Fire risk analysis

We identified areas of suitable NSO nesting habitat and non-habitat at risk of experiencing a wildfire likely to exhibit extreme fire behavior. We found approximately 86.8 km^2 (6.3%) of suitable nesting habitat at a "very high" risk of fire exhibiting these behaviors, with 708.4 km^2 (51.9%) at a "high" risk, 308 km^2 (22.5%) at a "moderate" risk, 155.3 km^2 (11.4%) at a "low" risk, and 107.9 km^2 (7.9%) at a "very low" risk. For non-habitat, we found approximately 263.1 km^2 (7.0%) at a "very high" risk, with 1017.7 km^2 (26.9%) at a "high" risk, 737.1 km^2 (19.5%) at a "moderate" risk, 1120.9 km^2 (29.7%) at a "low" risk, and 639.1 km^2 (16.9%) at a "very low" risk. In summary, non-habitat is predicted to have a greater total but proportionally fewer areas with a "high" or "very high" risk than suitable nesting habitat (Fig. 5).

In suitable habitat, areas of high/very high wildfire risk are scattered across the study area, with the category of high risk mostly spread evenly (Fig. 5). Zooming in more closely, we see that most areas of high risk are interspersed with low or very low and moderate risk in the far southern reaches and just south of Humboldt Bay, although high risk is the predominant category (Fig. 5a, b). In nonhabitat, areas near the coast are generally at a very low, low, or moderate risk while areas further inland tend to be at a higher risk (Fig. 5).

