California Spotted Owl Passive Acoustic Monitoring Program: Final Annual Report (2021–2024)

Jason M. Winiarski[1], Sheila A. Whitmore[1], Jonathan P. Eiseman[1], Erin C. Netoskie[1]
Matthias E. Bieber[1], H. Anu Kramer[1], Kevin G. Kelly[1], Connor M. Wood[2]
Kate A. McGinn[1], Stefan Kahl[2], Holger Klinck[2], and M. Zachariah Peery[1]

[1]*Department of Forest and Wildlife Ecology, University of Wisconsin - Madison*
[2]*K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University*

Submitted to:

US Forest Service Region 5: Pacific Southwest Region
1323 Club Drive
Vallejo, CA 94592

March 2025

Executive Summary

The California spotted owl (*Strix occidentalis occidentalis*) is associated with mature forests and has resided at the center of forest management planning for several decades in the Sierra Nevada. In 2021, population monitoring transitioned from intensive demographic surveys in local study areas to passive acoustic surveys conducted across much of the Sierra Nevada bioregion. Here, we report on patterns in California spotted owl site occupancy (i.e., the probability of a spotted owl occurring within a grid cell, after correcting for imperfect detection) for the first four years of passive acoustic surveys, 2021–2024. Key accomplishments and findings include:

- In 2024, we deployed 1,506 autonomous recording units (ARUs) across our study area, which encompasses seven national forests and nearly all suitable California spotted owl habitat on the western slope of the Sierra Nevada (Figure 1). ARU deployments occurred from early April to early August, with each ARU recording audio data over approximately five weeks.
- Weekly detection probability in 2024 (0.62) was lower than in previous years (Figure 4c), but the probability of detecting a spotted owl over a typical 5-week ARU deployment remained high (0.99).
- California spotted owls were widespread across the Sierra Nevada (Figure 2), and were most likely to occupy low-to-middle elevation sites with high canopy height that had experienced minimal high-severity wildfire (Figure 5).
- Colonization and extinction processes–which drive changes in annual site occupancy probability–were strongly affected by high-severity wildfire. As the proportion of a site burned at high-severity increased, colonization probability decreased and extinction probability increased (Figure 6). Accordingly, we found greater declines in occupancy for sites burned at $\geq$ 50% by high-severity wildfire compared to sites that burned at < 50% or had not experienced high-severity wildfire (Figure 9).
- Occupancy was lowest in Lassen National Forest (ψ_{2024}: 0.15), and highest in Stanislaus National Forest (ψ_{2024}: 0.46). Sierra Nevada-wide occupancy in 2024 was 0.28 (Figure 7).
- Trends in occupancy by national forest from 2021–2024 were variable: three forests showed a negative net change in occupancy ($\overline{\lambda}$: 0.86–0.92), two showed a positive net change in occupancy ($\overline{\lambda}$: 1.11–1.13), and two showed an uncertain net change in occupancy (λ: 0.98–1.02). We found with 83% certainty that California spotted owl occupancy was declining region-wide, and the annual rate of decline was 2% ($\overline{\lambda}$: 0.98; CRI: 0.93–1.02; Figure 8).
- The proportion of sites occupied by barred owls (*S. varia*; a dominant competitor with spotted owls) was very low (< 1% of surveyed cells in 2024), with nine or fewer occupied cells in each year from 2021–2024. Barred owls were detected in six cells on four national forests in 2024: Plumas, Lassen, Eldorado, and Sierra (Figure 2).

Collectively, these results highlight the feasibility of our passive acoustic monitoring program to 1) robustly estimate initial occupancy, colonization, and extinction processes driving California spotted owl occupancy dynamics, 2) detect the effects of severe wildfire on these ecological processes, 3) provide reliable trends in annual occupancy, and 4) assess the efficacy of barred owl removal efforts in the Sierra Nevada.

Table of contents

Cover photo: California spotted owl (*Strix occidentalis occidentalis*) by Danny Hofstadter

1 Background

The California spotted owl (*Strix occidentalis occidentalis*) is a territorial species associated with mature and old-growth forest that has resided at the center of forest management planning for several decades in the Sierra Nevada. California spotted owls are threatened, or potentially threatened, by a suite of anthropogenic and environmental factors. First, increasingly large, severe fires are causing localized losses of forest cover driving potentially decadal population declines in those areas (Jones et al. 2016, Jones et al. 2021). Second, forest management practices such as historical harvesting of large trees appears to have caused population declines in some but not all areas (Conner et al. 2013, Tempel et al. 2014b, Roberts et al. 2017), while suppression of historical disturbance regimes has reduced landscape heterogeneity, which can promote resource availability and provide energetic and reproductive benefits to spotted owls (Hobart et al. 2019, Zulla et al. 2022, Kuntze et al. 2023). Third, the barred owl (*S. varia*), a competitively dominant invasive species, which is in the process of driving northern spotted owls (*S. o. caurina*) extinct (Franklin et al. 2021, Wiens et al. 2021), has invaded the range of the California spotted owl and recently entered a rapid growth phase in the northern Sierra Nevada (Wood et al. 2020). The invasion motivated a lethal removal experiment in 2018 that, as of 2021, reduced barred owl densities across the Sierra Nevada (Hofstadter et al. 2022). Fourth, although population-level effects are unknown, the California spotted owl is widely exposed to environmental toxicity via anticoagulant rodenticides (Hofstadter et al. 2021). Fifth, rising temperatures driven by climate change will subject California spotted owls to increasing thermal stress (Weathers et al. 2001), which has potential implications for adult survival and reproduction (McGinn et al. 2023).

Concern over the status of California spotted owls has key implications for forest management activities intended to reduce forest fuels and curb increasingly large and severe wildfires. While reducing severe wildfire activity could reduce losses of suitable spotted owl habitat, fuels management activities have the potential to simplify the complex forest structure that spotted owls use for nesting and roosting. At the same time, the absence of disturbance can lead to forest homogenization, another form of simplification that can negatively impact habitat quality. Accordingly, there is an acute need to monitor the effects of fuels management on California spotted owls, particularly as natural resource agencies attempt to increase the pace and scale of forest restoration activities across the Sierra Nevada.

Since the late 1980's and early 1990's, California spotted owl populations have been monitored via four local demographic study areas in the Sierra Nevada (Tempel et al. 2016, Jones et al. 2018). These studies, while providing important insights regarding population trends and factors affecting populations at local scales, were not designed to monitor the subspecies at a bio-regional scale. Accordingly, trends in spotted owl populations across the Sierra Nevada are unknown, as are the relative impacts of environmental stressors and management activities (e.g., fuels reduction treatments) on the overall population.

Passive acoustic monitoring (PAM) is becoming an increasingly common approach for population assessments because it can enable broader and more continuous coverage than conventional, in-person surveys (Shonfield and Bayne 2017, Darras et al. 2018, Sugai et al. 2019). PAM involves deploying autonomous recording units (ARUs) to record acoustically

active species and extracting target signals from the audio data. Animal sounds identified in PAM data can then be readily adapted to detection/non-detection data that can, in turn, support occupancy modeling. The large sample sizes enabled by large-scale PAM projects can yield high statistical power to detect even small changes in occupancy over space and time (Wood et al. 2019). As a result, there is great potential for PAM to support population trend assessments at greater spatial scales than has previously been possible. Accordingly, in 2021 we initiated a PAM program to begin monitoring the subspecies across all seven national forests on the west side of the Sierra Nevada (Kelly et al. 2023).

2 Objectives

Here we report the results of the first four years (2021–2024) of passive acoustic monitoring for both California spotted owls and barred owls in the Sierra Nevada. Our primary objectives were to estimate site occupancy dynamics for California spotted owls and understand how site occupancy varies geographically (e.g., among national forests) and as a function of environmental variables, such as severe wildfire history. A secondary objective was to assess whether barred owl site occurrence remains low in the Sierra Nevada following the initiation of a lethal removal study in 2018 and less intensive removals conducted since 2020.

3 Methods

3.1 Study area

We conducted passive acoustic surveys as part of an ongoing, long-term effort to monitor California spotted owls (and the broader avian community) across 3,254,810 ha of foothill and montane forest in eastern California, USA (Figure 1). Our study area encompassed portions of seven national forests within the Sierra Nevada and Southern Cascades ecoregions (hereafter, Sierra Nevada), and ranged from 226–3,985 m in elevation. As the sampling design was optimized for monitoring California spotted owl populations, our study area consisted primarily of mixed-conifer forest on the western slope of the Sierra Nevada (Kelly et al. 2023), where most spotted owl habitat occurs (Verner et al. 1992). This region is characterized by a Mediterranean climate, with warm/dry summers and cool/wet winters, and tree species adapted to frequent, low- to moderate-severity fire including Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), and hardwoods such as black oak (*Quercus kelloggii*; North et al. 2016). The Sierra Nevada has recently seen an increase in the scale and severity of forest disturbance events (Stephens et al. 2022, Ayars et al. 2023), resulting in extensive habitat degradation and loss for older forest species such as California spotted owls. For example, Steel et al. (2023) found a rapid, 30% decline in mature forest habitat in the southern Sierra Nevada between 2011–2020 due to a combination of high-severity wildfires, drought, and drought-associated beetle attacks associated with a warming climate.

3.2 Acoustic sampling

We divided our study area into 8,087 400-ha hexagonal grid cells, which approximates spotted owl territory size in this region (Tempel et al. 2014a). From these, we randomly selected cells for passive acoustic surveys if: 1) they did not intersect highways, 2) were $\leq$ 50% water, and 3) were accessible from a road. Thus, we excluded cells within particularly steep and wilderness areas, but these accounted for < 5% of candidate cells (Kelly et al. 2023). We also avoided surveying adjacent cells to reduce the possibility of double-counting owl territories (Wood et al. 2019).

We typically deployed two ARUs (range = 1–4; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology Center, Ithaca, NY, USA) in each selected cell. To maximize sound quality and detection, ARUs were deployed at mid-slope and ridgetop locations with optimal sound propagation, away from roads and streams, and secured to small-diameter trees at a height of 1.5–2 m above the ground. When possible, we deployed ARUs $\geq$ 500 m apart and $\geq$ 250 m from cell borders (Figure 1). If a cell overlapped a spotted owl protected activity center (PAC; 121 ha area of high-quality habitat around historic spotted owl nest and roost sites), then we attempted to deploy at least one ARU inside the PAC; otherwise, deployments were made without prior knowledge of owl occupancy. Once selected, we aimed to monitor cells and ARU locations within cells for multiple years, unless access issues such as road closures prevented us from returning to these sites. ARUs were equipped with one omni-directional microphone with -25 dB sensitivity, and recorded from 18:00–09:00 Pacific Daylight Time (PDT) at a sample rate of 32 kHz, 16-bit resolution, and +33 dB gain. With these settings, it was possible to collect audio data continuously over a ~5-week period per ARU deployment. Deployments began in early April, with the latest recordings occurring in early August.

