

California Spotted Owl Passive Acoustic Monitoring Program: Final Annual Report (2021–2025)

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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 five years of passive acoustic surveys, 2021–2025. Key accomplishments and findings include:

- In 2025, we deployed 1,527 autonomous recording units (ARUs) across our study area, which encompasses 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 2025 (0.58) 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).
- In 2025, occupancy was lowest in Lassen National Forest (ψ : 0.12), and highest in Stanislaus National Forest (ψ : 0.46). Sierra Nevada-wide occupancy in 2025 was 0.27 (Figure 7).
- Trends in occupancy by management jurisdiction from 2021–2025 were variable: three management jurisdictions showed a negative net change in occupancy ($\bar{\lambda}$: 0.88–0.90), two showed a positive net change in occupancy ($\bar{\lambda}$: 1.07–1.10), and four showed an uncertain/stable net change in occupancy (λ : 0.96–1.01). We found with 92% certainty that California spotted owl occupancy was declining region-wide, and the annual rate of decline was 2% ($\bar{\lambda}$: 0.98; CRI: 0.95–1.01; Figure 8).
- The proportion of sites occupied by barred owls (*S. varia*; a dominant competitor with spotted owls) was very low ($< 2\%$ of surveyed cells in 2025), with fourteen or fewer occupied cells in each year from 2021–2025. Barred owls were detected in five national forests in 2025: Lassen, Plumas, Tahoe, Eldorado, and Stanislaus (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.

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Cover photo: California spotted owl (*Strix occidentalis occidentalis*) by Anu Kramer

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 the western slope of the Sierra Nevada (Kelly et al. 2023).

2 Objectives

Here we report the results of the first five years (2021–2025) 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 national parks) 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

We closely followed the methods of Winiarski et al. (2026), which are described below.

3.1 Study area

We conducted passive acoustic surveys from 2021 to 2025 as part of an ongoing, long-term effort to monitor avian biodiversity avian (>60 species; Brunk et al. 2025, McGinn et al. 2025) 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, three national parks, and some private lands within the Sierra Nevada and Southern Cascades ecoregions (hereafter, referred to as the Sierra Nevada) and ranged in elevation from 226–3,985 m. 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 (Wood et al. 2019, 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, a historic fire regime typified by frequent, low- to moderate-severity fire, and dominant tree species 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). Forest disturbance events in the Sierra Nevada have recently increased in scale and severity (Stephens et al. 2022, Ayars et al. 2023, Kramer et al. 2026), resulting in extensive habitat degradation and loss. For example, Steel et al. (2023) found a rapid, 30% decline in mature forest habitat in the southern Sierra Nevada between 2011 and 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 approximate spotted owl territory size in this region (Tempel et al. 2014a). From these, we randomly selected cells for passive acoustic surveys if they (1) 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; Swift or SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA) in each selected cell. To maximize sound quality and detection probability, ARUs were deployed at mid-slope and ridgetop locations with optimal sound propagation, 5–2245 m (mean distance = 34 m) from roads (the vast majority of which were unpaved and rarely traveled) and secured to 15–50 cm (diameter at breast height) trees at a height of 1.5–2 m above the ground. In situ testing and manual review of select audio indicated that spotted owl vocalizations could be detected up to 250 m from an ARU, so whenever possible we deployed ARUs ≥ 500 m apart and ≥ 250 m from cell borders (91% of deployments; 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 (14% of deployments); 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 or safety concerns prevented us from returning to these sites. ARUs were equipped with one omnidirectional microphone with -25 dB sensitivity, ± 0.9 V ADC clipping level, and recorded from 18:00 to 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.

Finally, we note that acoustic surveys were conducted on national parks in 2021 and 2023; otherwise national forests were sampled from 2021–2025.

3.3 Spotted and barred owl identification in acoustic data

We subset the raw audio data from 20:00 to 06:00 PDT (i.e., a “survey night”), when spotted owls are most vocally active (Reid et al. 2022). To identify spotted owl and barred owl vocalizations in the audio files, we used BirdNET <https://github.com/kahst/BirdNET-Analyzer>, a deep neural network designed to automate call classification for > 6000 species globally, most of them birds (Kahl et al. 2021, Wood and Kahl 2024). We used a customized version of BirdNET tailored explicitly to our PAM program (i.e., overfit to avian species in our study region and our recording hardware and specifications), 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-s segments, generating a “confidence” score ranging from 0 to 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 the 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 the mean canopy height for each cell from the California Forest Observatory (CFO) state-wide forest monitoring system (<https://forestobservatory.com>). 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 (i.e., 2019 Sentinel satellite imagery) collected 2 years prior to the 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 ≥ 4 ha from 1985–2024; 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 ≥ 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, and landscapemetrics packages ([Pebesma 2018](#), [Hesselbarth et al. 2019](#), [Wickham et al. 2019](#), [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 true-positive spotted owl observations across ARU(s) within a cell and secondary occasion were only coded as a 1 (i.e., a detection) when spotted owl observations occurred on ≥ 2 nights within the corresponding primary 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, spotted owl observations 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), and date:

$$\text{logit}(p_{i,t,j}) = \alpha_{jurisdiction} + \alpha_{year} + \beta_1 \times \log(hours)_{itj} + \beta_2 \times date_{itj} + \beta_3 \times date_{itj}^2. \quad (1)$$

Survey effort was log-transformed, as we expected detection probability to stabilize once a certain threshold of recording hours per week was reached (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 to accommodate seasonal variation in detection. We also included random intercepts, $\alpha_{jurisdiction}$ and α_{year} , to account for jurisdiction-level and annual detection heterogeneity.

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

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

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:

$$\text{logit}(\gamma_{i,t}) = \alpha_{jurisdiction} + \alpha_{year} + \beta_1 \times proportion\ high\ severity_{it} \quad (3)$$

where $\alpha_{jurisdiction}$ and α_{year} were random intercepts for management jurisdiction and year, respectively, and β_1 was the proportion of a cell burned by high-severity fire from 1985 to year $t-1$. 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 four chains for 4,000 iterations each with a warm-up of 2,000 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 (>400) 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 management jurisdiction, 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 management jurisdiction(s) but not affected by high-severity fire.

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

$$\bar{\lambda}_t = \overline{\psi_{t+1}} / \overline{\psi_t} \quad (4)$$

$$\bar{\lambda} = \frac{1}{T-1} \sum_{t=1}^T \bar{\lambda}_t \quad (5)$$

where $\bar{\lambda}_t$ is the change in mean occupancy across cells from year t to $t + 1$ (calculated per posterior draw), and $\bar{\lambda}$ is the mean of $\bar{\lambda}_t$ across years ($T - 1$). The $\bar{\lambda}$ 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 $\pm$ SD 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 $\bar{\lambda}$ 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 2021–2024 version of the report and the analysis of Winiarski et al. (2026) due to database updates (e.g., ARUs recovered in 2025 that were deployed in previous years), the inclusion of data from Yosemite and Sequoia-Kings Canyon national parks, and modifications to our dynamic

occupancy modeling framework (i.e., year parameterized as a random intercept rather than a fixed effect in the colonization, extinction, and detection submodels).

4.1 ARU sampling and detection summary

Our ecosystem-scale PAM program yielded 2,582,516 hours (295 years) of audio recordings from 2021–2025 (Table 1). ARU deployments occurred between 7 April and 8 August, and averaged 34 nights of surveys (± 7). ARUs were deployed at 2,123 locations, resulting in 933 unique grid cells surveyed across five years of monitoring (2.06 ± 0.42 ARUs per cell). Of these cells, 56% were monitored in all five years, 19% were monitored in four years, 7% were monitored in three years, 10% were monitored in two years, and 8% were monitored in a single year (Figure S1). Across all survey years, we manually validated 89,902 true-positive spotted owl detections, and 2,307 true-positive barred owl detections. We saw a marked reduction in spotted owl detections in 2023 ($n = 10,360$) 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 36–41% of cells with at least one spotted owl detected, and $<2\%$ 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 ≤ 14 cells 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 > 1600 (Table S1). Plots of submodel residuals and the Bayesian p -value (0.406) from the posterior predictive check also indicated adequate model fit (Figures. S2, S3).