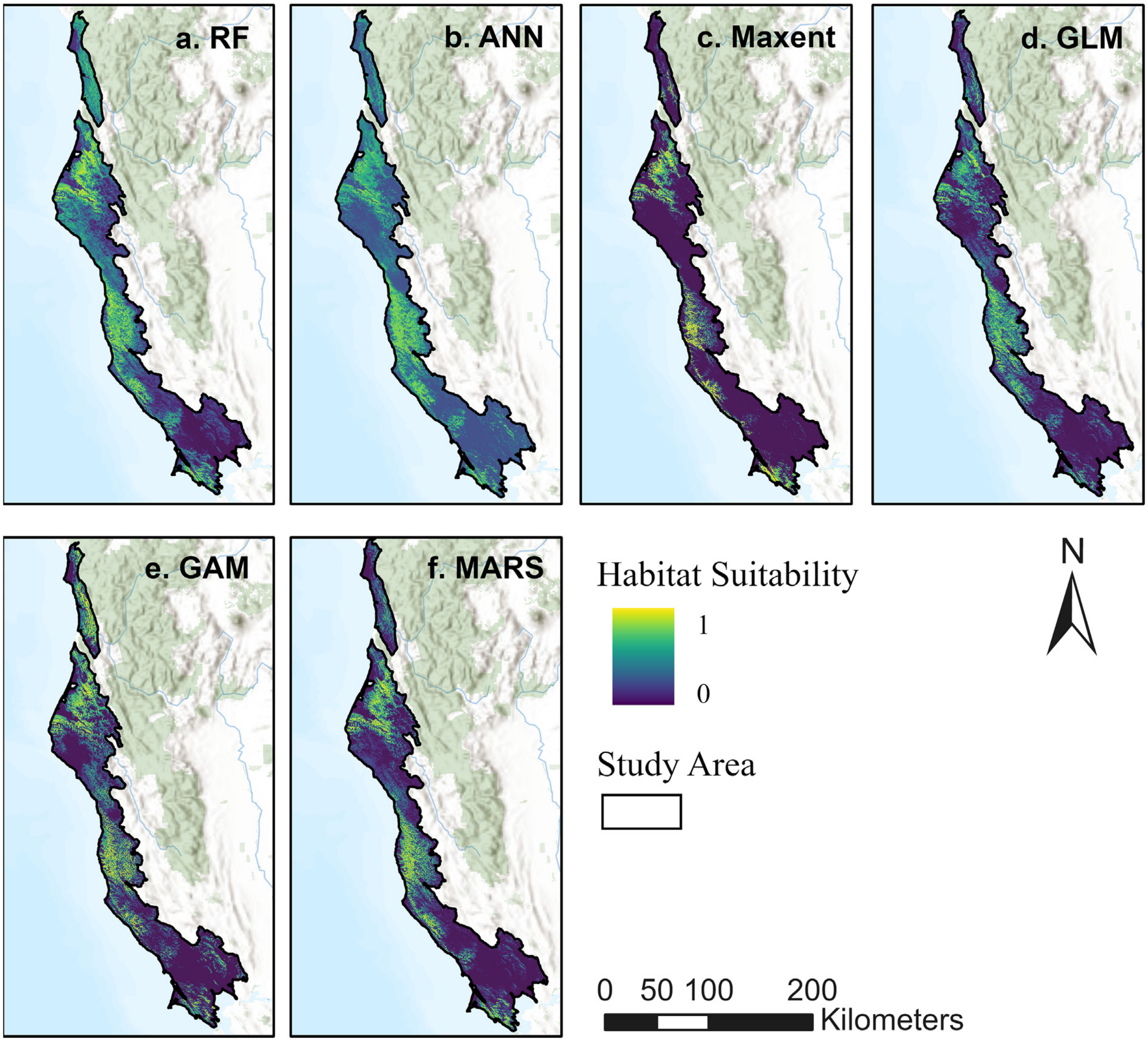

Fig. 2. Nesting habitat suitability maps for the redwood coast ecoregion (263a) using individual modeling approaches: (a) RF, (b) ANN, (c) MaxEnt, (d) GLM, (e) GAM, and (f) MARS.
Sources: Esri, USGS, NOAA.

We identified an area of 1027.5 km^2 of high-quality suitable nesting habitat at a high risk of experiencing a severe wildfire using a z-score threshold of $\sigma = +2$, 479.9 km^2 using $\sigma = +2.5$, and 96.2 km^2 using $\sigma = +3$. The areas identified using all three thresholds were concentrated in central Humboldt, Mendocino, and southern Marin County; they were located on a mixture of private and public lands (Fig. 6).

4. Discussion

4.1. Drivers of northern spotted owl habitat use

Our study presents the first scale-optimized habitat suitability model for NSOs, expanding current knowledge of habitat use by explicitly incorporating the scale of effect for each environmental relationship. Our model identified three environmental covariates (canopy cover, slope, and January precipitation) that are most important for NSO nesting habitat along the California redwood coast ecoregion. The relations of these covariates with habitat suitability as identified in our model are consistent with previous research on NSO nesting ecology in the region (LaHaye and Gutiérrez, 1999; Carroll, 2010; Sovern et al., 2019). Canopy cover was the most important covariate in our model. Northern spotted owls may select nesting habitat with a greater proportion of canopy cover since unfledged young are in a vulnerable state and parents need to maximize nesting success (Fig. 4). Areas with greater canopy cover typically have a more temperate microclimate (Jennings et al., 1999; Weathers et al., 2001) while providing protection against predators and adverse weather (Johnson, 1992). These benefits could be altered by high-severity wildfire, which could fragment the canopy, reducing canopy cover in the years following a wildfire (Karna et al., 2020).

January precipitation was also an important factor driving NSO nesting habitat use. Higher amounts of precipitation could decrease hunting efficiency and suppress prey activity, leading NSOs to prefer areas with more moderate amounts of precipitation during the winter (Franklin et al., 2000). As the climate changes the wet season in the region is expected to become shorter, with more rainfall occurring in more intense, frequent storms (Grantham, 2018). Further, a shorter, more intense wet season will likely lead to more summer droughts and a longer fire season (Grantham, 2018), expanding the window for high-severity wildfires to take place within NSO nesting habitat.

Similar to findings from LaHaye and Gutiérrez (1999), NSOs in the region also selected for areas with steep slopes. One plausible explanation for this behavior could be that areas with steeper slopes are less likely to have been harvested for timber in the past, supporting the presence of older trees capable of providing nesting structures for NSOs (Forsman and