3.3 Spotted and barred owl identification in acoustic data

We subset the raw audio data from 20:00–06:00 PDT (i.e., a "survey night"), when spotted owls are most vocally active (Reid et al. 2022). To identify spotted and barred owl vocalizations in passively recorded audio, we used BirdNET, a deep neural network designed to automate call classification for >6,000 species globally, most of them birds (Kahl et al. 2021, Wood and Kahl 2024). We used a customized version of BirdNET specifically tailored to our PAM program and capable of classifying the spotted owl's "four-note", "contact", "crow bark", "monkey hoot", and juvenile begging calls, and the barred owl's "eight-note" (or "who cooks for you") and "hoo-aw" calls. BirdNET analyzes audio data in 3-second segments, generating a "confidence" score ranging from 0–1 for each call type in a segment. While resembling probabilities, confidence scores are a unitless expression of the algorithm's predictive accuracy for a given classification, but are generally positively related to each other (Wood and Kahl 2024). Audio data were processed with BirdNET via the command line and Amazon Cloud Computing.

Following Kelly et al. (2023), we used a confidence score threshold of 0.989 for all spotted owl call types, and 0.970 for barred owl vocalizations to identify BirdNET predictions as potential detections requiring manual validation. While this process may miss individual calls that fall

below these thresholds, spotted and barred owl presence can be reliably confirmed because detection probabilities remain high over the entire sampling period (Kelly et al. 2023). We then manually validated all putative spotted and barred owl detections using Raven Pro sound analysis software (K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology Center, Ithaca, NY, USA); this was necessary to 1) obtain accurate presence data, which are important for coordinating barred owl removals and informing forest management activities that could affect spotted owl habitat quality, and 2) eliminate false-positive errors, as even moderate incidences of false-positives can severely bias occupancy and covariate estimates (Berigan et al. 2019, Clare et al. 2021). In our study system, false-positives can occur when non-target sounds are misclassified as a spotted owl (e.g., dog barks, cowbells), or when calls broadcast during spotted owl callback surveys are identified by BirdNET. Therefore, we also obtained spotted owl survey data from biologists in our study area, and discarded any BirdNET prediction occurring on the same survey night and within 1.5 km of a callback survey location.

3.4 Data processing and statistical analyses

All data processing and analyses–aside from automated classification with BirdNET and burn severity estimation with Google Earth Engine (Gorelick et al. 2017)–were conducted with Program R version 4.4.1 (R Core Team 2024).

3.4.1 Environmental variables

We considered four environmental variables that we hypothesized would influence spotted owl occupancy dynamics: latitude, elevation, canopy height, and proportion of a cell burned by high-severity wildfire. We extracted the northing spatial coordinate (California Albers projection; hereafter referred to as "latitude") of each cell's centroid. We obtained elevation data at a 10-m resolution from the 3D Elevation Program Digital Elevation Model (U.S. Geological Survey 2023), and calculated mean elevation within each cell. The elevational range of bird species in the Sierra Nevada varies depending on latitudinal position within the mountain range (Saracco et al. 2011, Siegel et al. 2011, Brunk et al. 2023). Therefore, we corrected elevation for geographic location within the Sierra Nevada by using the residuals from a linear regression of elevation on latitude.

We summarized mean canopy height for each cell from a state-wide forest monitoring system, the California Forest Observatory (CFO). CFO uses deep learning algorithms to derive a suite of forest structure metrics at a 10-m resolution from airborne lidar and satellite imagery (California Forest Observatory 2023). We used canopy height (CFO model mean absolute error = 1.97 m) from the 2020 CFO dataset, which was predicted from remotely-sensed products collected one year prior to initiation of our PAM program.

To quantify high-severity fire effects, we developed mapped predictions of the composite burn index (CBI; Key and Benson 2006) within our study area. CBI is a field-based measurement of fire severity ranging from 0–3 (unburned to high-severity), and is considered to be a more

ecologically meaningful metric of post-fire substrate and vegetation change compared with other indices of fire severity. Recently, Parks et al. (2019) developed a random forest model in Google Earth Engine to predict CBI at a 30-m resolution as a function of several spectral indices derived from Landsat imagery collected one year pre- and post-fire, latitude, and climatic water deficit, which performed well for wildfires in California (R^2 of observed vs. predicted CBI = 0.73). Following Cova et al. (2023), we applied the Parks et al. CBI model for wildfires $\geq$ 4 ha from 1985–2023; 1985 is the earliest year possible since Landsat was launched in 1984. First, we obtained wildfire perimeters intersecting our study area from the CAL FIRE Fire and Resource Assessment Program's historical fire perimeters geodatabase, and predicted CBI within each fire using the recommended Landsat image window dates for California (1 June–15 September; Parks et al. 2019). Specifically, we used the bias-corrected version of CBI, which more accurately predicts extreme CBI values (Parks et al. 2019). Next, we discretized bias-corrected CBI values into categorical fire severity classes, using $\geq$ 2.25 as a threshold for defining high-severity fire (Miller and Thode 2007). Finally, for each year of acoustic monitoring we calculated the proportion of each cell burned by high-severity fire from 1985 to the preceding fire season, which we assumed was representative of a quasi-permanent loss of habitat (Jones et al. 2016, Jones et al. 2021).

We relied primarily on the tidyverse, sf, terra, exactextractr, and rgee R packages (Pebesma 2018, Wickham et al. 2019, Aybar et al. 2020, Baston 2023, Hijmans 2024) for geospatial data processing.

3.4.2 Dynamic occupancy model description

We quantified spotted owl occupancy patterns using a dynamic occupancy model. Dynamic occupancy models estimate the ecological processes of initial occupancy, colonization, and extinction, while accounting for the observation process (MacKenzie et al. 2003). This occupancy modeling framework requires detection/non-detection data collected at sites using a hierarchical design, in which secondary sampling occasions (i.e., repeat surveys) are nested within primary occasions, such as seasons or years. Occupancy state of a site can change in subsequent primary occasions as a function of colonization and extinction probabilities, but is assumed to remain constant within a primary occasion. In our study, we consider each cell as a site (i) and primary occasions (t) were years, which were divided into 18, week-long secondary occasions (j). We used a stringent definition of occupancy when building detection histories, where detections across ARU(s) within a cell were only coded as a 1 when they occurred on $\geq$ 2 nights within a secondary occasion (Kelly et al. 2023) to distinguish site occupancy from less ecologically meaningful site use (e.g., extra-territorial movements) that could violate occupancy model assumptions of site closure and independence (Wood and Peery 2022). Otherwise, detections not meeting our criteria and non-detections were coded as a 0, and secondary occasions without acoustic monitoring were coded as NAs. We formatted detection histories using the CAbioacoustics package.

For the observation process, we modeled detection probability (p) as a function of survey effort (hours summed across one or more ARUs within a cell), date, and year (categorical effect):

$$logit(p_{i,t,j}) = \alpha_{[NF]} + \beta_1 \times log(hours)_{itj} + \beta_2 \times date_{itj} + \beta_3 \times date_{itj}^2 + \beta_4 \times year_{itj}. \quad (1)$$

Survey effort was log-transformed, as we expected detection probability to stabilize once a certain threshold of recording hours per week was met (Rugg et al. 2023). We included linear and quadratic terms for date to account for a potential peak in calling activity during the breeding season, and a fixed effect of year to accommodate annual variation in detection. We also included a national forest-level random intercept, $\alpha_{[NF]}$, to account for cell-level heterogeneity.

Initial occupancy (ψ_i) varied spatially as a function of national forest (random intercept), canopy height, elevation, latitude, and the proportion of a cell burned at high-severity from 1985–2020:

$$\begin{aligned} logit(\psi_{i,2021}) = \alpha_{[NF]} + \beta_1 \times canopy\ height_i + \beta_2 \times elevation_i + \beta_3 \times elevation_i^2 \\ + \beta_4 \times latitude_i + \beta_5 \times latitude_i^2 + \beta_6 \times proportion\ high\ severity_i. \end{aligned} \quad (2)$$

For elevation and latitude, we used linear and quadratic terms as we expected initial occupancy would be most strongly associated with intermediate levels of these variables.

We allowed colonization (γ) to vary spatially and temporally:

$$logit(\gamma_{i,t}) = \alpha_{[NF]} + \beta_1 \times proportion\ high\ severity_{it} + \beta_2 \times year_{it} \quad (3)$$

where $\alpha_{[NF]}$ was a random intercept by national forest, β_1 was the proportion of a cell burned by high-severity fire from 1985 to year *t-1*, and β_2 was a fixed, categorical effect of year. We used the same variables in the extinction (ϵ) submodel. Because the most recent CFO forest structure metrics were derived from satellite imagery collected in 2020, canopy height was only used to predict initial occupancy in 2021.

We fit the dynamic occupancy model in a Bayesian framework using the ubms package (Kellner et al. 2022) to interface with the probabilistic programming language Stan (Carpenter et al. 2017). We used the package's default, weakly informative priors for the model intercept, coefficients, and random effect standard deviation (Kellner et al. 2022), and ran three chains for 1,500 iterations each with a warm-up of 750 iterations. Prior to analysis, all continuous predictors were standardized by centering around the mean and dividing by the standard deviation. Parameter convergence was assessed visually with traceplots, and by evaluating effective sample size (> 300) and the $\hat{R}$ statistic for all parameters ($\hat{R} \leq 1.01$; Vehtari et al. 2021). We assessed model fit by plotting state and detection submodel residuals (Wright et al. 2019) and from posterior predictive checks of the MacKenzie-Bailey χ^2 fit statistic (MacKenzie and Bailey 2004).

3.4.3 Quantifying temporal trends in occupancy

Fitting the dynamic occupancy model in a Bayesian framework enabled us to derive additional metrics of ecological and management interest in a straightforward way. We used the fitted model to estimate spotted owl occupancy probability for the Sierra Nevada region, each national forest, and year by summarizing posterior draws of the projected occupancy trajectory of surveyed grid cells (Weir et al. 2009, Kellner et al. 2022). To examine the effects of recent high-severity wildfires on spotted owl occupancy, we repeated this procedure but summarized projected occupancy of grid cells burned at high-severity and reference cells in the same national forest(s) but not affected by high-severity fire.

We also quantified trends in occupancy for the Sierra Nevada region and each national forest by calculating the overall mean annual rate of change in occupancy or mean annual growth rate, $\overline{\lambda}$ (MacKenzie et al. 2017, Banner et al. 2019):

$$\overline{\lambda}_t = \overline{\psi_{t+1}} / \overline{\psi_t} \tag{4}$$

$$\overline{\lambda} = \frac{1}{T-1} \sum_{t=1}^{T} \overline{\lambda}_t \tag{5}$$

where $\overline{\lambda}_t$ is the change in mean occupancy across cells from year t to $t+1$ (calculated per posterior draw), and $\overline{\lambda}$ is the mean of $\overline{\lambda}_t$ across years ($T-1$). The $\overline{\lambda}$ parameter estimates a linear net change in occupancy, with values less than one indicating a decline in the number of occupied sites (Banner et al. 2019).

4 Results

Unless otherwise noted, we present the mean $\pm$ standard deviation for all descriptive statistics. To summarize parameter effects and their uncertainty, we provide the mean, 95% credible intervals (CRIs), and the probability of direction (PD). The PD is the proportion of a parameter's posterior distribution that is greater or less than zero, and provides an index of effect existence and direction (Makowski et al. 2019). We adapted this metric to evaluate the direction of occupancy trends, where the proportion of $\overline{\lambda}$ posterior samples greater or less than one represents certainty of a trend being positive or negative, respectively.

Finally, we note that there are minor differences in the results presented below compared to the 2021–2023 version of the report due to database updates (e.g., ARUs recovered in 2024 that were deployed in previous years), and the new, multi-season occupancy modeling framework used here.

