Bioregional-scale acoustic monitoring can support fire-prone forest restoration planning

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In many forests globally, resilience-focused restoration is necessary to prevent fire-driven regime shifts. However, restoration planning is challenged by limited resources for monitoring biodiversity responses to management intervention and to natural disturbances. Bioregional-scale passive acoustic monitoring, when combined with automated species identification tools and management-relevant habitat data, can be a tractable method to simultaneously monitor suites of complementary indicator species and rapidly generate species-specific information for resource managers. We demonstrate these methods by mapping the occurrence of ten avian indicator species while examining the impact of fire history on patterns of occurrence across 25,000 km^2 of California's Sierra Nevada mountains. Monitoring complementary indicator species with rapidly developing bioacoustics technology and relating their occurrence to policy-ready habitat metrics have the potential to transform restoration planning by providing managers with high-resolution, ecosystem-scale information that facilitates adaptive management in an era of rapid environmental change.

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Declining ecosystem resilience threatens biodiversity at a global scale (Forzieri *et al.* 2022). Loss of resilience leaves ecosystems vulnerable to potentially irreversible regime shifts (eg conversion of forests to shrubland; Folke *et al.* 2004), which can have cascading impacts, including loss of biodiversity and degradation of ecosystem services (Scheffer *et al.* 2001). To enhance resilience, managers increasingly rely on restoration in an adaptive management framework (Jacobs *et al.* 2015). This framework involves setting specific and measurable goals in terms of habitat structure and cover, and then iteratively assessing whether management intervention is effective in reaching those goals (Jacobs *et al.* 2015). Thus, monitoring is an essential component of adaptive management that facilitates an understanding of how species respond to habitat changes resulting from both natural disturbance and management intervention itself. However, the capacity to monitor biodiversity at sufficiently high resolutions and across broad spatial scales is often limited, which results in an inadequate understanding of species–habitat relationships that can compound uncertainty and slow the pace of adaptive management.

The forests of western North America exemplify these issues—a warming climate and changing disturbance regimes are causing large-scale conversion of forests to shrub-dominated systems (Coop *et al.* 2020), often at a faster rate than managers can track changes in landcover or wildlife populations. In the Sierra Nevada mountains of California, increasingly frequent megafires limit forest regeneration (Coop *et al.* 2020), threatening species persistence and ecosystem services in a global hotspot for both biodiversity and agricultural production (Adams 2013). Although restoring forest resilience is a priority, the pace and scale of forest restoration are well below what is necessary to avert massive ecosystem change (North *et al.* 2012; Knight *et al.* 2022). One factor slowing restoration in the Sierra Nevada is the perceived trade-off between restoration and conservation of one of the most prominent species in the western US: the spotted owl (*Strix occidentalis*) (Stephens *et al.* 2020; Jones *et al.* 2022). While the spotted owl has played a defining role in forest management for decades (Gutiérrez 2008; Stephens *et al.* 2020), it is just one of the more than 200 bird species occurring in the Sierra Nevada. Research on most other Sierra Nevada species, even federally designated indicator species (USFS 2007), is limited to small-scale, opportunistic studies. Lack of bioregional-scale information—about how Sierra Nevadan bird communities are associated with current forest conditions and are impacted by changing disturbance regimes and management intervention—forces managers to plan restoration with considerable uncertainty about intervention outcomes.

Emerging conservation technologies have the potential to address monitoring shortfalls and provide managers with more complete information for restoration planning (Wood *et al.* 2024). Here, we demonstrate the synthesis of