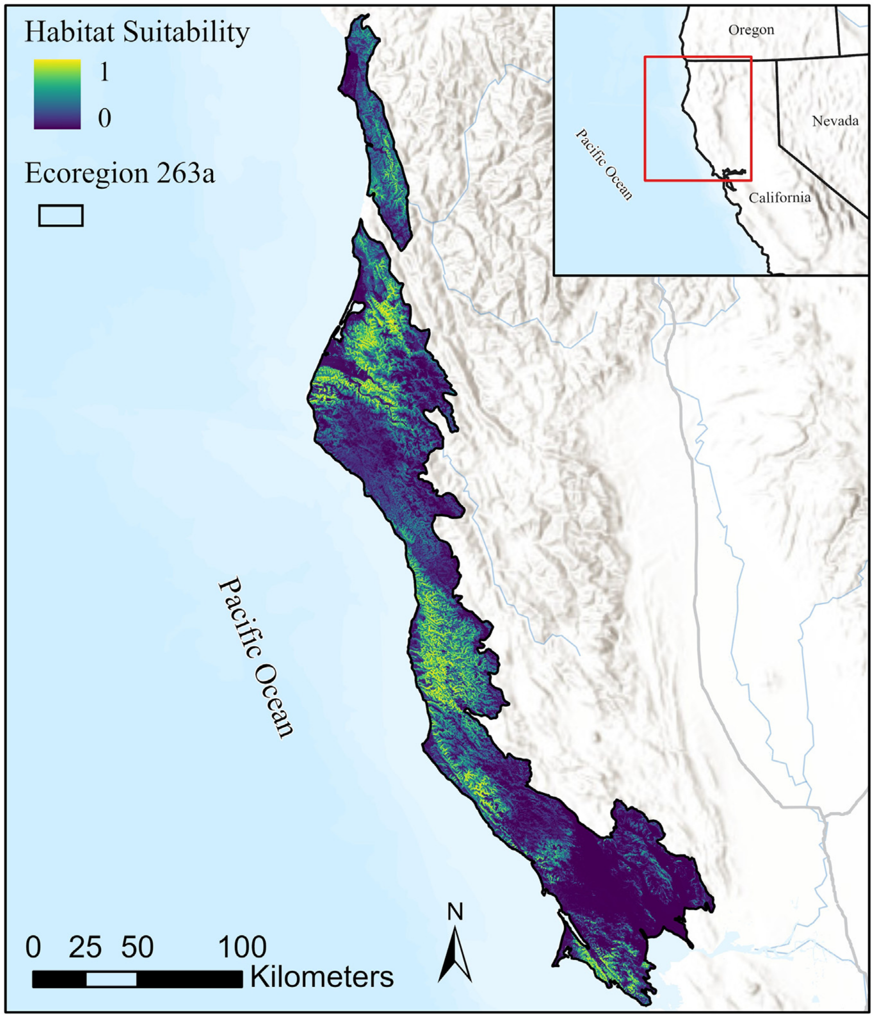

Fig. 3. Nesting habitat suitability map for the redwood coast ecoregion (263a) using the ensemble model.
Sources: Esri, USGS, NOAA.