4.1 ARU sampling and detection summary

Our ecosystem-scale PAM program yielded 1,936,476 hours (221 years) of audio recordings from 2021–2024 (Table 1). ARU deployments occurred between 7 April and 8 August, and averaged 34 nights of surveys ($\pm$ 7). ARUs were deployed at 1,935 locations, resulting in 841 unique grid cells surveyed across four years of monitoring (2.05 $\pm$ 0.44 ARUs per cell). Of these cells, 64% were monitored in all four years, 21% in three years, 7% in two years, and 7% for a single year (Figure S1). Across all survey years, we manually validated 63,709 true-positive spotted owl detections, and 2,078 true-positive barred owl detections. We saw a marked reduction in spotted owl detections in 2023 (n = 9,730) compared to other years, coinciding with lower survey effort due to a combination of SD card formatting issues (restricted to 86 ARUs in the Stanislaus, Sierra, and Sequoia National Forests) and record snowpack in the Sierra Nevada that hindered our ability to deploy ARUs early in the season and at higher elevations (Table 1).

These detections corresponded with 36–40% of cells with at least one spotted owl detected, and 1% or less of cells with at least one barred owl detected in any given year (Table 1; Figure 2); given these consistently low naïve occupancy rates and high barred owl detection probabilities (Kelly et al. 2023), we did not attempt to formally model barred owl occupancy (i.e., while accounting for imperfect detection). Barred owls continued to remain at very low densities across the Sierra Nevada bioregion, with barred owls occurring in $\leq$ 9 cells and 3–4 national forests in each year (Table 1; Figure 2).

Year-specific sampling and detection summaries can be found in Table 1.

4.2 Model evaluation

Our model showed adequate convergence with all $\hat{R} \leq 1.01$ and effective sample sizes > 750 (Table S1). Plots of submodel residuals and the Bayesian p-value (0.301) from the posterior predictive check also indicated adequate model fit.

4.3 Detection process

We found a strong, non-linear relationship (β: 0.58; 95% CRI: 0.51–0.65; PD: 1.00) between spotted owl detection probability and ARU survey effort, with detection probability sharply increasing then plateauing with additional recording beyond ~100 hours per week (Figure 4a; Table S1). Date had moderate linear (β: 0.28; 95% CRI: -0.07–0.65; PD: 0.94) and quadratic effects (β: -0.27; 95% CRI: -0.64–0.10; PD: 0.93), corresponding to a slight peak in detection probability in mid-June (Figure 4b). Detection probability was lower in 2024 (β: -0.17; 95% CRI: -0.37–0.03; PD: 0.96) compared to the first three years of monitoring (Figures 3, 4c). Nevertheless, weekly detection probability in 2024 was 0.62 (95% CRI: 0.54–0.68), and the probability of detecting a spotted owl over a typical 5-week survey period–if present–was high (0.99; 95% CRI: 0.98–1.00).

4.4 Initial occupancy, colonization, and extinction processes

Mean canopy height was the most important predictor of spotted owl initial occupancy (Figure 3, Table S1), and had a positive relationship with initial occupancy probability (β: 1.13; 95% CRI: 0.88–1.38; PD: 1.00; Figure 5a). There were strong linear (β: -0.24; 95% CRI: -0.48– -0.02; PD: 0.98) and quadratic (β: -0.56; 95% CRI: -0.81– -0.32; PD: 1.00) effects of elevation after correcting for latitudinal position within the Sierra Nevada, with spotted owls most likely to occur at low-to-middle elevations (Figure 5b). Latitude had a strong linear effect (β: -0.69; 95% CRI: -1.21– -0.14; PD: 0.99), but a moderate quadratic effect (β: -0.24; 95% CRI: -0.63–0.14; PD: 0.88), suggesting higher occupancy in the southern Sierra Nevada (Figure 5c).

Spotted owls showed strong, negative relationships with higher proportions of high-severity fire for initial occupancy (β: -0.22; 95% CRI: -0.45–0.00; PD: 0.98; Figure 6a) and colonization (β: -0.76; 95% CRI: -0.99– -0.55; PD: 1.00; Figure 6b). Conversely, extinction probability increased with a higher proportion of high-severity fire (β: 0.71; 95% CRI: 0.44–0.98; PD: 1.00; Figure 6c). There was moderate-to-strong support for an effect of year on colonization (β_{2022}: 0.28; 95% CRI: -0.07–0.64; PD: 0.94; β_{2023}: -0.37; 95% CRI: -0.83–0.08; PD: 0.95), but the effect was uncertain for the extinction process (β_{2022}: -0.14; 95% CRI: -0.57–0.31; PD: 0.73; β_{2023}: -0.16; 95% CRI: -0.60–0.28; PD: 0.75; Figure 3).

4.5 Temporal trends in occupancy

Year-specific occupancy estimates can be found in Table S2. Across the entire study period, predicted occupancy was lowest in Lassen National Forest (ψ_{2023}: 0.15; 95% CRI: 0.09–0.21), and highest in Stanislaus National Forest (ψ_{2023}: 0.48; 95% CRI: 0.40–0.56; Figure 7; Table S2). Trends in occupancy by national forest were variable: Lassen, Eldorado, and Sequoia showed a negative net change in occupancy ($\overline{\lambda}$: 0.86–0.92; probability of declining trend: 0.85–1.00), Plumas and Sierra showed a positive net change in occupancy ($\overline{\lambda}$: 1.11–1.13; probability of a stable or increasing trend: 0.94–0.96), and Tahoe and Stanislaus showed an uncertain net change in occupancy ($\overline{\lambda}$: 0.98–1.02; probability of declining or increasing trend: 0.64–0.67); Table S3; Figure 8). Sierra Nevada-wide occupancy estimates ranged from 0.30 (95% CRI: 0.27–0.34) in 2023 to 0.28 (95% CRI: 0.24–0.31) in 2024, and we detected a 2% annual decline in occupancy from 2021–2024 ($\overline{\lambda}$: 0.98; 95% CRI: 0.93–1.02; probability of a declining trend: 0.83).

Occupancy of cells burned at high-severity generally declined in the years after a wildfire (Figure 9). The largest declines occurred one year post-fire, and were most pronounced when the proportion of a grid cell burned was $\geq$ 0.5. Indeed, occupancy estimates of cells in this high-severity category approached zero by 2024 for every recent wildfire we examined. In contrast, occupancy of reference cells (cells within a wildfire footprint or the surrounding national forest(s) that had not burned at high-severity from 1985–2023) either remained constant or increased slightly in the years following a wildfire.

5 Discussion

Our results demonstrate that California spotted owl occupancy dynamics can be monitored effectively across a large portion of the Sierra Nevada bioregion using passive acoustic surveys. Importantly, weekly detection probabilities exceeded 0.62 (translating to very high seasonal probabilities of detecting at least one spotted owl), and Sierra Nevada-wide estimates of site occupancy were reasonably precise, with standard deviations of posterior distributions ranging from 0.01–0.02. Forest-level annual occupancy was also estimated with reasonable precision. We also found a high probability of negative or positive trends in occupancy for five national forests, and detected a 2% decline in occupancy for the entire region, which is consistent with estimates from three demographic study areas in the Sierra Nevada (Conner et al. 2013, Tempel et al. 2014b, Jones et al. 2018). We note however that certainty of a region-wide decline was 83%, and our PAM program was not designed to estimate occupancy trends in the short-term (i.e., < 10 years) or for individual national forests. Nevertheless–while it remains somewhat premature to estimate trends in occupancy–the first four years of surveys indicate that PAM monitoring of California spotted owls is logistically feasible, and that it is possible to detect ecologically meaningful changes in populations within individual national forests and region-wide (perhaps with less than 10 years of acoustic surveys).

We were also able to detect the effects of high-severity wildfire on California spotted owl occupancy dynamics. We found that high-severity fire decreased initial occupancy and colonization probabilities, and increased extinction probability, which is consistent with numerous studies using territory occupancy information derived from call-based surveys (e.g., Jones et al. 2016, Jones et al. 2021, Tempel et al. 2022). Further, by modeling the dynamic processes driving changes in the occupancy state, we were able to produce robust annual occupancy estimates of cells monitored pre- and post-fire. For recent fires across the Sierra Nevada, spotted owl occupancy declined substantially, particularly at sites with a relatively a high proportion of severe wildfire ($\geq$ 0.5). Our analysis, in conjunction with previous studies (Jones et al. 2016, Jones et al. 2021) and current work (McGinn et al., *in review*) indicate that megafires are increasingly creating gaps in the distribution of California spotted owls in the Sierra Nevada, with the potential to fragment the species into smaller, less viable populations. Nevertheless, California spotted owls (while a rare species in the Sierra Nevada) remain well-distributed across the region (i.e., ψ_{2024}: 0.28; detected in each of the 22 USFS Ranger Districts surveyed in 2024), and we suspect that this core population–which has been proposed for listing as a Threatened species by the US Fish and Wildlife Service–is recoverable. As suggested by previous modeling studies (Tempel et al. 2015, Jones et al. 2022), increasing fuels management activities to curb the frequency and intensity of large, severe fires could help promote the recovery of California spotted owls, so long as they minimize impacts to key habitat elements.

Our results also reflect the enduring success of the northern Sierra Nevada barred owl lethal removal study, which was initiated in 2018 and fully implemented in 2019, with 76 removals of barred owls and hybrids during this period (Hofstadter et al. 2022). Prior to removals, barred owl modeled site occupancy based on acoustic surveys was 0.19 in 2018 and declined to 0.03 in 2020 as a result of removals (Hofstadter et al. 2022). Passive acoustic surveys suggest that

naïve barred owl occupancy in the Sierra Nevada has remained very low (barred owls detected in $\leq$ 1% of cells), with 15 or fewer removals conducted per year across the entire region from 2020–2024 (59 removals total; W. Berigan, *unpublished data*). Accordingly, low-level lethal removals appear to be a viable means for preventing barred owl-driven extirpation of California spotted owls from the Sierra Nevada, so long as the PAM program–which provides barred owl locational information as well as a means to monitor removal success–is maintained.

5.1 Related work

Ongoing work with the PAM program aims to understand the extent to which it can be used to monitor the effects of fuels management on California spotted owls. We first tested how well our PAM network sampled areas with differing amounts and intensities of fuel management activities. To do so, we integrated FACTS and remote sensing products to develop the first-ever Sierra Nevada-wide annual map of forest disturbance (wildfire and drought-related tree mortality) since 2003 (Kramer et al., *in prep.*). We refined treated areas into newer (1–10 years old), older (11–20 years old), all existing (1–20 years old), and future treatments. We also classed past treatments into 'heavy' or 'light' intensity, depending on whether there was a substantial canopy cover loss in the remote sensing data. Overall, monitored hexes had roughly 1% of their area treated each year, with 10% of their area treated in the last 10 years, 12% treated 11–20 years ago, and 18% treated in the last 20 years. We leveraged this dataset in two studies to evaluate the responses of spotted owls to disturbance and fuels treatments. In the first, we detected strong relationships between spotted owl occupancy and severe wildfire, severe drought-related tree mortality, and fuels management (Ng et al., *in prep.*). In the second, we found that relatively intensive fuels management reduced spotted owl occupancy in unburned areas but, importantly, improved occupancy in burned areas by curbing severe wildfire behavior (McGinn et al., *in prep.*). Together, these results indicate that our sampling effort is sufficient to detect the effects of key forms of forest disturbance and management. Thus, in cooperation with the USFS Region 5, we have decided not to alter our sampling design or increase sampling effort.