4.3 Detection process

We found a strong, non-linear relationship (β : 0.56; 95% CRI: 0.50–0.61; 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 an uncertain linear effect (β : 0.03; 95% CRI: -0.03–0.08; PD: 0.83) and a moderate quadratic effect (β : -0.06; 95% CRI: -0.10– -0.01; PD: 0.99), corresponding to a slight peak in detection probability in mid-June (Figure 4b). Detection probability in 2025 was relatively low ($p = 0.58$; 95% CRI: 0.48–0.70), but remained within the range of among-year variation

(Figure 4c). Nevertheless, 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 occupancy probability (β : 1.09; 95% CRI: 0.86–1.33; PD: 1.00; Figure 5a). There were strong linear (β : -0.33; 95% CRI: -0.55– -0.10; PD: 1.00) and quadratic (β : -0.50; 95% CRI: -0.69– -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 : -0.85; 95% CRI: -1.36– -0.37; PD: 1.00), but a moderate quadratic effect (β : -0.22; 95% CRI: -0.55–0.10; PD: 0.91), 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 : -0.19; 95% CRI: -0.39–0.02; PD: 0.96; Figure 6a) and colonization (β : -0.78; 95% CRI: -0.96– -0.60; PD: 1.00; Figure 6b). Conversely, extinction probability increased with a higher proportion of high-severity fire (β : 0.58; 95% CRI: 0.34–0.82; PD: 1.00; Figure 6c).

4.5 Temporal trends in occupancy

Sierra Nevada-wide occupancy estimates ranged from 0.30 (95% CRI: 0.27–0.33) in 2024 to 0.27 (95% CRI: 0.24–0.30) in 2025, and we detected a 2% annual decline in occupancy from 2021–2025 ($\bar{\lambda}$: 0.98; 95% CRI: 0.95–1.01; probability of a declining trend: 0.92; Table S2; Figure 7). Across the entire study period, predicted occupancy was lowest in Lassen National Forest (ψ_{2025} : 0.12; 95% CRI: 0.08–0.17), and highest in Stanislaus National Forest (ψ_{2024} : 0.49; 95% CRI: 0.41–0.57). Trends in occupancy by management jurisdiction were variable: Sequoia, Eldorado, and Lassen showed a negative net change in occupancy ($\bar{\lambda}$: 0.88–0.90; probability of declining trend: 0.96–1.00), Plumas and Sierra showed a positive net change in occupancy ($\bar{\lambda}$: 1.07–1.10; probability of a stable or increasing trend: 0.91–0.96), and Sequoia-Kings Canyon, Tahoe, Yosemite, and Stanislaus showed an uncertain net change in occupancy ($\bar{\lambda}$: 0.96–0.99; probability of declining, stable, or increasing trend: 0.57–0.76; Table S3; Figure 8).

Occupancy of cells burned at high-severity generally declined in the years following a wildfire (Figure 9). The most significant declines occurred 1-year post-fire and were most pronounced when the proportion of a grid cell burned was ≥ 0.5 . Indeed, occupancy estimates of cells more than half burned at high-severity approached zero by 2025 for every recent wildfire we examined. In contrast, occupancy of reference cells (cells within a wildfire footprint or the surrounding management jurisdiction(s) that had not burned at high-severity from 1985 to 2024) 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 0.58 (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 0.02–0.07. Management jurisdiction-level annual occupancy was also estimated with reasonable precision. We found a high probability of negative or positive trends in occupancy for five management jurisdictions, 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 92%, and our PAM program was not designed to estimate occupancy trends in the short-term (i.e., <10 years) or for individual management jurisdictions. Nevertheless—while it remains somewhat premature to estimate trends in occupancy—the first five 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 management jurisdictions 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 high proportion of severe wildfire (≥ 0.5). Our analysis, in conjunction with previous studies (Jones et al. 2016, Jones et al. 2021) and recent work (McGinn et al. 2026b, Winiarski et al. 2026, Ng et al. 2026) 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_{2025} : 0.27; Figure 1), 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) and recently completed work leveraging data from the PAM program and novel Sierra Nevada-wide annual raster maps of forest disturbance (Kramer et al. 2026, McGinn et al. 2026a, Ng et al. 2026) 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.

Finally, our results 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 <2% of cells annually), with 16 or fewer removals conducted per year across the entire region from 2020–2025 (75 removals total from 2021 to 2025; 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.

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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, 2021–2025.

Management jurisdiction	Year	ARUs	Grid cells	Survey hours	Number of detections	
					CSOW	BDOW
Lassen NF	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
	2025	223	111	77,756	422	162
Plumas NF	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
	2025	295	133	106,539	2,358	54
Tahoe NF	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
	2025	203	101	72,933	3,691	3
Eldorado NF	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	214	107	69,417	3,320	2
	2025	201	98	72,410	2,945	1
Stanislaus NF	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	169	78	61,295	5,720	0
	2025	207	94	72,696	6,675	9
Yosemite NP	2021	104	53	34,513	684	0
	2023	92	46	30,988	345	0
Sierra NF	2021	222	113	72,965	954	0
	2022	268	128	94,682	2,544	0
	2023	154	80	39,768	486	0
	2024	219	107	76,829	2,265	15
	2025	232	115	82,371	4,344	0
Sequoia-Kings Canyon NP	2021	74	38	24,403	1,788	0
	2023	35	18	10,989	146	0
Sequoia NF	2021	125	63	44,532	3,566	16
	2022	176	85	62,992	2,989	98
	2023	141	71	40,273	988	257
	2024	163	82	58,211	2,432	0
	2025	166	81	58,333	2,653	0
Region-wide	2021	1,654	849	549,739	19,759	1,174
	2022	1,616	778	515,692	17,535	572

(continued)

Management jurisdiction	Year	ARUs	Grid cells	Survey hours	Number of detections	
					CSOW	BDOW
	2023	1,453	689	468,416	10,360	271
	2024	1,511	725	505,631	19,160	61
	2025	1,527	733	543,038	23,088	229