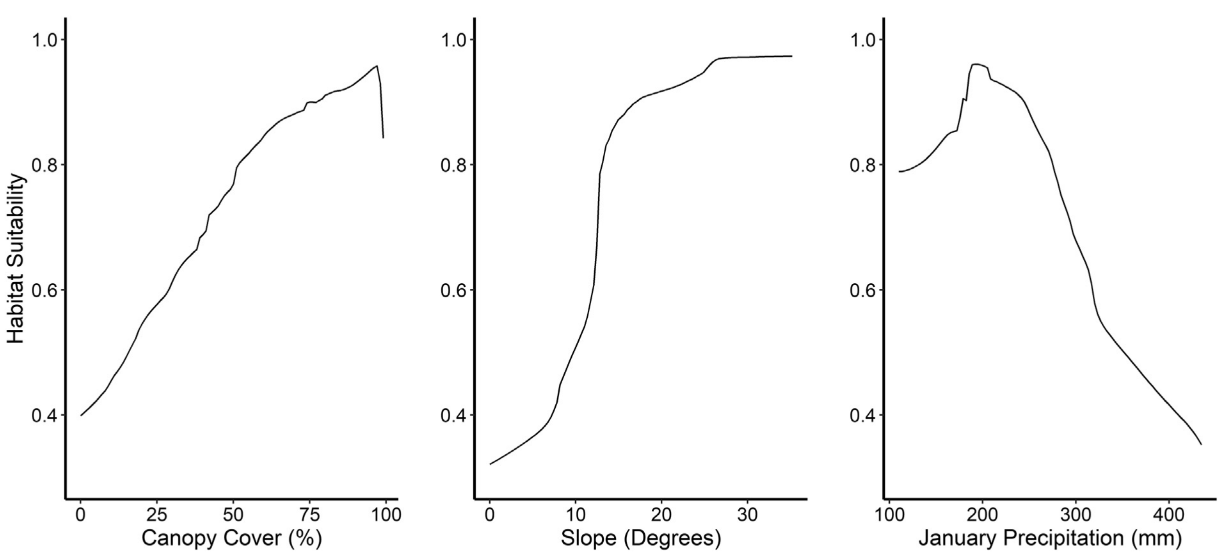

Fig. 4. Response curves for the three most important environmental covariates obtained by varying one covariate while holding the remaining covariates constant at their mean value in the ensemble model.

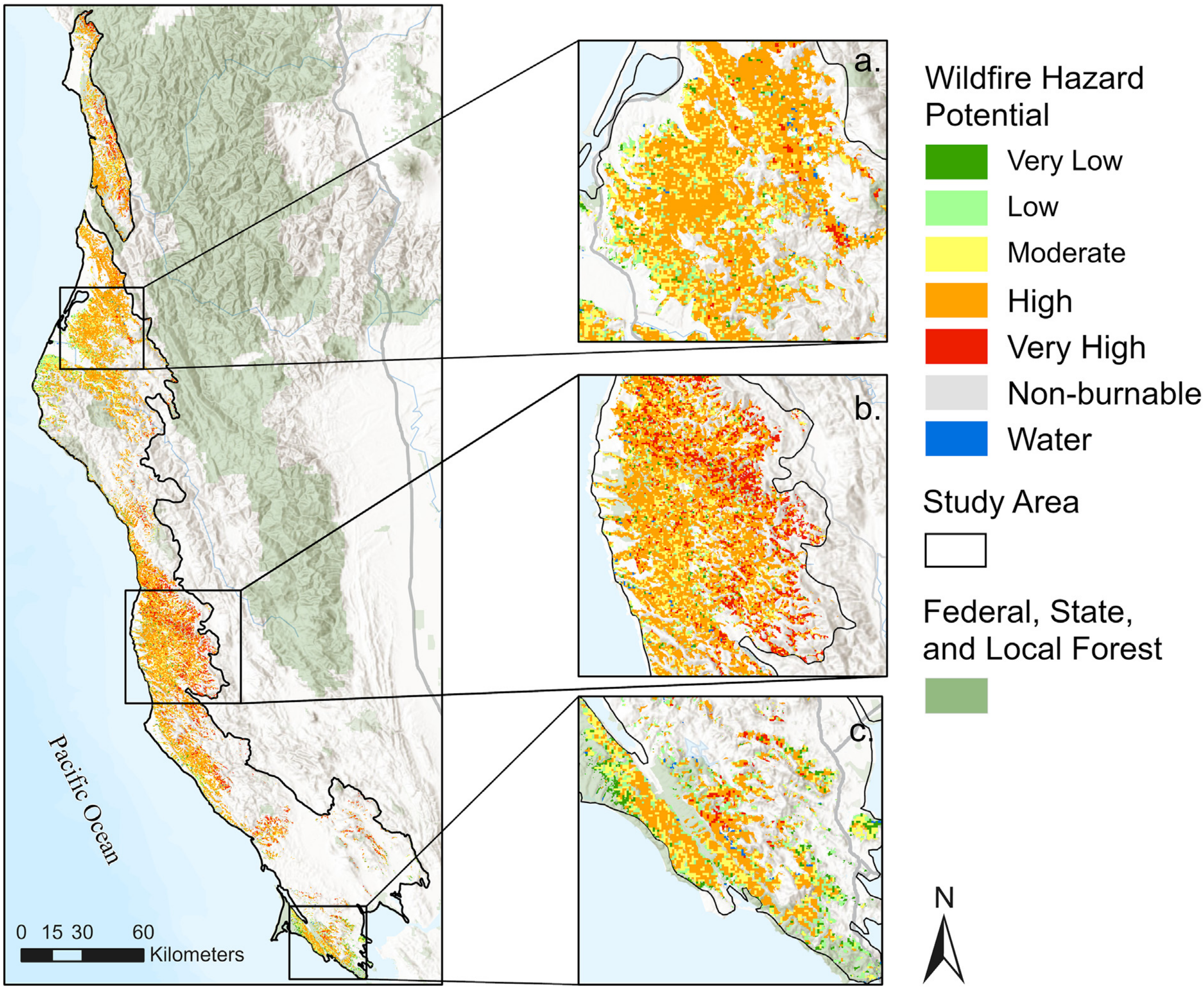

Fig. 5. Fire risk within suitable nesting habitat using the Wildfire Hazard Potential Index.
Sources: Esri, USGS, NOAA.