6 Acknowledgments

Funding for this project was provided by US Forest Service Region 5 and the National Fish and Wildlife Foundation. We thank Christian Alderson, Jason Banaszak, Elijah Bradshaw, James Canada, Tom Kelly, Elizabeth Ng, and Emmanuel Sepúlveda-Ramírez for their hard work deploying and recovering ARUs throughout the Sierra Nevada in 2024. Numerous biologists from the US Forest Service, Institute for Bird Populations, and Sierra Pacific Industries also provided assistance and broadcast survey data. Vince Berigan and Kylie Magnus helped to manually vet spotted and barred owl detections. Finally, we thank Garrett Smith and Jeffrey Hwang for their technical assistance and development of the bioacoustics database.

7 Literature cited

Ayars, J., H. A. Kramer, and G. M. Jones. 2023. The 2020 to 2021 California megafires and their impacts on wildlife habitat. Proceedings of the National Academy of Sciences 120:e2312909120.

Aybar, C., Q. Wu, L. Bautista, R. Yali, and A. Barja. 2020. rgee: An R package for interacting with Google Earth Engine. Journal of Open Source Software 5:2272.

Banner, K. M., K. M. Irvine, T. J. Rodhouse, D. Donner, and A. R. Litt. 2019. Statistical power of dynamic occupancy models to identify temporal change: Informing the North American Bat Monitoring Program. Ecological Indicators 105:166–176.

Baston, D. 2023. exactextractr: fast extraction from raster datasets using polygons. C++.

Berigan, W. J., G. M. Jones, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2019. Cryptic wide-ranging movements lead to upwardly biased occupancy in a territorial species. Journal of Applied Ecology 56:470–480.

Brunk, K. M., R. J. Gutiérrez, M. Z. Peery, C. A. Cansler, S. Kahl, and C. M. Wood. 2023. Quail on fire: changing fire regimes may benefit mountain quail in fire-adapted forests. Fire Ecology 19:19.

California Forest Observatory. 2023. A Statewide Tree-Level Forest Monitoring System. Salo Sciences, Inc. San Francisco, CA.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. Journal of Statistical Software 76:1–32.

Clare, J. D. J., P. A. Townsend, and B. Zuckerberg. 2021. Generalized model-based solutions to false-positive error in species detection/nondetection data. Ecology 102:e03241.

Conner, M. M., J. J. Keane, C. V. Gallagher, G. Jehle, T. E. Munton, P. A. Shaklee, and R. A. Gerrard. 2013. Realized population change for long-term monitoring: California spotted owl case study. The Journal of Wildlife Management 77:1449–1458.

Cova, G., V. R. Kane, S. Prichard, M. North, and C. A. Cansler. 2023. The outsized role of California's largest wildfires in changing forest burn patterns and coarsening ecosystem scale. Forest Ecology and Management 528:120620.

Darras, K., P. Batáry, B. Furnas, A. Celis-Murillo, S. L. Van Wilgenburg, Y. A. Mulyani, and T. Tscharntke. 2018. Comparing the sampling performance of sound recorders versus point counts in bird surveys: A meta-analysis. Journal of Applied Ecology 55:2575–2586.

Franklin, A. B., K. M. Dugger, D. B. Lesmeister, R. J. Davis, J. D. Wiens, G. C. White, J. D. Nichols, J. E. Hines, C. B. Yackulic, C. J. Schwarz, S. H. Ackers, L. S. Andrews, L. L. Bailey, R. Bown, J. Burgher, K. P. Burnham, P. C. Carlson, T. Chestnut, M. M. Conner, K. E. Dilione, E. D. Forsman, E. M. Glenn, S. A. Gremel, K. A. Hamm, D. R. Herter, J. M. Higley, R. B. Horn, J. M. Jenkins, W. L. Kendall, D. W. Lamphear, C. McCafferty, T. L. McDonald, J. A. Reid, J. T. Rockweit, D. C. Simon, S. G. Sovern, J. K. Swingle, and H. Wise. 2021. Range-wide declines of northern spotted owl populations in the Pacific Northwest: A meta-analysis. Biological Conservation 259:109168.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Hijmans, R. J. 2024. terra: spatial data analysis.
Hobart, B. K., G. M. Jones, K. N. Roberts, B. P. Dotters, S. A. Whitmore, W. J. Berigan, M. G. Raphael, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2019. Trophic interactions mediate the response of predator populations to habitat change. Biological Conservation 238:108217.
Hofstadter, D. F., N. F. Kryshak, M. W. Gabriel, C. M. Wood, G. M. Wengert, B. P. Dotters, K. N. Roberts, E. D. Fountain, K. G. Kelly, J. J. Keane, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2021. High rates of anticoagulant rodenticide exposure in California Barred Owls are associated with the wildland–urban interface. Ornithological Applications 123:duab036.
Hofstadter, D. F., N. F. Kryshak, C. M. Wood, B. P. Dotters, K. N. Roberts, K. G. Kelly, J. J. Keane, S. C. Sawyer, P. A. Shaklee, H. A. Kramer, R. Gutiérrez, and M. Z. Peery. 2022. Arresting the spread of invasive species in continental systems. Frontiers in Ecology and the Environment 20:278–284.
Jones, G. M., R. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2016. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment 14:300–306.
Jones, G. M., J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2018. Declining old-forest species as a legacy of large trees lost. Diversity and Distributions 24:341–351.
Jones, G. M., A. R. Keyser, A. L. Westerling, W. J. Baldwin, J. J. Keane, S. C. Sawyer, J. D. Clare, R. Gutiérrez, and M. Z. Peery. 2022. Forest restoration limits megafires and supports species conservation under climate change. Frontiers in Ecology and the Environment 20:210–216.
Jones, G. M., H. A. Kramer, W. J. Berigan, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2021. Megafire causes persistent loss of an old-forest species. Animal Conservation 24:925–936.
Kahl, S., C. M. Wood, M. Eibl, and H. Klinck. 2021. BirdNET: A deep learning solution for avian diversity monitoring. Ecological Informatics 61:101236.
Kellner, K. F., N. L. Fowler, T. R. Petroelje, T. M. Kautz, D. E. Beyer Jr., and J. L. Belant. 2022. ubms: An R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. Methods in Ecology and Evolution 13:577–584.
Kelly, K. G., C. M. Wood, K. McGinn, H. A. Kramer, S. C. Sawyer, S. Whitmore, D. Reid, S. Kahl, A. Reiss, J. Eiseman, W. Berigan, J. J. Keane, P. Shaklee, L. Gallagher, T. E. Munton, H. Klinck, R. J. Gutiérrez, and M. Z. Peery. 2023. Estimating population size for California spotted owls and barred owls across the Sierra Nevada ecosystem with bioacoustics. Ecological Indicators 154:110851.
Key, C. H., and N. C. Benson. 2006. Landscape Assessment (LA). FIREMON: Fire Effects Monitoring and Inventory System. US Department of Agriculture Forest Service Rocky Mountain Research Station, Fort Collins, CO, USA.
Kuntze, C. C., J. N. Pauli, C. J. Zulla, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, and M. Z. Peery. 2023. Landscape heterogeneity provides co-benefits to predator and prey. Ecological Applications 33:e2908.
MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.
MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.
MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species

Occurrence. Second edition.
Makowski, D., M. S. Ben-Shachar, S. H. A. Chen, and D. Lüdecke. 2019. Indices of effect existence and significance in the Bayesian framework. Frontiers in Psychology 10.
McGinn, K. A., B. Zuckerberg, J. N. Pauli, C. J. Zulla, W. J. Berigan, Z. A. Wilkinson, J. M. Barry, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2023. Older forests function as energetic and demographic refugia for a climate-sensitive species. Oecologia 202:831–844.
Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.
North, M., B. Collins, H. Safford, and N. L. Stephenson. 2016. Montane Forests. Ecosystems of California. University of California Press, Berkeley, CA.
Parks, S. A., L. M. Holsinger, M. J. Koontz, L. Collins, E. Whitman, M.-A. Parisien, R. A. Loehman, J. L. Barnes, J.-F. Bourdon, J. Boucher, Y. Boucher, A. C. Caprio, A. Collingwood, R. J. Hall, J. Park, L. B. Saperstein, C. Smetanka, R. J. Smith, and N. Soverel. 2019. Giving ecological meaning to satellite-derived fire severity metrics across North American forests. Remote Sensing 11:1735.
Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. The R Journal 10:439.
R Core Team. 2024. R: A Language and Environment for Statistical Computing.
Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, H. A. Kramer, N. F. Kryshak, J. J. Keane, S. C. Sawyer, R. J. Gutiérrez, H. Klinck, and M. Z. Peery. 2022. Breeding status shapes territoriality and vocalization patterns in spotted owls. Journal of Avian Biology 2022:e02952.
Roberts, K. N., W. E. Hall, A. J. Shufelberger, M. A. Reno, and M. M. Schroeder. 2017. California spotted owl occupancy on mixed-ownership lands in the Sierra Nevada of California, 2012 through 2016. Northwestern Naturalist 98:101–116.
Rugg, N. M., J. M. A. Jenkins, and D. B. Lesmeister. 2023. Western screech-owl occupancy in the face of an invasive predator. Global Ecology and Conservation 48:e02753.
Saracco, J. F., R. B. Siegel, and R. L. Wilkerson. 2011. Occupancy modeling of Black-backed woodpeckers on burned Sierra Nevada forests. Ecosphere 2:art31.
Shonfield, J., and E. M. Bayne. 2017. Autonomous recording units in avian ecological research: current use and future applications. Avian Conservation and Ecology 12:art14.
Siegel, R. B., R. L. Wilkerson, J. F. Saracco, and Z. L. Steel. 2011. Elevation ranges of birds on the Sierra Nevada's west slope. Western Birds 42.
Steel, Z. L., G. M. Jones, B. M. Collins, R. Green, A. Koltunov, K. L. Purcell, S. C. Sawyer, M. R. Slaton, S. L. Stephens, P. Stine, and C. Thompson. 2023. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. Ecological Applications 33:e2763.
Stephens, S. L., A. A. Bernal, B. M. Collins, M. A. Finney, C. Lautenberger, and D. Saah. 2022. Mass fire behavior created by extensive tree mortality and high tree density not predicted by operational fire behavior models in the southern Sierra Nevada. Forest Ecology and Management 518:120258.
Sugai, L. S. M., T. S. F. Silva, J. W. Ribeiro Jr, and D. Llusia. 2019. Terrestrial passive acoustic monitoring: review and perspectives. BioScience 69:15–25.
Tempel, D. J., R. J. Gutiérrez, J. J. Battles, D. L. Fry, Y. Su, Q. Guo, M. J. Reetz, S. A. Whitmore, G. M. Jones, B. M. Collins, S. L. Stephens, M. Kelly, W. J. Berigan, and M. Z. Peery. 2015.

Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. Ecosphere 6:1–18.

Tempel, D. J., R. J. Gutiérrez, S. A. Whitmore, M. J. Reetz, R. E. Stoelting, W. J. Berigan, M. E. Seamans, and M. Z. Peery. 2014a. Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. Ecological Applications 24:2089–2106.