9 Figures

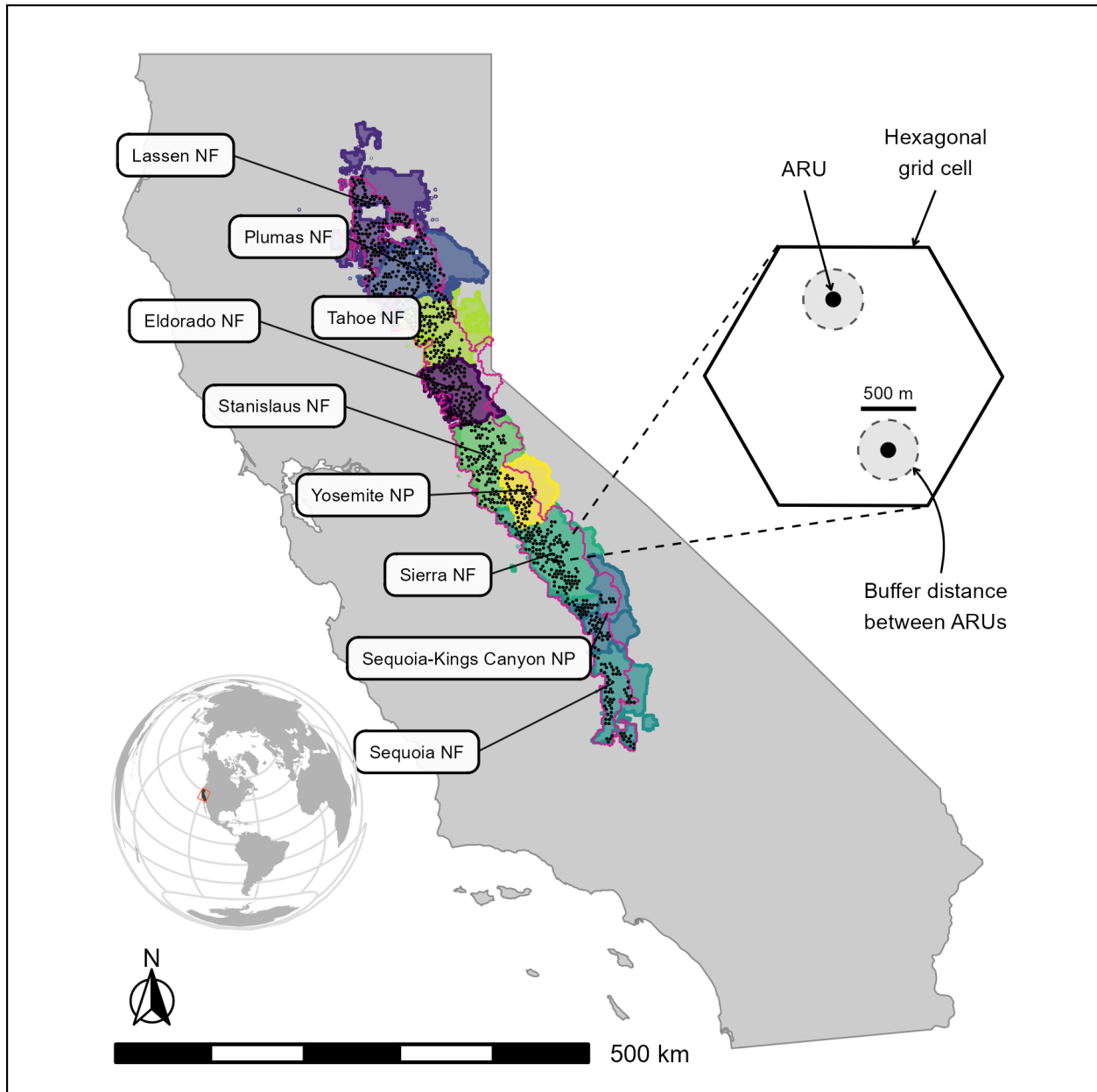


Figure 1. Location of the Sierra Nevada bioacoustic monitoring program in California, USA. The study area (pink border) encompasses suitable spotted owl habitat across seven US national forests and two national parks (colored polygons), and was divided into a grid of 400 ha hexagonal cells. Within each surveyed cell, we deployed 1–4 (but generally 2) autonomous recording units (ARUs) ≥ 500 m apart and in acoustically advantageous locations (e.g., ridgetops). Black points represent cells surveyed in 2021–2025.

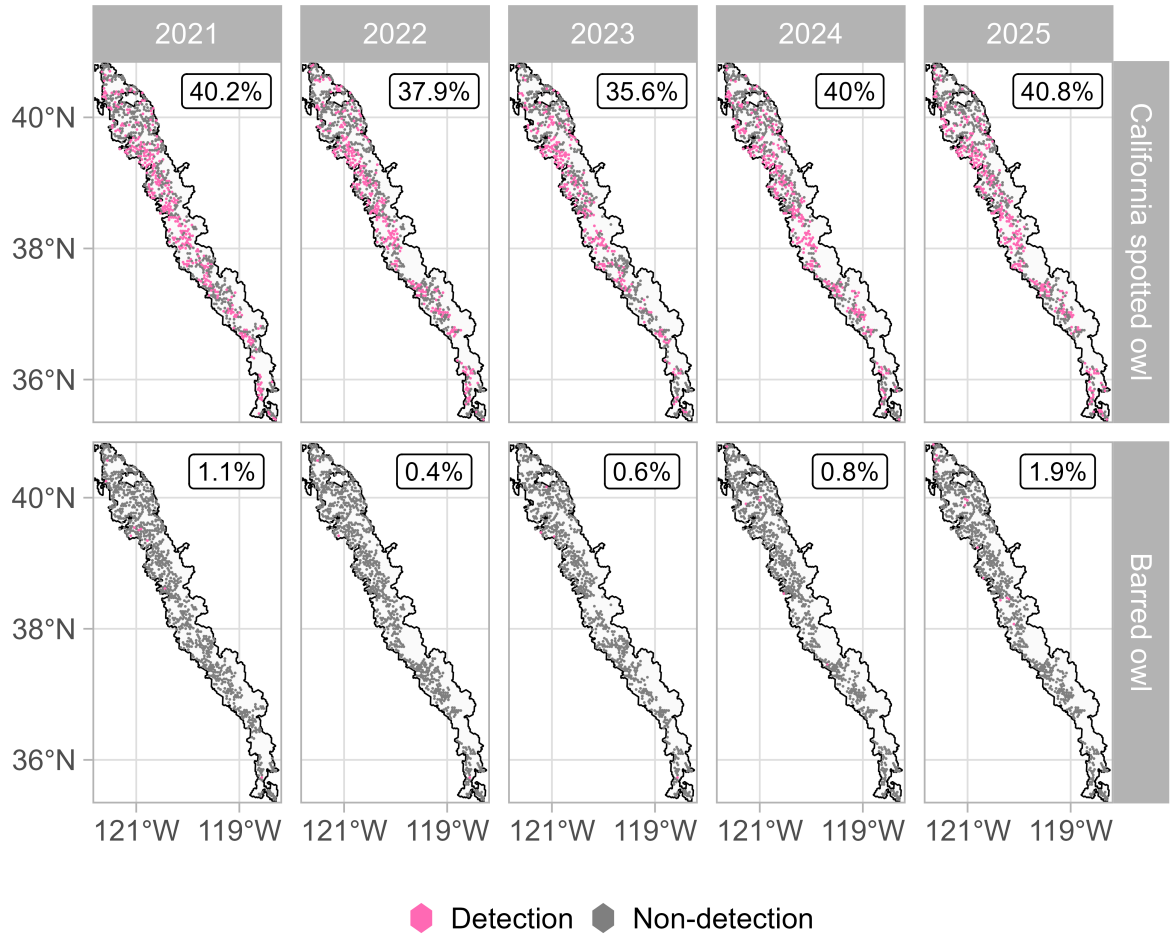


Figure 2. Grid cells with detections (owl observation(s) on at least one night; pink hexagons) and non-detections (gray hexagons) of California spotted owls (top panels) and barred owls (bottom panels) in the Sierra Nevada study region, 2021–2025. Labels in top right corner of each panel indicate naïve occupancy (i.e., the percent of grid cells with detections).