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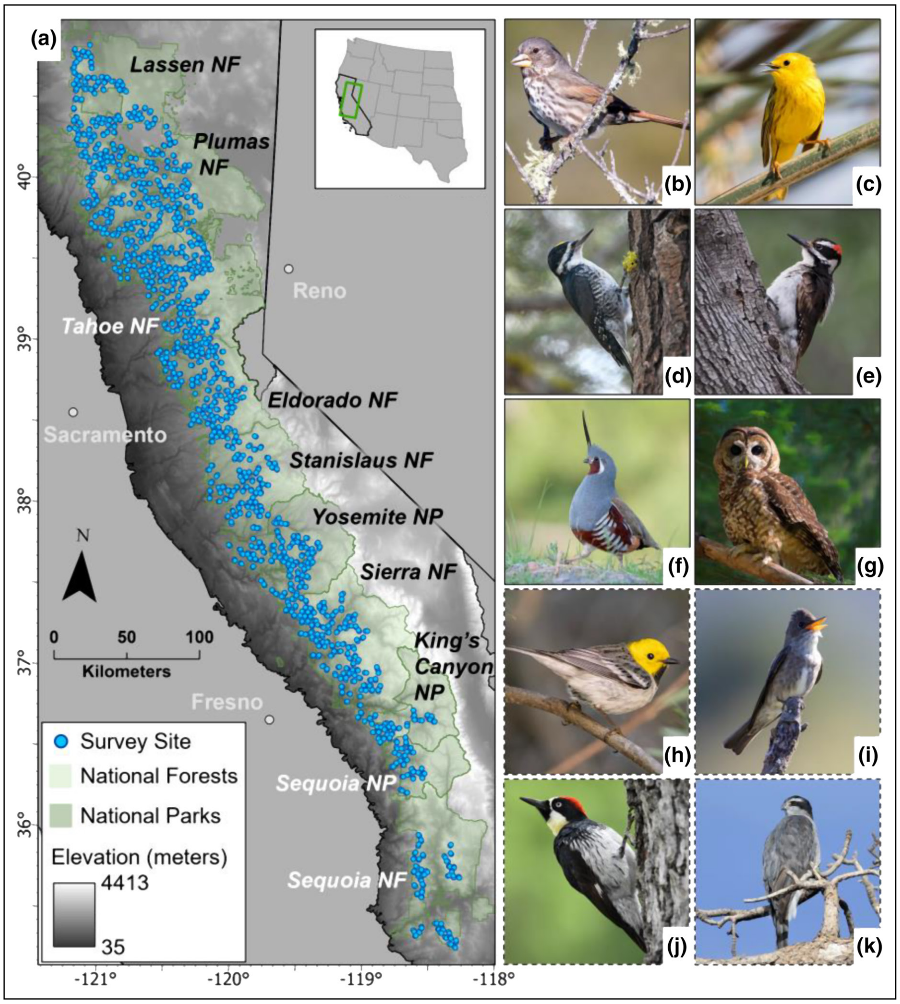

Figure 1. (a) Map of the study area with elevation and the survey locations for the Sierra Nevada bioregion. (b–k) The indicator species included in this study (with image credit and Macaulay Library unique identifier): (b) fox sparrow (*Passerella megarhyncha*) (Connor Cochrane, ML417831361); (c) yellow warbler (*Setophaga petechia*) (Bradley Hacker, ML102888141); (d) black-backed woodpecker (*Picoides arcticus*) (Vladimir Pravosudov, ML474401111); (e) hairy woodpecker (*Leuconotopicus villosus*) (Aidan Brubaker, ML450485851); (f) mountain quail (*Oreortyx pictus*) (Shailesh Pinto, ML586116811); (g) California spotted owl (*Strix occidentalis occidentalis*) (Danny Hofstadter); (h) hermit warbler (*Setophaga occidentalis*) (Marky Mutchler, ML438636841); (i) olive-sided flycatcher (*Contopus cooperi*) (Michael Stubblefield, ML465414131); (j) acorn woodpecker (*Melanerpes formicivorus*) (Steve Tucker, ML167275911); and (k) American goshawk (*Astur atricapillus*) (Eric Tipton, ML384343761). Species photos with solid borders are designated USDA Forest Service indicator species; species photos with dashed borders were selected for this study.

bioregional-scale passive acoustic monitoring, a machine-learning animal sound identification algorithm (Kahl *et al.* 2021), and remotely sensed data that are "management-ready"—directly compatible with metrics used by forest managers for restoration planning across the bioregion. We conducted a high-resolution, bioregional-scale study of ten Sierra Nevada avian indicator species, six of which are federally designated indicator species for this region. Specifically, we mapped current habitat suitability for indicator species to facilitate short-term restoration planning and examined the additional explanatory power gained by including natural disturbance (ie fire) in our models. Our work offers more comprehensive insight into the links between forest conditions and biodiversity by mapping suitability for species beyond the spotted owl, lays the groundwork for understanding future trade-offs between restoration and biodiversity at a broad spatial scale, and demonstrates how emerging conservation tools can facilitate adaptive management strategies.

Methods

Study site and species

Our study area spanned 24,494 km^2 of California's Sierra Nevada, including seven national forests and three national parks (Figure 1a). We modeled the occurrence of fox sparrow (*Passerella megarhyncha*), yellow warbler (*Setophaga petechia*), black-backed woodpecker (*Picoides arcticus*), hairy woodpecker (*Leuconotopicus villosus*), mountain quail (*Oreortyx pictus*), California spotted owl (*Strix occidentalis occidentalis*), hermit warbler (*Setophaga occidentalis*), olive-sided flycatcher (*Contopus cooperi*), acorn woodpecker (*Melanerpes formicivorus*), and American goshawk (*Astur atricapillus*) (Figure 1, b–k; see Appendix S1: Table S1 for habitat associations). The first six species are federally designated management indicators (USFS 2007) in the Sierra Nevada. We chose the remaining four based on affiliations with important habitat types in the Sierra Nevada that were not represented by the first six species and on the ability of our machine-learning algorithm to accurately identify them (see below).