Tempel, D. J., J. J. Keane, R. J. Gutiérrez, J. D. Wolfe, G. M. Jones, A. Koltunov, C. M. Ramirez, W. J. Berigan, C. V. Gallagher, T. E. Munton, P. A. Shaklee, S. A. Whitmore, and M. Z. Peery. 2016. Meta-analysis of California spotted owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: habitat associations and their implications for forest management. The Condor 118:747–765.

Tempel, D. J., H. A. Kramer, G. M. Jones, R. J. Gutiérrez, S. C. Sawyer, A. Koltunov, M. Slaton, R. Tanner, B. K. Hobart, and M. Z. Peery. 2022. Population decline in California spotted owls near their southern range boundary. The Journal of Wildlife Management 86:e22168.

Tempel, D. J., M. Z. Peery, and R. J. Gutiérrez. 2014b. Using integrated population models to improve conservation monitoring: California spotted owls as a case study. Ecological Modelling 289:86–95.

U.S. Geological Survey. 2023. 1/3rd arc-second Digital Elevation Models (DEMs) - USGS National Map 3DEP Downloadable Data Collection.

Vehtari, A., A. Gelman, D. Simpson, B. Carpenter, and P.-C. Bürkner. 2021. Rank-normalization, folding, and localization: an improved R^ for assessing convergence of MCMC (with discussion). Bayesian Analysis 16:667–718.

Verner, J., K. McKelvey, B. Noon, R. Gutierrez, G. Gould, T. Beck, and Technical Coordinators. 1992. The California Spotted Owl: A Technical Assessment of Its Current Status. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Weathers, W. W., P. J. Hodum, and J. A. Blakesley. 2001. Thermal ecology and ecological energetics of California spotted owls. The Condor 103:678–690.

Weir, L., I. J. Fiske, and J. A. Royle. 2009. Trends in anuran occupancy from northeastern states of the North American Amphibian Monitoring Program. Herpetological Conservation and Biology 4:389–402.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache, K. Müller, J. Ooms, D. Robinson, D. P. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. Welcome to the Tidyverse. Journal of Open Source Software 4:1686.

Wiens, J. D., K. M. Dugger, J. M. Higley, D. B. Lesmeister, A. B. Franklin, K. A. Hamm, G. C. White, K. E. Dilione, D. C. Simon, R. R. Bown, P. C. Carlson, C. B. Yackulic, J. D. Nichols, J. E. Hines, R. J. Davis, D. W. Lamphear, C. McCafferty, T. L. McDonald, and S. G. Sovern. 2021. Invader removal triggers competitive release in a threatened avian predator. Proceedings of the National Academy of Sciences 118:e2102859118.

Wood, C. M., R. J. Gutiérrez, J. J. Keane, and M. Z. Peery. 2020. Early detection of rapid barred owl population growth within the range of the California spotted owl advises the Precautionary Principle. The Condor 122:duz058.

Wood, C. M., and S. Kahl. 2024. Guidelines for appropriate use of BirdNET scores and other detector outputs. Journal of Ornithology 165:777–782.

Wood, C. M., and M. Z. Peery. 2022. What does "occupancy" mean in passive acoustic surveys? Ibis 164:1295–1300.

Wood, C. M., V. D. Popescu, H. Klinck, J. J. Keane, R. J. Gutiérrez, S. C. Sawyer, and M. Z. Peery. 2019. Detecting small changes in populations at landscape scales: a bioacoustic site-occupancy framework. Ecological Indicators 98:492–507.

Wright, W. J., K. M. Irvine, and M. D. Higgs. 2019. Identifying occupancy model inadequacies: can residuals separately assess detection and presence? Ecology 100:e02703.

Zulla, C. J., H. A. Kramer, G. M. Jones, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, S. A. Whitmore, W. J. Berigan, K. G. Kelly, A. K. Wray, and M. Z. Peery. 2022. Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls. Ornithological Applications 124:duac024.

8 Tables

Table 1. Summary of passive acoustic monitoring effort, and the number of manually confirmed California spotted owl (CSOW) and barred owl (BDOW) vocalizations, 2021–2024.

					Number of detections	
National Forest	**Year**	**ARUs**	**Grid cells**	**Survey hours**	**CSOW**	**BDOW**
Lassen	2021	235	120	73,157	1,172	47
	2022	230	114	66,329	814	31
	2023	213	93	71,101	158	0
	2024	249	119	82,464	485	6
Plumas	2021	268	147	83,356	1,069	0
	2022	323	144	73,169	1,092	0
	2023	310	131	101,213	1,573	12
	2024	316	139	102,235	2,742	38
Tahoe	2021	235	119	82,255	4,121	1,110
	2022	197	103	73,433	3,970	443
	2023	170	87	58,750	1,608	2
	2024	181	93	55,180	2,196	0
Eldorado	2021	207	103	71,975	1,856	1
	2022	210	107	72,928	1,728	0
	2023	202	100	71,537	2,571	0
	2024	213	107	69,327	3,320	2
Stanislaus	2021	184	93	62,583	4,549	0
	2022	212	97	72,159	4,398	0
	2023	136	63	43,797	2,485	0
	2024	168	78	61,125	5,717	0
Sierra	2021	222	113	72,965	954	0
	2022	268	128	94,682	2,544	0
	2023	154	80	39,768	486	0
	2024	216	106	75,719	2,265	15
Sequoia	2021	125	63	44,532	3,566	16
	2022	176	85	62,992	2,989	98
	2023	139	70	39,534	849	257
	2024	163	82	58,211	2,432	0
All forests	2021	1,476	758	490,823	17,287	1,174
	2022	1,616	778	515,692	17,535	572
	2023	1,324	624	425,700	9,730	271
	2024	1,506	724	504,261	19,157	61

9 Figures

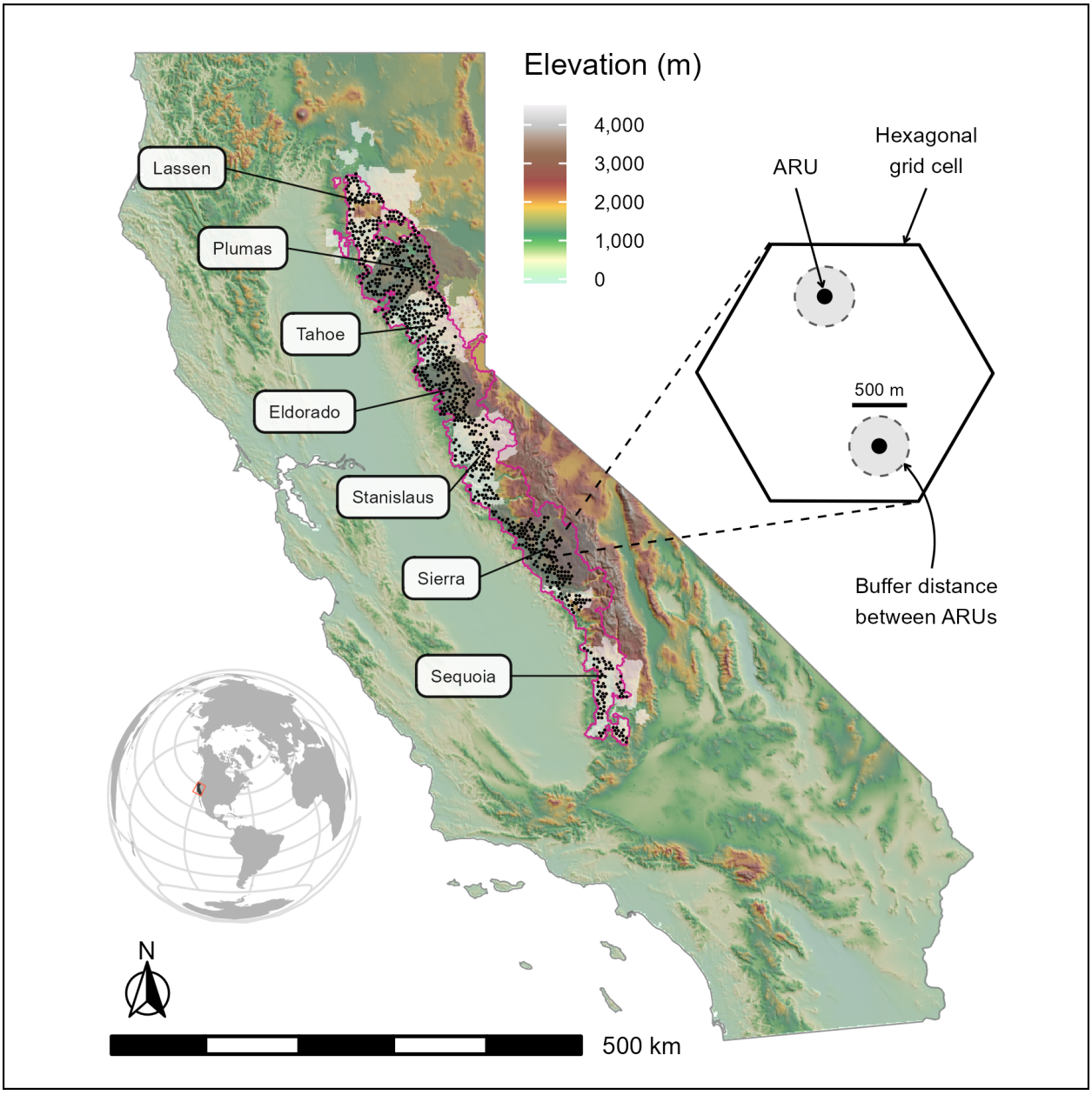

Figure 1. Location of the Sierra Nevada bioacoustic monitoring program in California, USA. The study area (pink border) encompasses suitable spotted owl habitat across seven US national forests (white and gray polygons), and was divided into a grid of 400 ha hexagonal cells. Within each surveyed cell, we deployed 1–4 (but generally 2) autonomous recording units (ARUs) $\geq$ 500 m apart and in acoustically advantageous locations (e.g., ridgetops). Black points represent cells surveyed in 2021–2024.