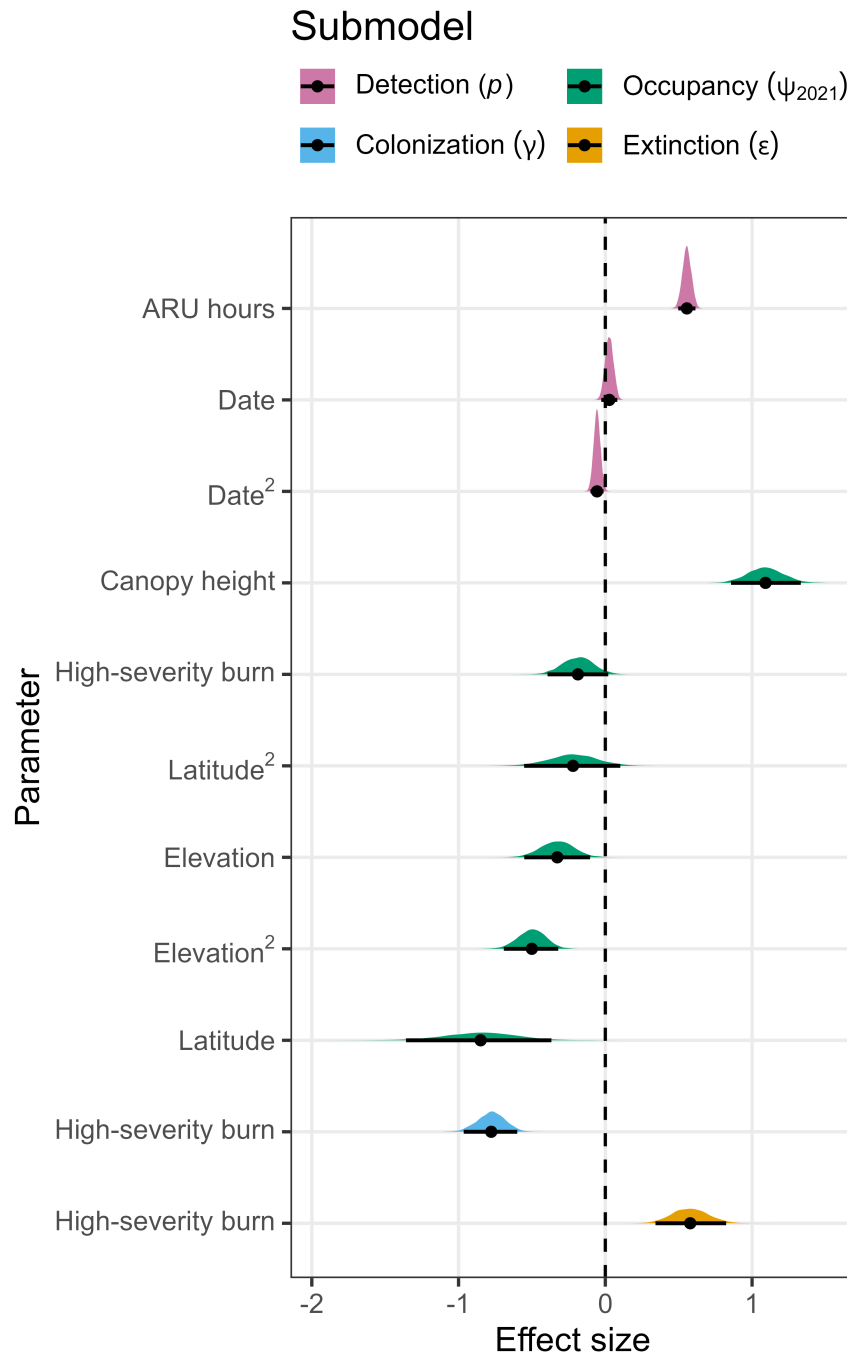


Figure 3. Effect sizes of covariates on detection, initial occupancy, colonization, and extinction. Colored polygons represent full posterior distributions of covariates, while black points and lines represent means and 95% credible intervals. Values greater than zero show a positive effect on the respective 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.

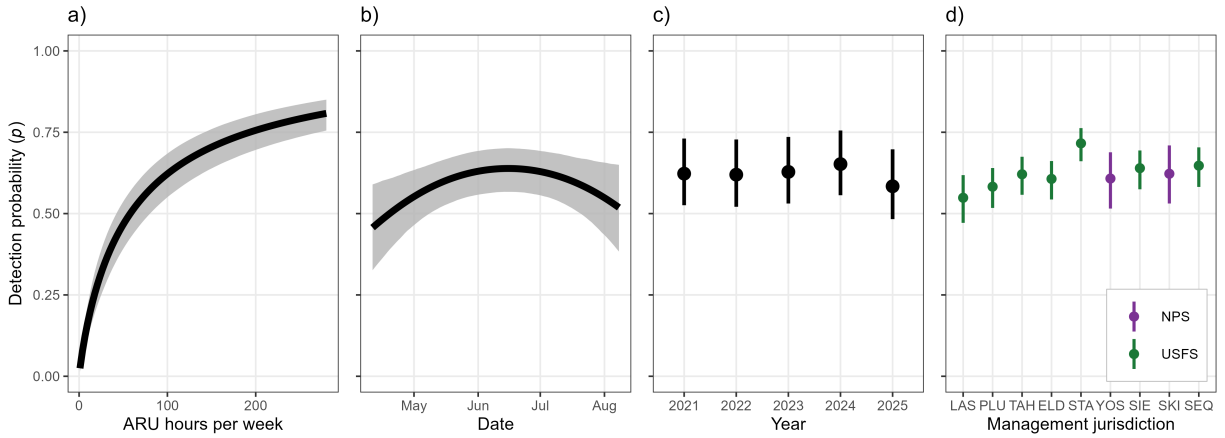


Figure 4. Estimated relationships between detection probability (p) and weekly autonomous recording unit (ARU) survey effort (a), date (b), year (c), and management jurisdiction (d). Predictions are shown with all other submodel covariates held at their mean value. Black lines represent posterior means and gray shaded areas represent 95% credible intervals (a, b); black points and lines represent posterior means and 95% credible intervals, respectively (c); points and lines represent posterior means and 95% credible intervals for national forests (green) and national parks (purple; d). Management jurisdictions are Lassen National Forest (LAS), Plumas National Forest (PLU), Tahoe National Forest (TAH), Eldorado National Forest (ELD), Stanislaus National Forest (STA), Yosemite National Park (YOS), Sierra National Forest (SIE), Sequoia-Kings Canyon National Park (SKI), and Sequoia National Forest (SEQ).

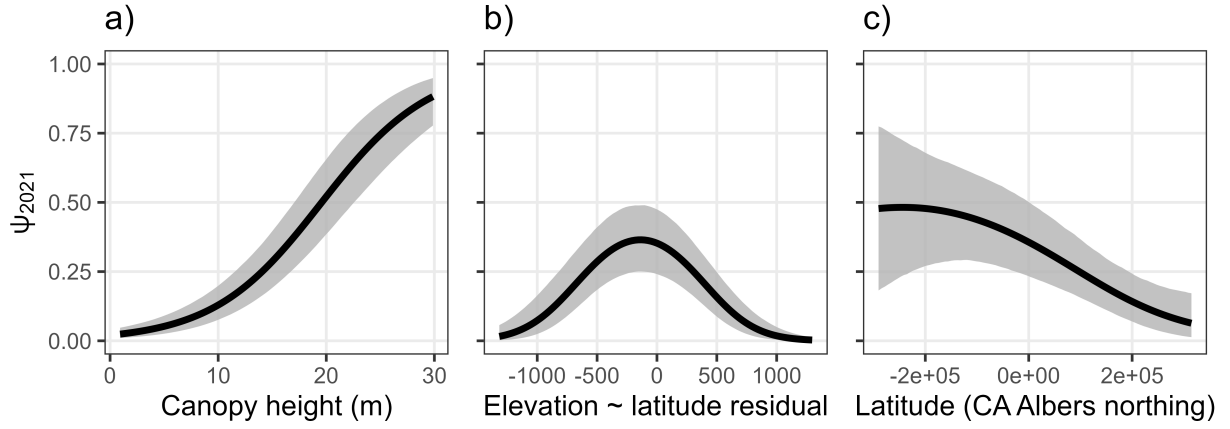


Figure 5. Estimated relationships between canopy height (a), latitude-corrected elevation (residuals of elevation regressed against latitude; b), latitude (in California Albers projection; c) and initial occupancy probability (ψ_{2021}). Predictions are shown with all other submodel covariates held at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