Giese, 1997; LaHaye and Gutiérrez, 1999). Further, studies in other parts of the NSO's range have not found a habitat association with slope (Buchanan et al., 1993; LaHaye and Gutiérrez, 1999). Thus, steep slopes may not necessarily be an ecological requirement for NSO nesting habitat (LaHaye and Gutiérrez, 1999). This could also be due to physiographic differences between the different regions where NSOs are found and reinforces the need to consider nonstationarity when modeling habitat (LaHaye and Gutiérrez, 1999; Wan et al., 2017; Dunk et al., 2019). While NSOs select steep slopes for nesting habitat in our study area, wildfire often travels up steeper slopes more quickly than less steep slopes due to preheating and more loosely packed burnable material (Butler et al., 2007). As a result, a preference for steeper slopes could place NSO nesting habitat at a greater risk of experiencing severe wildfire.

4.2. Variation in the scale of habitat selection across environmental covariates

Our model explicitly incorporates spatial scale and allows us to gain a more detailed understanding of how NSOs use habitat. We found that canopy cover and slope were most important at finer spatial scales (Table 1). This suggests that NSOs select nesting locations with high canopy cover and steep slopes near the nesting structure, possibly because these habitat qualities nearby nests make it more difficult for predators to see or reach the nests (Sovern et al., 2019). In addition, higher canopy cover contributes to a more temperate microclimate, which generally occurs at a fine scale and can result in hospitable conditions for raising young (Weathers et al., 2001). Moreover, LaHaye and Gutiérrez (1999) showed that NSOs select lower portions of slope probably due to the better productivity and the availability of large trees and forest structure required for NSO nesting.

January precipitation and other climatic covariates were most important at broader spatial scales (Table 1), suggesting that BSO respond to climatic conditions over a wider area compared to structural and topographic elements of the landscape. Northern spotted owls typically hunt throughout their home range, not necessarily directly near the nesting structure (USFWS, 2011). Therefore, higher precipitation throughout the home range during the wet season could contribute to reduced hunting success and therefore reduced survival and fecundity (Franklin et al., 2000). However, the lack of a pattern at finer spatial scales could also be due to a lack of fine-scale climate data in the region. By including each environmental covariate at its scale of effect, we were able to effectively elucidate important species-habitat relationships, identify areas of suitable NSO nesting habitat, and then identify where that habitat is most at risk of experiencing a severe wildfire.

4.3. Habitat at risk of wildfire

Consistent with our hypothesis, more areas of suitable habitat are at a high or very high risk of severe wildfire than nonhabitat. When compared to areas of nonhabitat, this suggests that the habitat NSOs rely on for nesting could be among the most heavily impacted by future wildfire. This might seem contradictory to recent findings that old-growth NSO habitat acts as fire refugia (Lesmeister et al., 2021), although many NSO nests in our study were not located in old-growth forests. Old-growth forest is