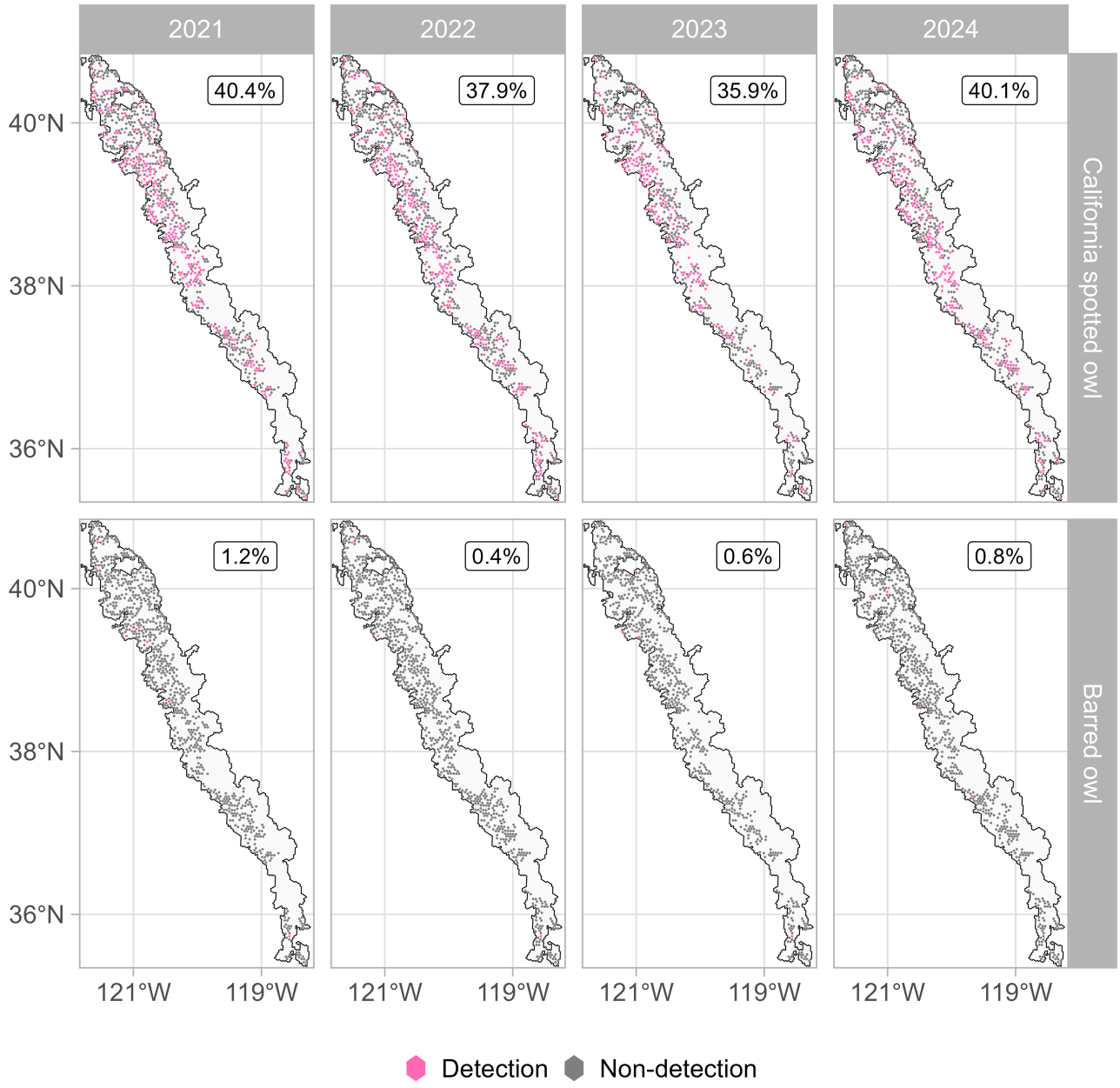

Figure 2. Grid cells with detections (pink hexagons) and non-detections (gray hexagons) of California spotted owls (top panels) and barred owls (bottom panels) in the Sierra Nevada study region, 2021–2024. Labels in top right corner of each panel indicate the percent of grid cells with detections.

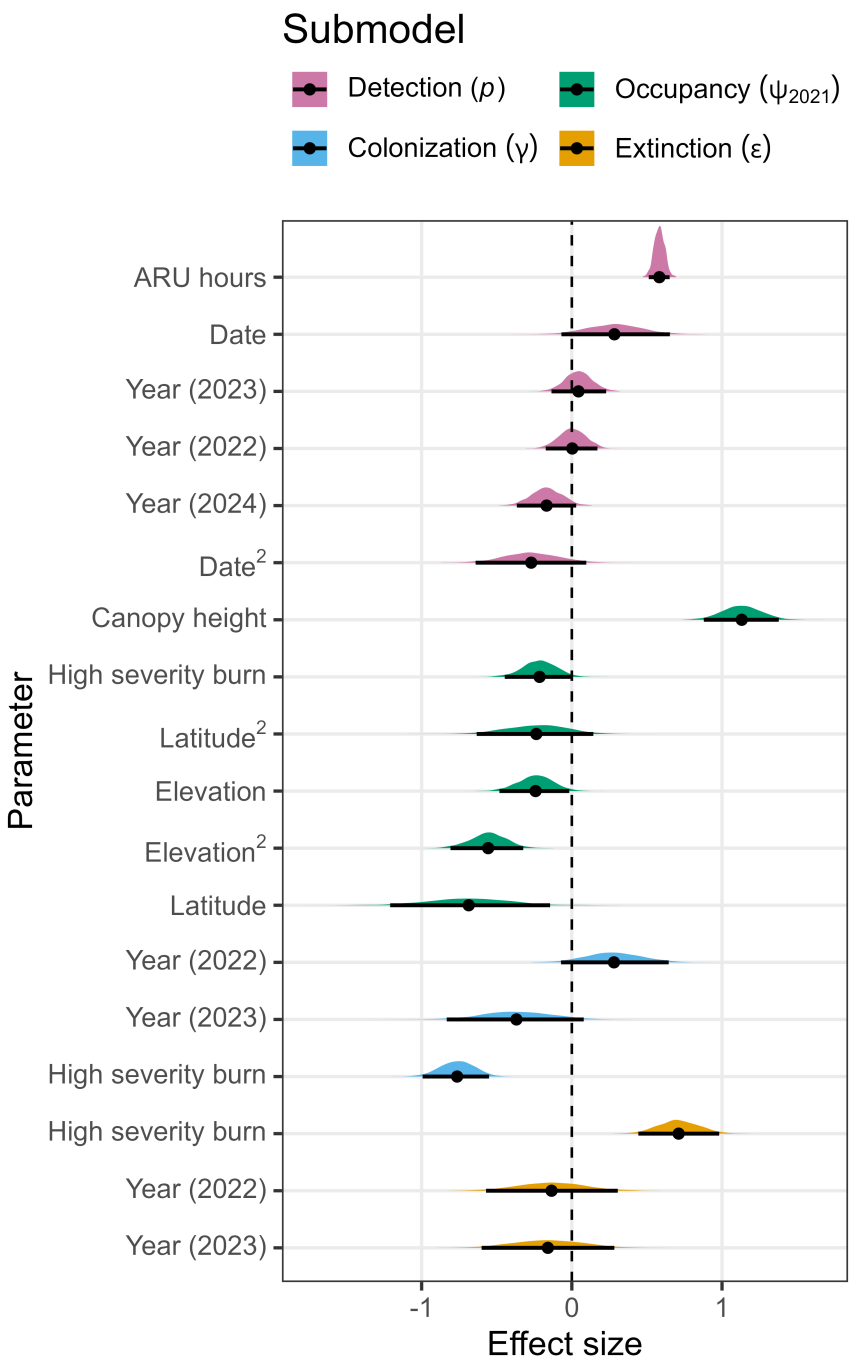

Figure 3. Effect sizes of covariates on detection, initial occupancy, colonization, and extinction. Colored polygons represent full posterior distributions of covariates, while black points and lines represent means and 95% credible intervals. Values greater than zero show a positive effect on the respective observation or ecological process, and mean values lower than zero show a negative effect. Uncertainty in the existence of a positive or negative effect increases with greater overlap of the posterior distribution with zero.

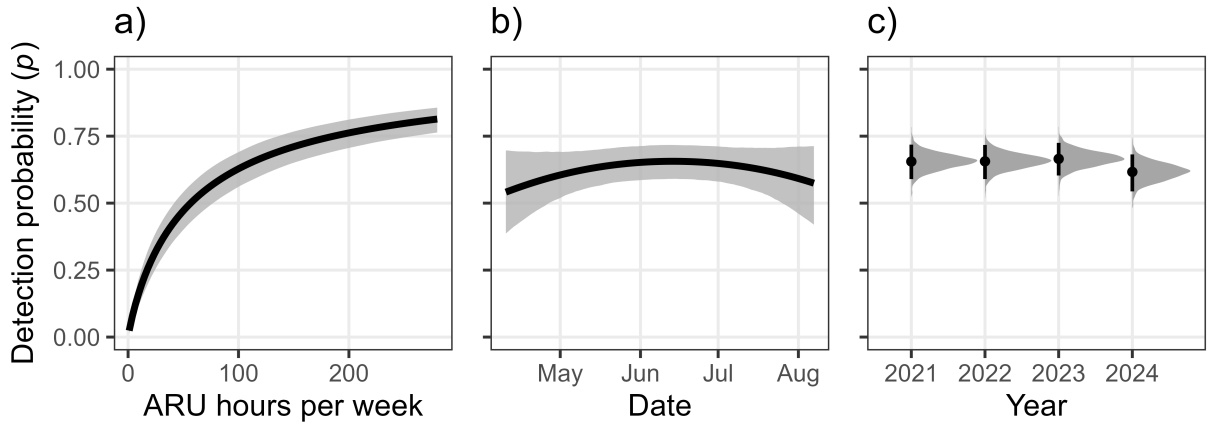

Figure 4. Estimated relationships between detection probability (p) and weekly autonomous recording unit (ARU) survey effort (a), date (b), and year (c). Predictions are shown with all other submodel covariates held at their mean value. Black lines represent posterior means and gray shaded areas represent 95% credible intervals (a, b); gray polygons represent full posterior distributions of annual p estimates, and black points and lines represent posterior means and 95% credible intervals, respectively (c).

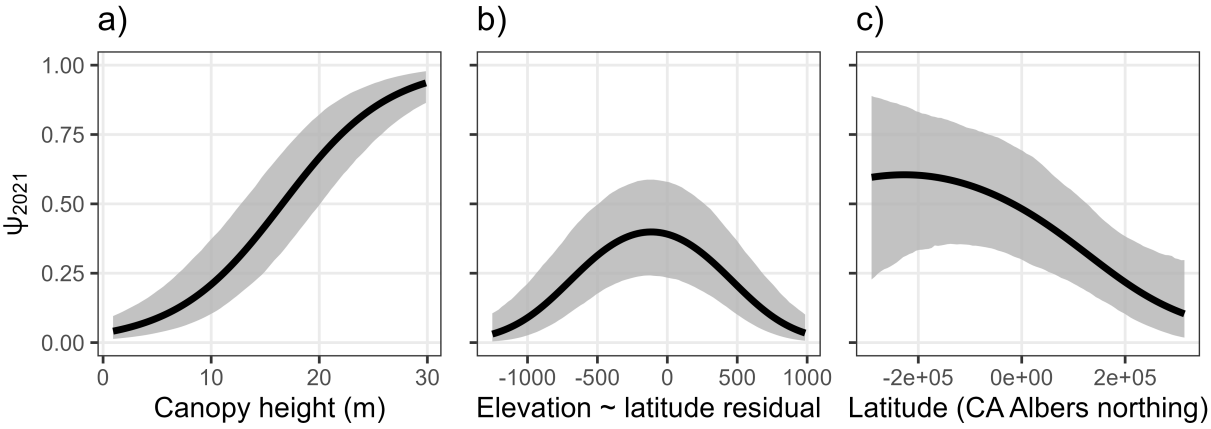

Figure 5. Estimated relationships between canopy height (a), latitude-corrected elevation (residuals of elevation regressed against latitude; b), latitude (in California Albers projection; c) and initial occupancy probability (ψ_{2021}). Predictions are shown with all other submodel covariates held at their mean value. Black lines represent posterior means and gray shaded areas represent 95% credible intervals.