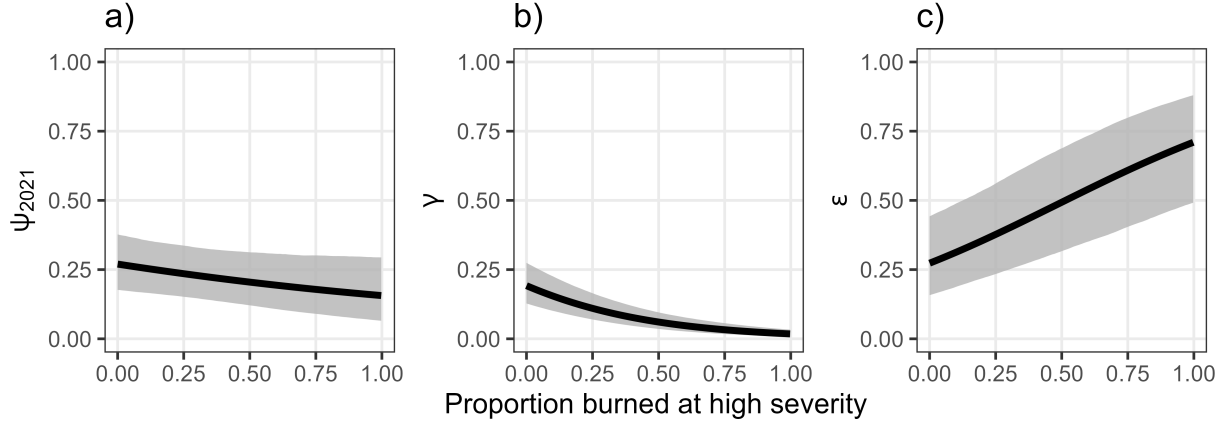


Figure 6. Estimated relationships between the proportion of a cell burned by high-severity fire and probability of initial occupancy (ψ_{2021} ; a), colonization (γ ; b), and extinction (ϵ ; c). Predictions are shown with all other submodel covariates held at their mean value. Black lines represent posterior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

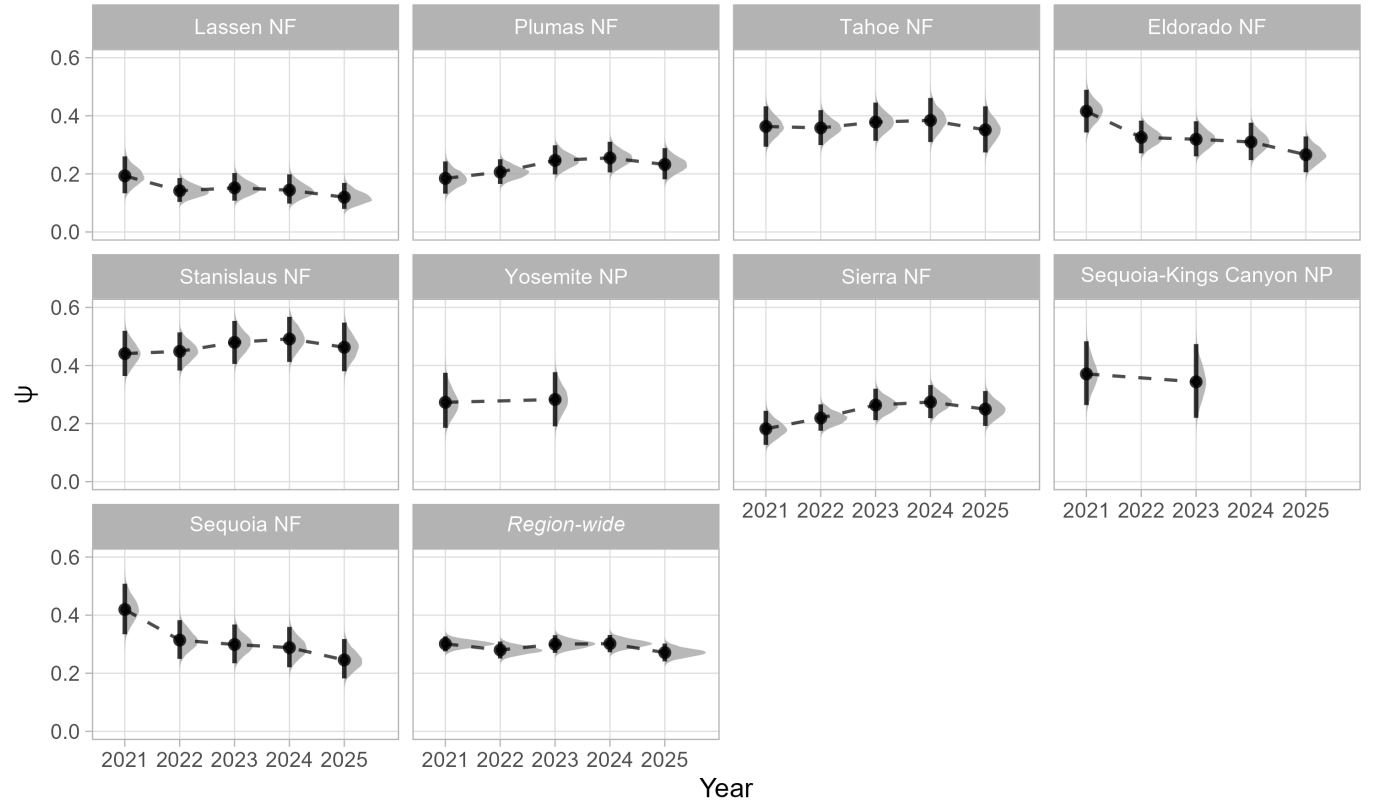


Figure 7. Model-projected occupancy estimates (ψ) by management jurisdiction and year. Gray polygons represent full posterior distributions of annual ψ estimates, while black points and vertical lines represent means and 95% credible intervals. Note that passive acoustic monitoring was not conducted on national park lands in 2022, 2024, and 2025.