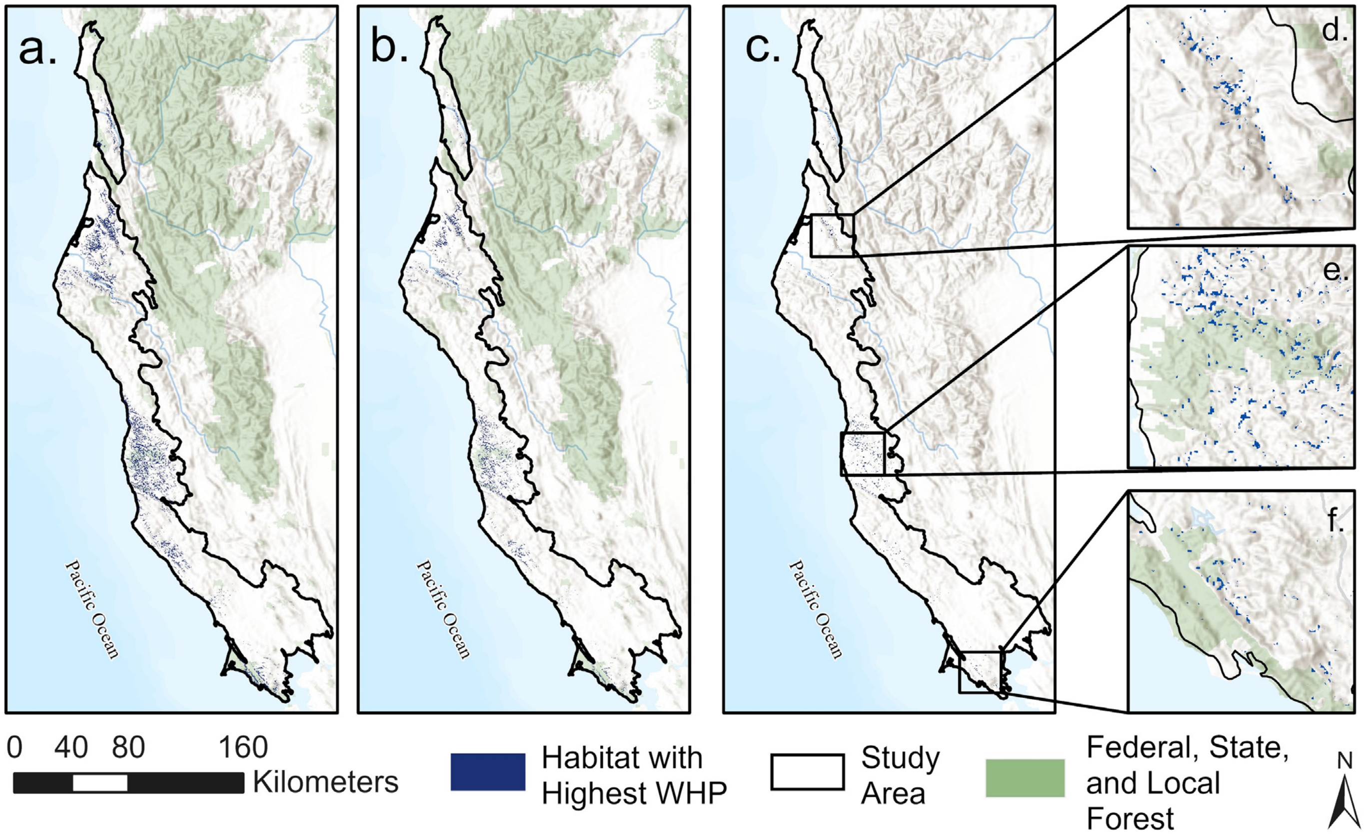

Fig. 6. Highly suitable habitat at the most risk of experiencing a severe wildfire using three z-score thresholds, (a) σ = +2, (b) σ = +2.5, and (c) σ = +3. We identified three general areas for further attention based on the amount of highly suitable habitat at risk: (d) the Maple Creek area, mostly consisting of private land, (e) the Jackson State Demonstration Forest area, mostly state-owned land, and (f) Point Reyes National Seashore area, mostly consisting of federally owned and private land.
Sources: Esri, USGS, NOAA.

relatively rare in our study area, with <5% of old-growth redwood stands in particular remaining (Mooney and Zavaleta, 2016). Northern spotted owls are commonly found in younger forests here than in other parts of their range since redwoods are typically larger and taller than other tree species and forests in northwestern California are highly productive (Thome et al., 1999; Mooney and Zavaleta, 2016; Lesmeister et al., 2021). As a result, younger redwood stands could possibly provide suitable nesting structures equivalent to old growth stands of other species. This is also true of areas focused on in Fig. 5a, b, and c that represent a large proportion of suitable nesting habitat (Fig. 6). Given that there is a consistently high or very high risk of severe wildfire across a high proportion of suitable nesting habitat, we suggest that these areas are prime candidates for prioritizing future study and management attention.