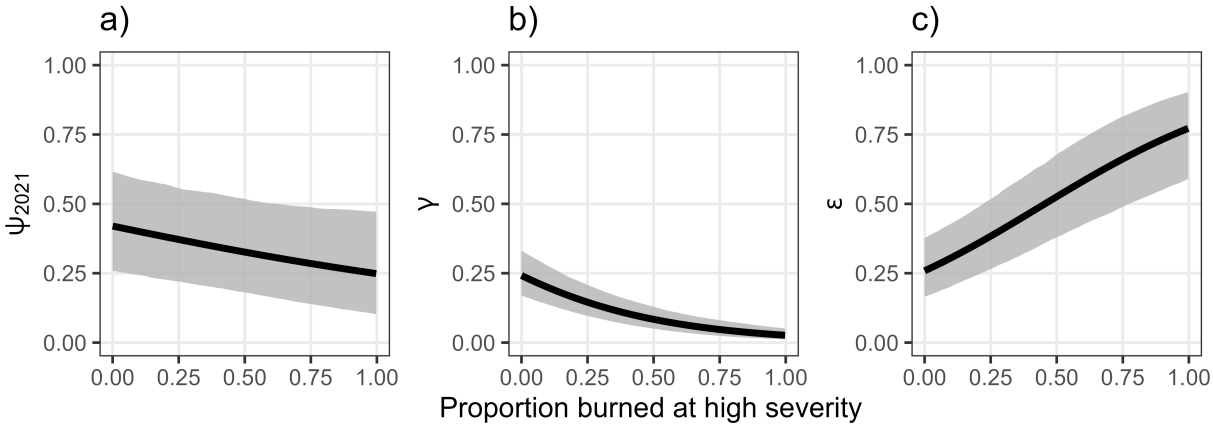

Figure 6. Estimated relationships between the proportion of a cell burned by high-severity fire and probability of initial occupancy (ψ_{2021}; a), colonization (γ; b), and extinction (ϵ; c). Predictions are shown with all other submodel covariates held at their mean value. Black lines represent posterior means and gray shaded areas represent 95% credible intervals.

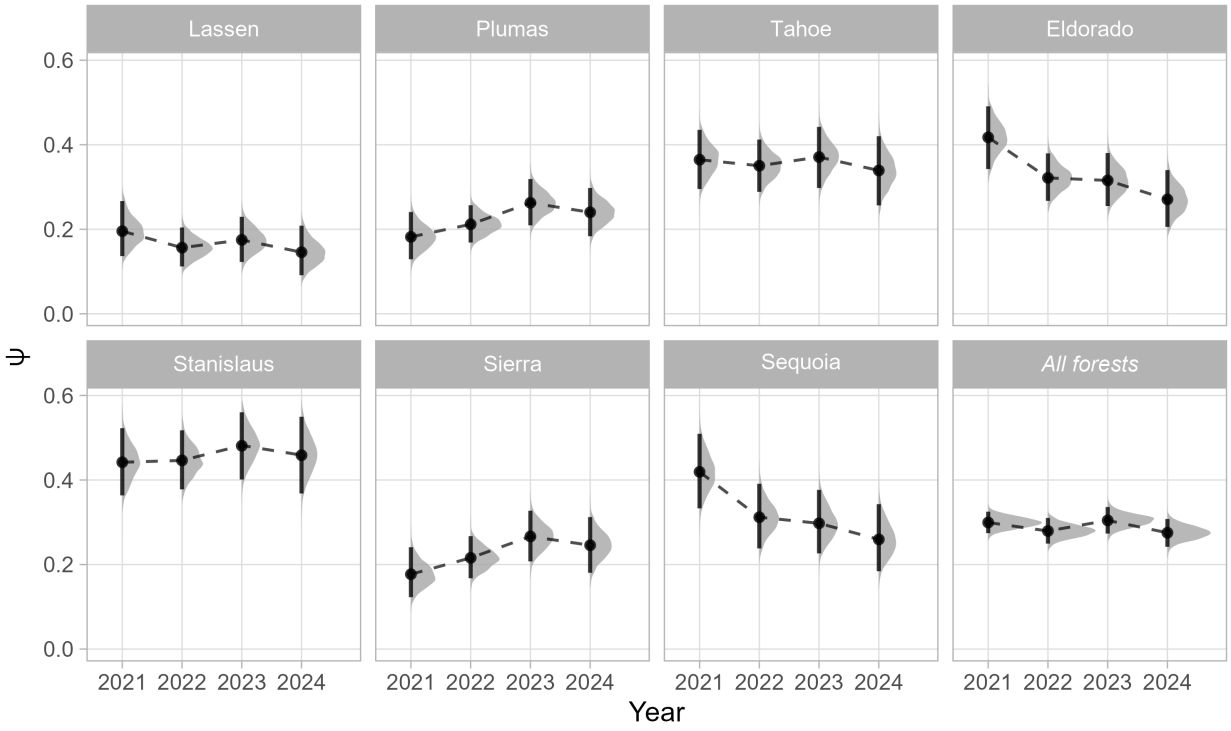

Figure 7. Model-projected occupancy estimates (ψ) by national forest and year. Gray polygons represent full posterior distributions of annual ψ estimates, while black points and vertical lines represent means and 95% credible intervals.

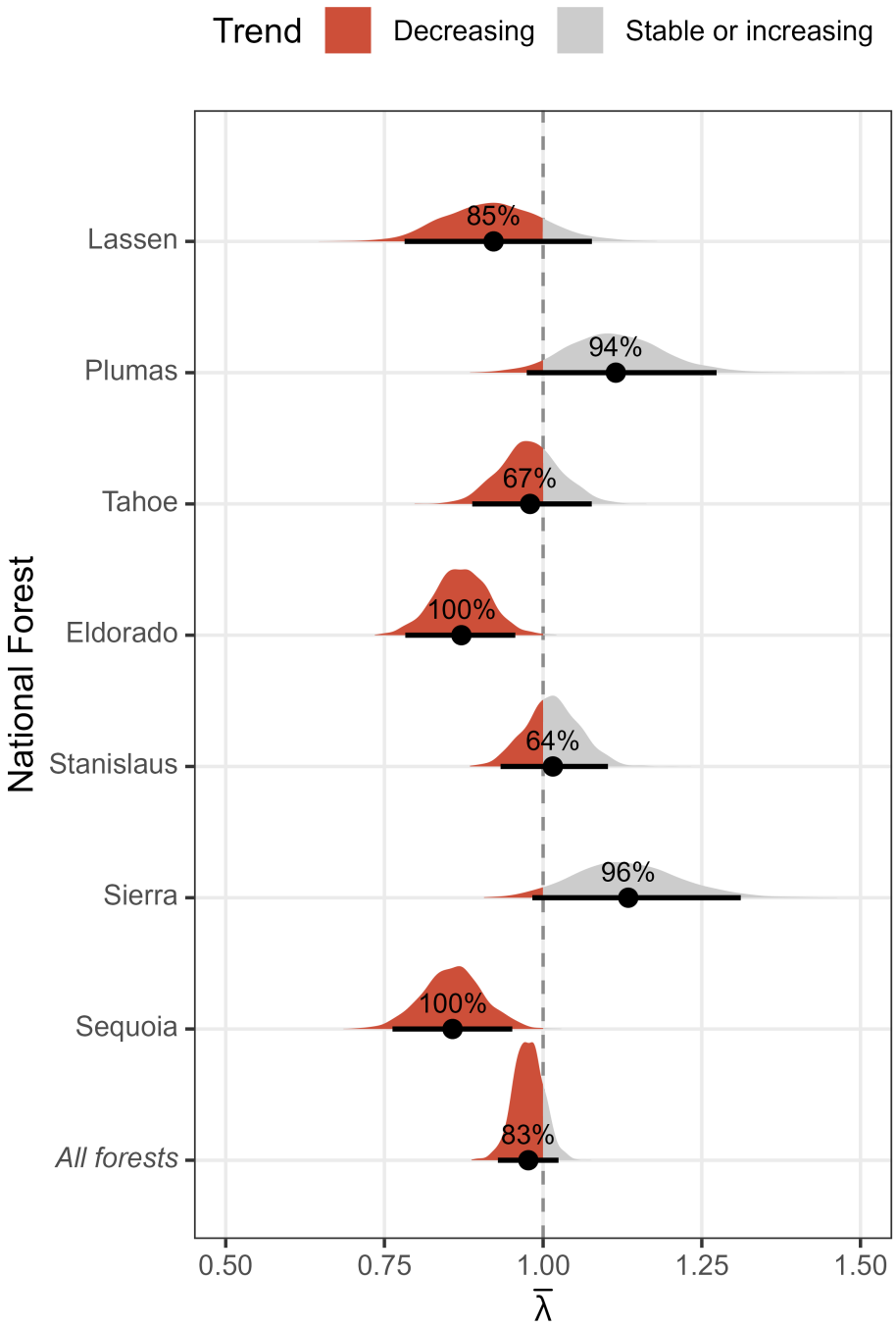

Figure 8. Estimates of net change in occupancy ($\overline{\lambda}$) by national forest from 2021–2024. Shaded polygons represent full posterior distributions of $\overline{\lambda}$, while black points and vertical lines represent means and 95% credible intervals. The portion of posterior draws with $\overline{\lambda}$ estimates < 1 or ≥ 1 are shown in red and gray, respectively. Labels above mean $\overline{\lambda}$ estimates indicate the percent of posterior draws with a decreasing or stable/increasing trend.