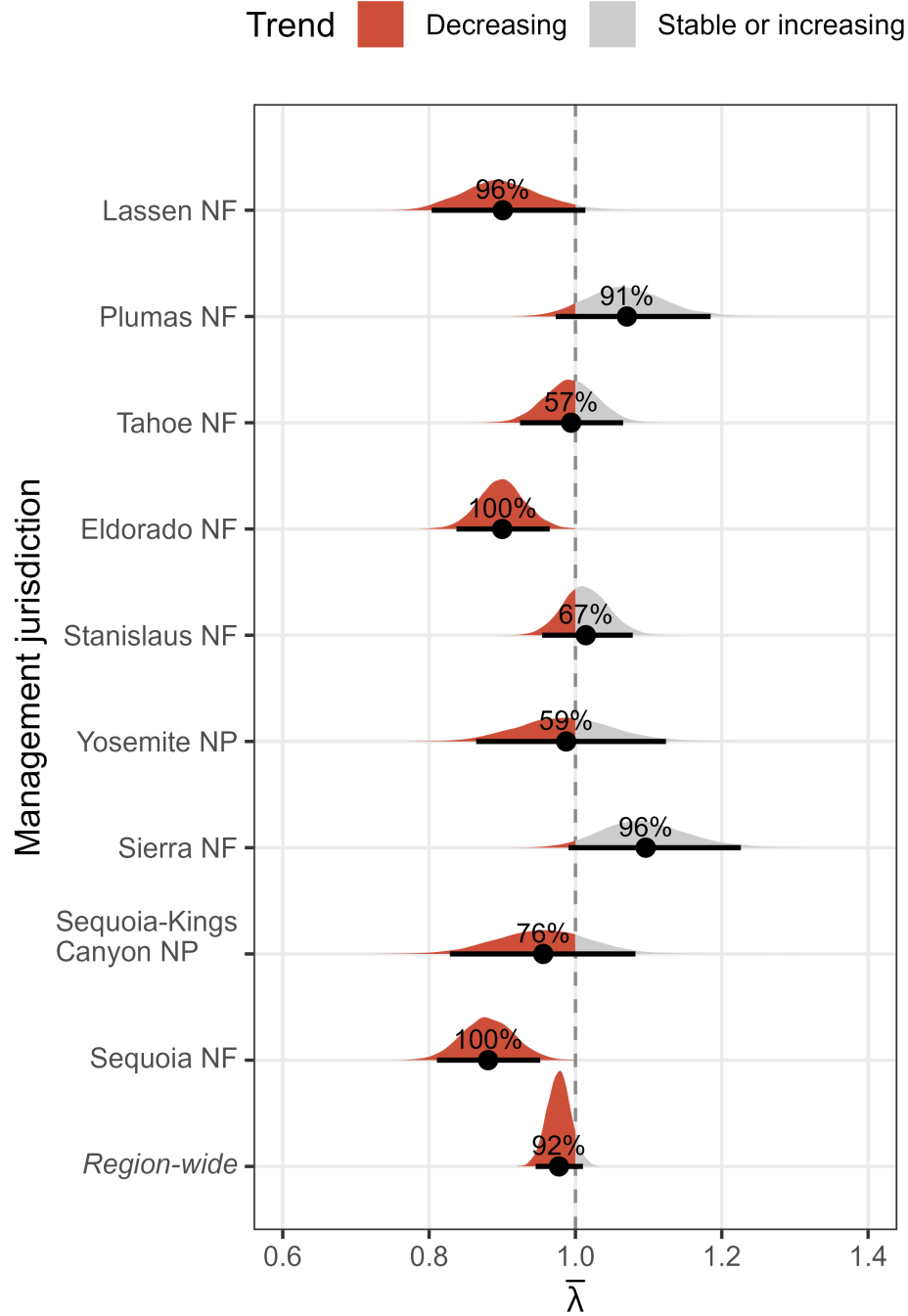


Figure 8. Estimates of net change in occupancy ($\bar{\lambda}$) by management jurisdiction from 2021–2025. Shaded polygons represent full posterior distributions of $\bar{\lambda}$, while black points and vertical lines represent means and 95% credible intervals. The portion of posterior draws with $\bar{\lambda}$ estimates <1 or ≥ 1 are shown in red and gray, respectively. Labels above mean $\bar{\lambda}$ estimates indicate the percent of posterior draws with a decreasing or stable/increasing trend.

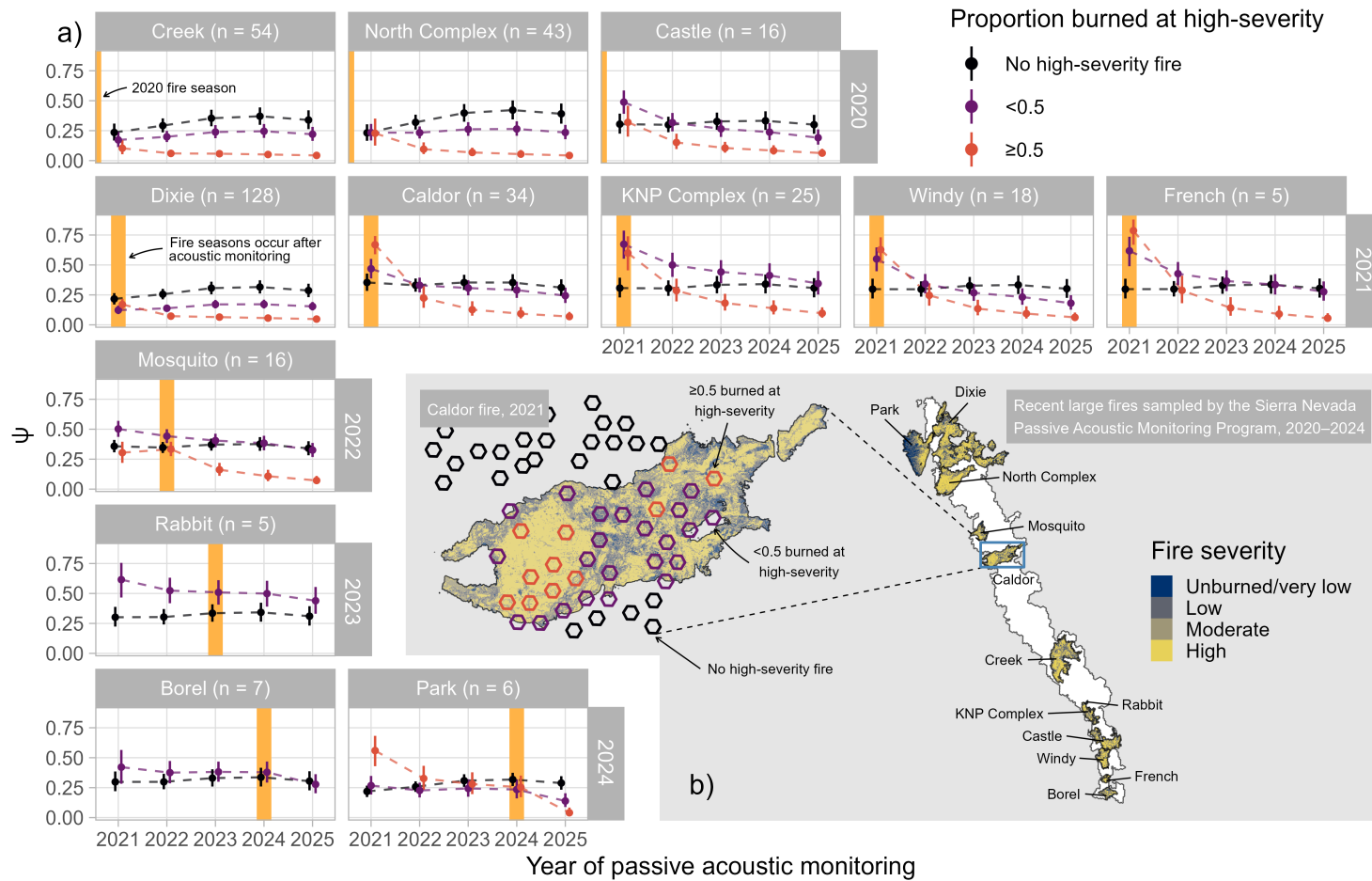


Figure 9. Model-projected occupancy estimates (ψ ; a) for 12 recent wildfires monitored in the Sierra Nevada study region (b). Panel rows are organized by wildfire ignition year (also indicated by orange vertical shading). Fire categories are unburned at high-severity (i.e., reference cells in the same management jurisdictions 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 and solid vertical lines denote posterior means and 95% credible intervals, respectively. Warmer colors in (b) indicate higher fire severity, with an inset map of the 2021 Caldor Fire illustrating the acoustic sampling and occupancy estimation framework.

10 Supporting Information

10.1 Supplemental tables

Table S1. Mean, standard deviation (SD), 95% credible intervals, and convergence diagnostics ($\hat{R}$ and effective sample size; ESS) of parameter estimates from California spotted owl dynamic occupancy model fit to ARU data from 2021–2025.

Submodel	Parameter	Mean	SD	2.5%	97.5%	Rhat	ESS
<i>Initial occupancy</i>	Intercept	-0.397	0.304	-0.979	0.210	1.00	2473
	Elevation	-0.327	0.114	-0.552	-0.104	1.00	6367
	Elevation ²	-0.501	0.095	-0.692	-0.321	1.00	6793
	Latitude	-0.850	0.253	-1.358	-0.367	1.00	3078
	Latitude ²	-0.220	0.167	-0.553	0.102	1.00	4067
<i>Colonization</i>	Canopy height	1.091	0.120	0.857	1.332	1.00	6792
	High-severity burn	-0.187	0.106	-0.393	0.020	1.00	7012
	$\sigma_{\text{jurisdiction}}$	0.683	0.232	0.355	1.266	1.00	3952
	Intercept	-2.069	0.239	-2.543	-1.580	1.00	2449
	High-severity burn	-0.777	0.094	-0.965	-0.600	1.00	7444
<i>Extinction</i>	$\sigma_{\text{jurisdiction}}$	0.473	0.296	0.132	1.203	1.00	4673
	σ_{year}	0.329	0.178	0.071	0.757	1.00	1787
	Intercept	-0.550	0.364	-1.215	0.207	1.00	1894
	High-severity burn	0.579	0.124	0.342	0.824	1.00	8036
	$\sigma_{\text{jurisdiction}}$	0.732	0.393	0.220	1.708	1.00	4156
<i>Detection</i>	σ_{year}	0.512	0.217	0.209	1.050	1.00	2127
	Intercept	0.569	0.148	0.266	0.846	1.00	1624
	Date	0.027	0.028	-0.028	0.082	1.00	8778
	Date ²	-0.057	0.023	-0.101	-0.012	1.00	7564
	log(ARU hours)	0.556	0.030	0.497	0.614	1.00	7749
	$\sigma_{\text{jurisdiction}}$	0.271	0.157	0.077	0.677	1.00	2848
	σ_{year}	0.222	0.081	0.108	0.419	1.00	2962