There are several management actions that can be taken to reduce wildfire risks in the high priority forests as identified by our models. One action that has been shown to effectively mitigate wildfire risk is thinning (Roberts and Harrington, 2008), although this is often more effective in dry forests that typically burn frequently (Agee and Skinner, 2005). Thinning is also a widely employed technique for removing dead and small-diameter trees, which generally reduces forest density and removes fuel that might lead to large and severe wildfires (Mooney and Zavaleta, 2016). Thinning is suggested to improve NSO foraging habitat quality, increasing the density and abundance of prey species (Dodson et al., 2008; Irwin et al., 2015). As for nesting habitat, thinning has been suggested to shorten the time required for development of favorable NSO nesting structure in forest stands (Andrews et al., 2005). However, thinning has also been suggested to reduce habitat quality for California spotted owls, both in the short- and long-term (Tempel et al., 2015; Bond et al., 2022). Therefore, we recommend careful planning and small-scale experimental studies be conducted when selecting sites for thinning.

Actions like the installation of fuel breaks, which can slow the spread of wildfire near important resources such as habitat for at-risk species, can also be used and provide an alternative to direct impacts on NSO nesting habitat (Syphard et al., 2011). Prescribed burning, historically used by indigenous communities prior to European colonization (Lorimer et al., 2009), is another approach that is effective at reducing fuel loads in treated areas (Cowman and Russell, 2021). In dry forests, careful prescribed burning promotes the dominance of large fire-resistant trees and increases heterogeneity in closed-canopy forests, which is suggested to reduce habitat availability for NSOs in the short term while improving the resiliency of these forests over the long-term (Stephens et al., 2019). However, highly restrictive government regulations, high investment in fire suppression, and underfunding of prescribed fire have limited its implementation (Marks-Block and Tripp, 2021). While these approaches are generally effective at reducing the risk of high severity wildfire, there is limited information on how species like the NSO respond to treatment; thus, these procedures require careful implementation and research (Wan et al., 2018).

This study provides crucial information regarding spatial patterns of suitability and wildfire risk for a threatened species at a pivotal time. The management of the publicly owned forests within our study area is governed by various forest plans, which were amended by the Northwest Forest Plan in 1994 with the express purpose of protecting NSO habitat while maintaining a sustainable forest products industry (USDA & USDI, 1994; Lesmeister et al., 2019). These plans are currently undergoing revision as required by the National Forest Management Act (NFMA) of 1976, which requires that Forest Plans be revised every 10–15 years based on changing conditions, trends, and new science. The role of fire in northwestern forests is a major consideration in this revision process and will continue to have a major impact on forest management over the next decade. The timely information provided in this study will aid in the revision process by helping to identify areas of concern for a key species in the forest plans and ultimately help create more robust, accurate plans that influence much of the forests and other species associated with these forests in the region.

The three areas of high fire risk and highly suitable nesting habitat encompass large tracts of land that are under a mosaic of different ownerships. The northern-most focal area is the Maple Creek area of Humboldt County, which is mostly composed of privately held land (e.g., timber companies). In this area, the NSO nesting habitat most at risk of experiencing severe wildfire mostly follows the Mad River Valley, an area with steeper slopes than much of the surrounding terrain. The focal area in the central part of the study area consists of land within and around the state-owned Jackson State Demonstration Forest near the coast. Here, the habitat at risk of experiencing severe wildfire is more dispersed across the landscape rather than being confined to a single valley. Finally, the southernmost focal area consists of land within and nearby Point Reyes National Seashore, which is federally owned. This area has relatively mild climatic conditions as a result of its proximity to San Francisco Bay, and the areas that are most at risk of experiencing a severe wildfire are set back from the coast.

Future studies in these areas should consider the effect of different management strategies on wildfire impacts to NSO habitat. Since these areas have quite different land ownership patterns, it is intractable to implement one-size-fits-all conservation and management actions (Daley et al., 2004). For example, the Northwest Forest Plan put into place similar management requirements across federally owned lands in the Northwestern United States and was quite successful at restoring habitat for NSOs (USDA & USDI, 1994). However, this plan did not apply to state-owned lands or privately-owned lands (USDA & USDI, 1994). Since the NSO is listed by the Endangered Species Act, the federal government does play a role in its management on non-federal lands, but private land regulation is limited and varying. For example, landowners and managers may have different attitudes toward wildfire and listed species like the NSO, which could impact management priorities (Bruskotter et al., 2018; Ghasemi et al., 2020). This necessitates clear communication and collaboration between the different management entities and stakeholders to design cross-boundary management approaches for wildfire and endangered species management, allowing all voices to be heard and come to a concrete solution.