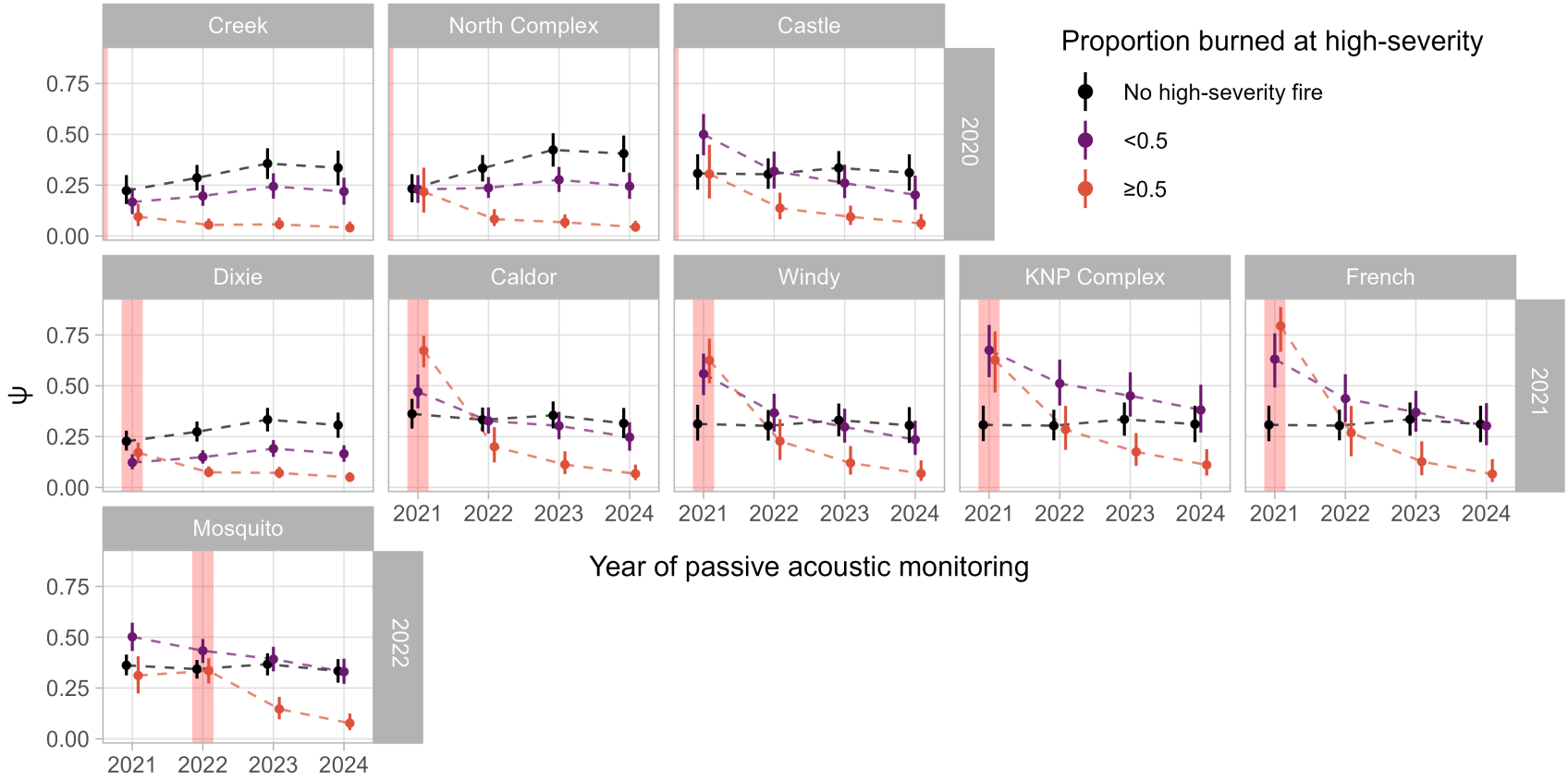

Figure 9. Model-projected occupancy estimates (ψ) by wildfire, proportion of cell burned by high-severity fire, and year. Panel rows are organized by wildfire ignition year (also indicated by red vertical shading). Fire categories are unburned at high-severity (i.e., reference cells in the same national forest(s) and potentially within a fire perimeter, but not burned at high-severity; black), proportion burned less than 0.5 (purple), and proportion burned greater than 0.5 (red). Points represent posterior means and solid lines represent 95% credible intervals.

10 Supporting Information

10.1 Supplemental tables

Table S1. Mean, standard deviation (SD), 95% credible intervals, and convergence diagnostics ($\widehat{R}$ and effective sample size; ESS) of parameter estimates from California spotted owl dynamic occupancy model fit to ARU data from 2021–2024.

Submodel	Parameter	Mean	SD	2.5%	97.5%	Rhat	ESS
Initial occupancy	Intercept	-1.101	0.326	-1.714	-0.436	1.00	757
	Elevation	-0.242	0.117	-0.482	-0.017	1.00	2723
	Elevation^2	-0.557	0.122	-0.808	-0.324	1.00	3352
	Latitude	-0.686	0.276	-1.209	-0.145	1.00	1275
	Latitude^2	-0.236	0.203	-0.633	0.143	1.00	1694
	Canopy height	1.131	0.129	0.879	1.378	1.00	2371
	High severity burn	-0.215	0.111	-0.447	-0.005	1.00	2579
	σ_{Forest}	0.804	0.328	0.365	1.642	1.00	1113
Colonization	Intercept	-2.049	0.234	-2.499	-1.572	1.00	860
	Year (2022)	0.281	0.184	-0.072	0.645	1.00	2324
	Year (2023)	-0.369	0.233	-0.833	0.079	1.00	2304
	High severity burn	-0.764	0.114	-0.993	-0.551	1.00	2681
	σ_{Forest}	0.413	0.197	0.155	0.906	1.00	811
Extinction	Intercept	-0.365	0.268	-0.897	0.192	1.00	842
	Year (2022)	-0.135	0.220	-0.571	0.306	1.00	2740
	Year (2023)	-0.159	0.231	-0.601	0.283	1.00	2588
	High severity burn	0.711	0.138	0.443	0.981	1.00	3169
	σ_{Forest}	0.539	0.235	0.191	1.120	1.00	1088
Detection	Intercept	0.475	0.142	0.201	0.770	1.00	758
	Year (2022)	0.003	0.090	-0.174	0.170	1.00	1978
	Year (2023)	0.044	0.090	-0.135	0.228	1.00	1960
	Year (2024)	-0.168	0.102	-0.366	0.029	1.00	1959
	Date	0.283	0.184	-0.069	0.653	1.00	1760
	Date^2	-0.270	0.186	-0.641	0.096	1.00	1741
	log(ARU hours)	0.583	0.035	0.512	0.651	1.00	3731
	σ_{Forest}	0.320	0.132	0.161	0.648	1.00	1309

Table S2. California spotted owl occupancy (ψ) estimates for the Sierra Nevada region, by forest, and year. Mean, standard deviation, and 95% credible intervals of ψ are shown.

Year	National Forest	Mean	SD	2.5%	97.5%
2021	Lassen	0.195	0.033	0.136	0.267
2022		0.156	0.024	0.112	0.204
2023		0.175	0.028	0.123	0.229
2024		0.146	0.029	0.091	0.208
2021	Plumas	0.182	0.029	0.129	0.241
2022		0.212	0.023	0.169	0.257
2023		0.263	0.028	0.209	0.319
2024		0.240	0.029	0.184	0.298
2021	Tahoe	0.365	0.036	0.295	0.435
2022		0.350	0.032	0.289	0.412
2023		0.371	0.037	0.298	0.442
2024		0.339	0.041	0.257	0.420
2021	Eldorado	0.417	0.038	0.343	0.491
2022		0.322	0.029	0.267	0.380
2023		0.316	0.033	0.255	0.380
2024		0.271	0.034	0.206	0.340
2021	Stanislaus	0.442	0.042	0.364	0.523
2022		0.446	0.036	0.378	0.518
2023		0.482	0.042	0.401	0.564
2024		0.459	0.046	0.368	0.551
2021	Sierra	0.177	0.030	0.123	0.241
2022		0.216	0.026	0.168	0.267
2023		0.266	0.031	0.207	0.327
2024		0.246	0.034	0.181	0.312
2021	Sequoia	0.419	0.046	0.333	0.509
2022		0.312	0.038	0.238	0.391
2023		0.298	0.039	0.226	0.377
2024		0.259	0.041	0.184	0.343
2021	*All forests*	0.299	0.013	0.274	0.325
2022		0.279	0.015	0.250	0.310
2023		0.304	0.016	0.273	0.336
2024		0.275	0.017	0.242	0.308

Table S3. Estimates of net change in occupancy ($\overline{\lambda}$) for the Sierra Nevada region and by national forest. Mean, standard deviation, and 95% credible intervals of $\overline{\lambda}$ are shown, along with probability of a declining or stable/increasing trend.

National Forest	Mean	SD	2.5%	97.5%	Probability of trend
Lassen	0.92	0.08	0.78	1.08	0.85
Plumas	1.11	0.08	0.97	1.27	0.94
Tahoe	0.98	0.05	0.89	1.08	0.67
Eldorado	0.87	0.04	0.78	0.96	1.00
Stanislaus	1.02	0.04	0.93	1.10	0.64
Sierra	1.13	0.08	0.98	1.31	0.96
Sequoia	0.86	0.05	0.76	0.95	1.00
All forests	0.98	0.02	0.93	1.02	0.83

10.2 Supplemental figures

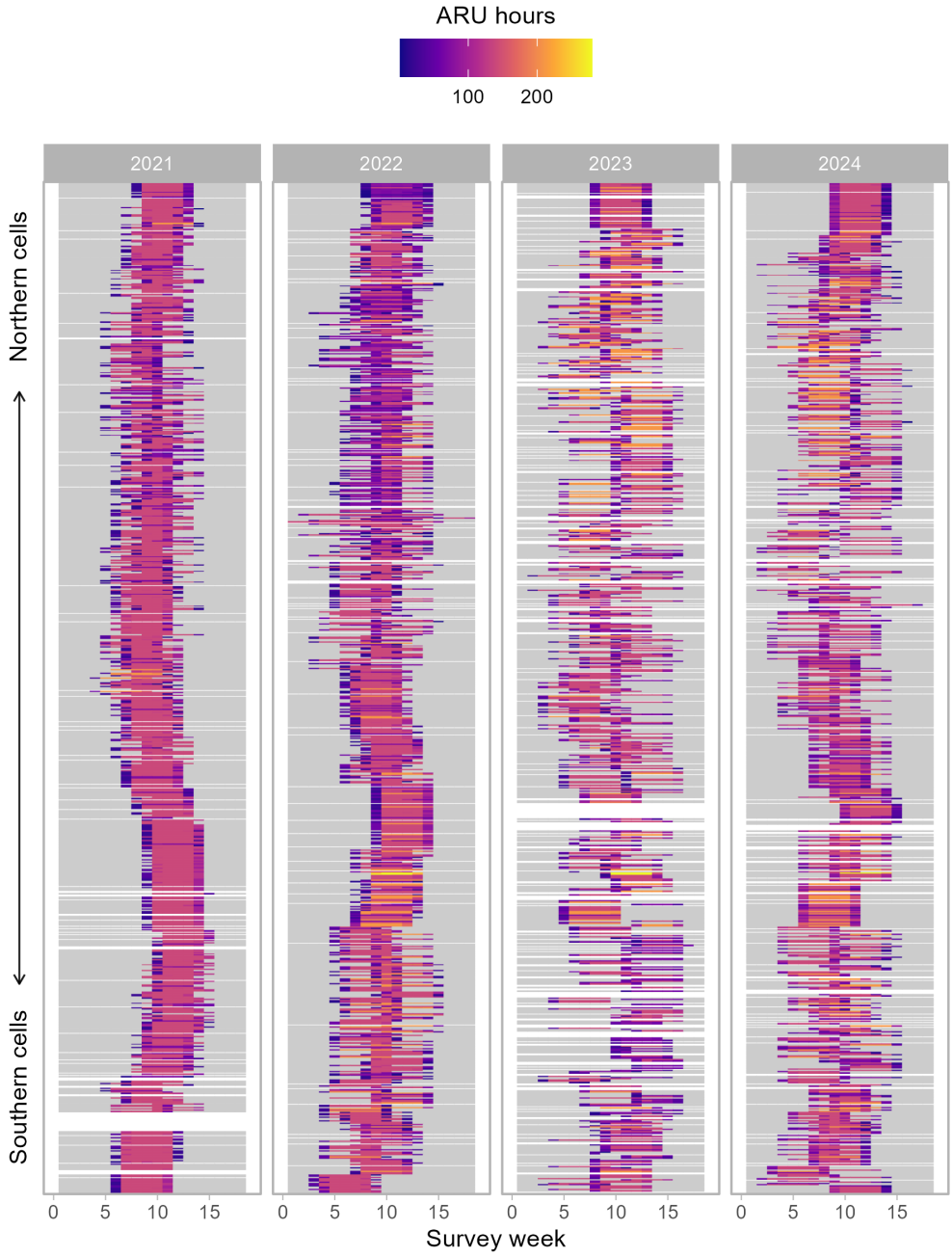

Figure S1. Passive acoustic monitoring effort and timing by hexagonal grid cell in the Sierra Nevada region, 2021–2024. Cells are ordered by latitudinal position, with warmer colors indicating greater survey effort, and gray shading indicating weeks without survey effort. Missing rows show cells that were not surveyed in one or more years.