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

Management jurisdiction	Year	Mean	SD	2.5%	97.5%
Lassen NF	2021	0.193	0.032	0.133	0.260
	2022	0.142	0.021	0.103	0.186
	2023	0.152	0.024	0.108	0.203
	2024	0.144	0.026	0.098	0.198
	2025	0.120	0.023	0.079	0.169
Plumas NF	2021	0.185	0.029	0.132	0.243
	2022	0.206	0.022	0.165	0.250
	2023	0.246	0.026	0.198	0.298
	2024	0.255	0.027	0.205	0.311
	2025	0.232	0.027	0.181	0.289
Tahoe NF	2021	0.363	0.035	0.294	0.433
	2022	0.358	0.030	0.299	0.419
	2023	0.379	0.034	0.314	0.445
	2024	0.384	0.039	0.310	0.461
	2025	0.351	0.041	0.274	0.433
Eldorado NF	2021	0.416	0.037	0.343	0.490
	2022	0.326	0.029	0.271	0.383
	2023	0.319	0.031	0.260	0.381
	2024	0.310	0.033	0.247	0.376
	2025	0.266	0.031	0.205	0.329
Stanislaus NF	2021	0.441	0.040	0.364	0.519
	2022	0.449	0.033	0.383	0.514
	2023	0.480	0.038	0.405	0.554
	2024	0.492	0.041	0.412	0.570
	2025	0.463	0.043	0.380	0.548
Yosemite NP	2021	0.273	0.048	0.185	0.375
	2023	0.283	0.048	0.190	0.377
Sierra NF	2021	0.182	0.030	0.127	0.244
	2022	0.219	0.023	0.175	0.266
	2023	0.264	0.028	0.212	0.320
	2024	0.274	0.029	0.219	0.333
	2025	0.250	0.031	0.192	0.312
Sequoia-Kings Canyon NP	2021	0.371	0.056	0.264	0.483
	2023	0.344	0.064	0.220	0.475
Sequoia NF	2021	0.419	0.045	0.334	0.508
	2022	0.314	0.034	0.250	0.383

(continued)

Management jurisdiction	Year	Mean	SD	2.5%	97.5%
	2023	0.299	0.034	0.234	0.368
	2024	0.288	0.035	0.221	0.359
	2025	0.246	0.035	0.182	0.318
<i>Region-wide</i>	2021	0.301	0.013	0.275	0.327
	2022	0.280	0.015	0.251	0.309
	2023	0.300	0.016	0.270	0.331
	2024	0.302	0.015	0.272	0.332
	2025	0.271	0.015	0.241	0.302

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

Management jurisdiction	Mean	SD	2.5%	97.5%	Probability of trend
Lassen NF	0.90	0.05	0.80	1.01	0.96
Plumas NF	1.07	0.05	0.97	1.18	0.91
Tahoe NF	0.99	0.04	0.92	1.07	0.57
Eldorado NF	0.90	0.03	0.84	0.96	1.00
Stanislaus NF	1.01	0.03	0.95	1.08	0.67
Yosemite NP	0.99	0.07	0.86	1.12	0.59
Sierra NF	1.10	0.06	0.99	1.23	0.96
Sequoia-Kings Canyon NP	0.96	0.06	0.83	1.08	0.76
Sequoia NF	0.88	0.04	0.81	0.95	1.00
<i>Region-wide</i>	0.98	0.02	0.95	1.01	0.92

10.2 Supplemental figures

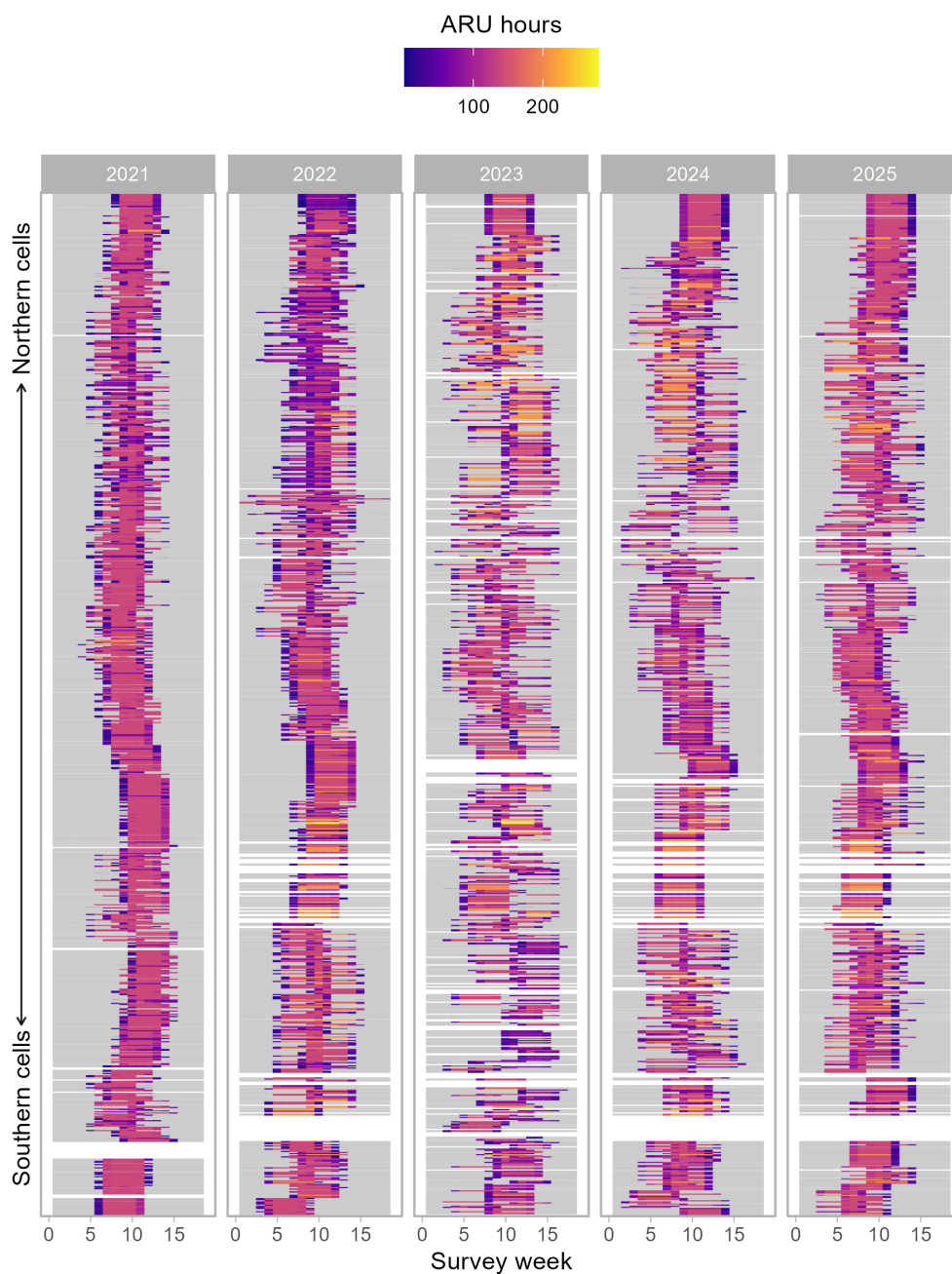


Figure S1. Passive acoustic monitoring effort and timing by hexagonal grid cell in the Sierra Nevada region, 2021–2025. Cells are ordered by latitudinal position, with warmer colors indicating greater survey effort, and gray shading indicating weeks without survey effort. Missing rows show cells that were not surveyed in one or more years.