4.4. Complicated future for northern spotted owls

As Pacific Northwest summers become hotter and drier as a result of climate change, wildfires are predicted to increase in extent and severity (Fried et al., 2004; Westerling et al., 2011; Littell et al., 2018). As a result, larger and more contiguous areas of a wildfire's footprint could burn at a high severity (Ganey et al., 2017). However, it is still unclear how many species, such as the NSO, respond to wildfire or could be at risk of wildfire across their ranges. In addition, forests recently burned by high-severity wildfire in northwestern California are thought to be avoided by barred owls (*Strix varia*), an invasive generalist species that outcompetes NSOs where their ranges overlap (Duchac et al., 2021). As a result, barred owls may be more likely to settle in unburned areas, which are also thought to be preferred by NSOs (LaHaye and Gutiérrez, 1999; Sovern et al., 2019; Duchac et al., 2021). More research is needed to understand how barred owls respond to wildfire and how this could impact NSO populations moving forward. More research is needed to understand how other species in the region respond and how management can best address wildfire impacts, especially on species of conservation concern and their habitats.

5. Conclusions

The extent and severity of wildfire activity is increasing across the western United States, potentially altering the habitats of many species (Bowman and Johnston, 2014; Littell et al., 2018; Wan et al., 2019; Parks and Abatzoglou, 2020). Spatially explicit information from multi-scale habitat selection models has been increasingly used to aid species conservation and management and can pinpoint where habitat and its associated features are most at risk (Macdonald et al., 2019; Khosravi et al., 2022). We found that suitable nesting habitat identified for NSOs, which often corresponds with unique forest habitat in northwestern California, was at a higher risk of experiencing a severe fire than nonhabitat. We used this information to identify three areas of suitable habitat in northwestern California most at risk of experiencing a severe wildfire and suggested prioritizing them for management actions to mitigate the severity of future wildfire. We stress that wildfire does not always have negative impacts; in fact, many terrestrial ecosystems are adapted to a historical fire regime (Agee, 1996; Bond and Keeley, 2005). However, rapid increases in fire size, frequency, and severity could alter this balance (Kasischke and Turetsky, 2006; Abatzoglou and Williams, 2016; McKenzie and Littell, 2017; Wan et al., 2020). Since resources to manage and conserve at-risk species are often limited, the spatially explicit information we provide can help prioritize areas for more effective planning. This could be examined further in future studies by optimizing the implementation of wildfire management strategies across the landscape that also preserve biodiversity, provide habitat for at-risk species, and promote multifunctional landscapes (Law et al., 2017; Iglesias et al., 2022). In addition, while the spotted owl is often considered an indicator species for other old-growth forest species, we believe there is value in considering multiple species in future studies when examining tradeoffs between different wildfire management approaches and their impacts to ecosystem services like habitat provisioning or human well-being (Regos et al., 2018). Lastly, we emphasize the importance of considering multiple spatial scales when evaluating habitat suitability and quantifying impacts of disturbances in order to make appropriate management decisions for NSOs and other forest-dependent species (Wan et al., 2020).

CRediT authorship contribution statement

Logan B. Hysen: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Samuel A. Cushman:** Writing – review & editing. **Frank A. Fogarty:** Writing – review & editing. **Erin C. Kelly:** Writing – review & editing. **Danial Nayeri:** Writing – review & editing. **Ho Yi Wan:** Conceptualization, Data curation, Methodology, Writing – review & editing.

Data availability

The authors do not have permission to share data.

Declaration of competing interest

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

Acknowledgments

This research was supported by a Joint Venture with the USDA Forest Service, Sponsor Award # 20-JV-11221633-152. We thank the California Department of Fish and Wildlife for making northern spotted owl data available through the Spotted Owl Observations Database (SPOWDB). We thank the people from California Department of Fish and Wildlife, the United States Forest Service, Green Diamond Resource Company, and more who collected the data for their hard work and dedication. Maps were created using ArcGIS® software by Esri. ArcGIS® and ArcGIS Pro™ are the intellectual property of Esri and are used herein under license.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.163414.

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