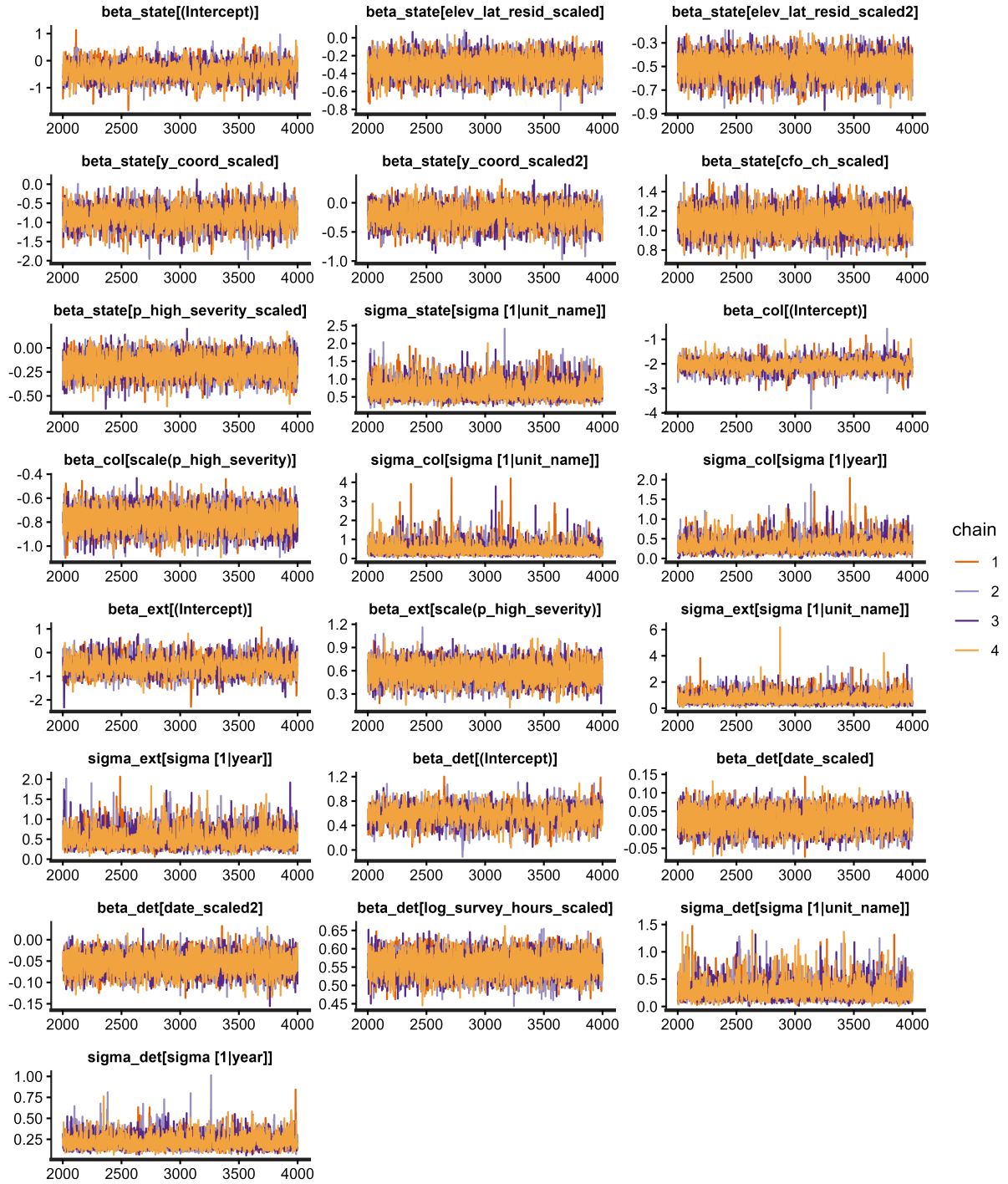


Figure S2. Traceplots for the California spotted owl dynamic occupancy model.

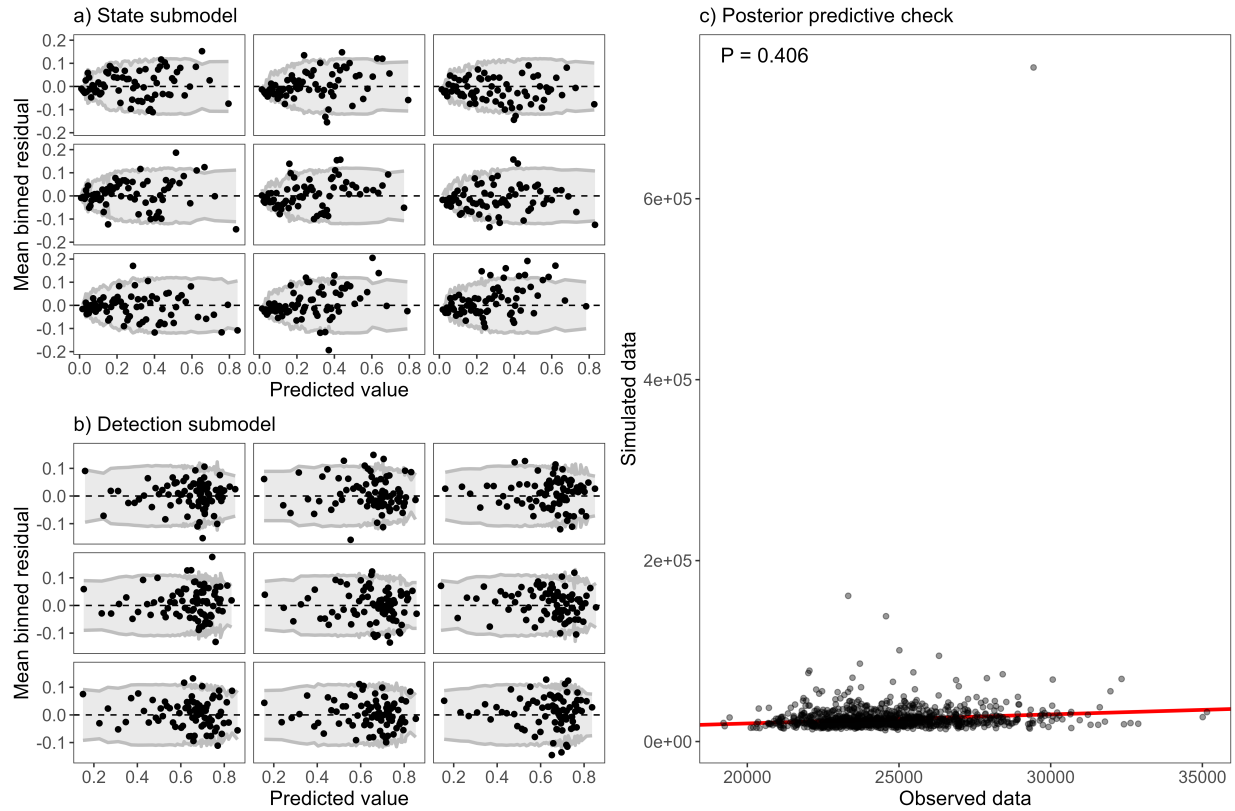


Figure S3. Residual plots for state (a) and detection (b) submodels and posterior predictive check plot (c) for California spotted owl dynamic occupancy model. Goodness-of-fit test (Bayesian p -value = 0.406) and posterior predictive check plot indicated adequate model fit.