Passive acoustic surveys and audio processing

Between May and August 2021, we conducted passive acoustic surveys at 1652 sites within 400-ha hexagonal grid cells. Survey cells were randomly selected but non-contiguous and accessible by road, resulting in relatively uniform coverage across the study area. In each cell, we deployed two autonomous recording units (ARUs; Swift recorder, K Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology) at least 500 m apart (Wood *et al.* 2019) for ≥5 weeks. ARUs were set to record continuously from 1800 to 0900 every day using one omnidirectional microphone at a sample rate of 32 kHz. For diurnal species, we analyzed data from 0400 to 0900 and 1800 to 2000; for the largely nocturnal spotted owl, we analyzed data from 2000 to 0400. We identified species' vocalizations in the audio data using a customized version of the machine-learning algorithm BirdNET (Kahl *et al.* 2021). We applied rigorous, species-specific, quality-control standards to detector outputs, and then manually reviewed all (for spotted owl and American goshawk) or many (for the other eight species) putative observations for each species to generate detection/non-detection datasets, which mitigated false positive detections (see Appendix S1: Panel S1 for details).

Occupancy modeling and influence of fire history

We used a Bayesian formulation of single-species, single-season occupancy models (Mackenzie *et al.* 2002) to relate species occurrence to habitat features and fire history. Because our objectives related to facilitating species conservation in the context of forest restoration, we represented forest vegetation with metrics that are widely used in forest management planning (as opposed to using metrics that could be more ecologically precise but that could not be readily incorporated into forest management decision making). In addition, we limited all analyses and inference to sites with ≥75% forest cover. Our goal was not to generate the best possible explanation of where these species might occur across the ecosystem, but rather to directly relate their distributions to management-relevant and manipulatable dimensions of the ecosystem.

We fit two occupancy models for each species: a baseline forest-only model composed of vegetation covariates (forest structure and cover), and a forest+fire model that included the same covariates plus three fire history covariates (Appendix S1: Panel S2). We used the month of June (for non-raptors) or the period from May 20 to June 30 (for raptors) as our primary survey season, and compiled detections from each ARU in each 6-day period into five (non-raptors) or seven (raptors) secondary survey periods. We quantified vegetation and fire history in circular buffers around each ARU at species-specific resolutions (12.6 ha, 113 ha, or 452 ha), which were selected based on empirical evidence about home range sizes and a broadly observed positive relationship between body size and home range size (Haskell *et al.* 2002; Appendix S1: Table S1). Forest structure was represented by mean biomass, canopy cover, canopy height, trees per hectare, and basal area per hectare. For species with >5% naïve occupancy, we also included an interaction between trees per hectare and basal area per hectare (ie basal area per hectare may have a different impact on occupancy in areas with low tree density versus areas with high tree density). Forest cover was represented as the proportion of the buffer around an ARU composed of mixed deciduous/conifer, conifer, and shrub/scrub cover. We derived vegetation (ie forest structure and cover) data from the most recent gradient nearest neighbor dataset created by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group at Oregon State University (Ohmann and Gregory 2002; Bell *et al.* 2024), a forest structure product derived from forest inventory and analysis plots. We also included the linear and quadratic forms of the residuals of elevation regressed on latitude, which represent the effect of elevation on occupancy, corrected for latitude (Saracco *et al.* 2011). The forest+fire models also included the proportion of a buffer burned at low-to-moderate severity in the past 5 years, the proportion of a buffer burned at high severity in the past 5 years, and the proportion of a buffer burned at high severity in the past 6–10 years. Fire history was summarized from a fire severity atlas (Cova *et al.* 2023).

Comparing parameter estimates between the forest-only models and the forest+fire models enabled assessment of the extent to which forest structure and cover covariates accounted for species' responses to fire. If inclusion of the fire covariates improved model performance (as measured by the widely applicable information criterion [WAIC]; Watanabe 2010) and the 95% credible intervals of fire parameter estimates did not include zero, then this suggested that fire history influenced habitat suitability in ways that are not fully represented by forest structure and cover as we quantified them (see above); if WAIC was not reduced and fire covariate credible intervals included zero, then the data did not provide evidence that fire history offered additional explanatory power above and beyond vegetation. Thus, fitting two models for each species allowed identification of indicator species whose responses to fire may be more nuanced than simple responses to changes in forest structure or cover as represented by our management-oriented covariates.

Results and discussion

We demonstrate that indicator species can be monitored in a unified bioacoustic framework, and that their occurrence can be related to vegetation characteristics that are central to defining forest restoration objectives. Our passive acoustic surveys resulted in >700,000 hours of acoustic recordings across >1600 sites spanning 25,000 km^2, a magnitude of simultaneous survey effort that would be cost-prohibitive when relying solely on human surveyors. We fit occupancy models for all indicator species using our management-ready vegetation and fire history covariates (Appendix S1: Table S2; Figures 2 and 3), such that results can be directly applied to forest management policy.

Our results reflect the known ecology of better-studied species well, suggesting that they are also a useful tool for lesser-studied species in the region. For example, spotted owls displayed a negative association with recent high-severity fire and a neutral-to-positive relationship with low-to-moderate severity fire (Figure 2a), while black-backed woodpeckers had generally positive associations with recent fire (Figure 2b; Saracco *et al.* 2011). Thus, the spotted owl was predicted to be absent from recent fire footprints

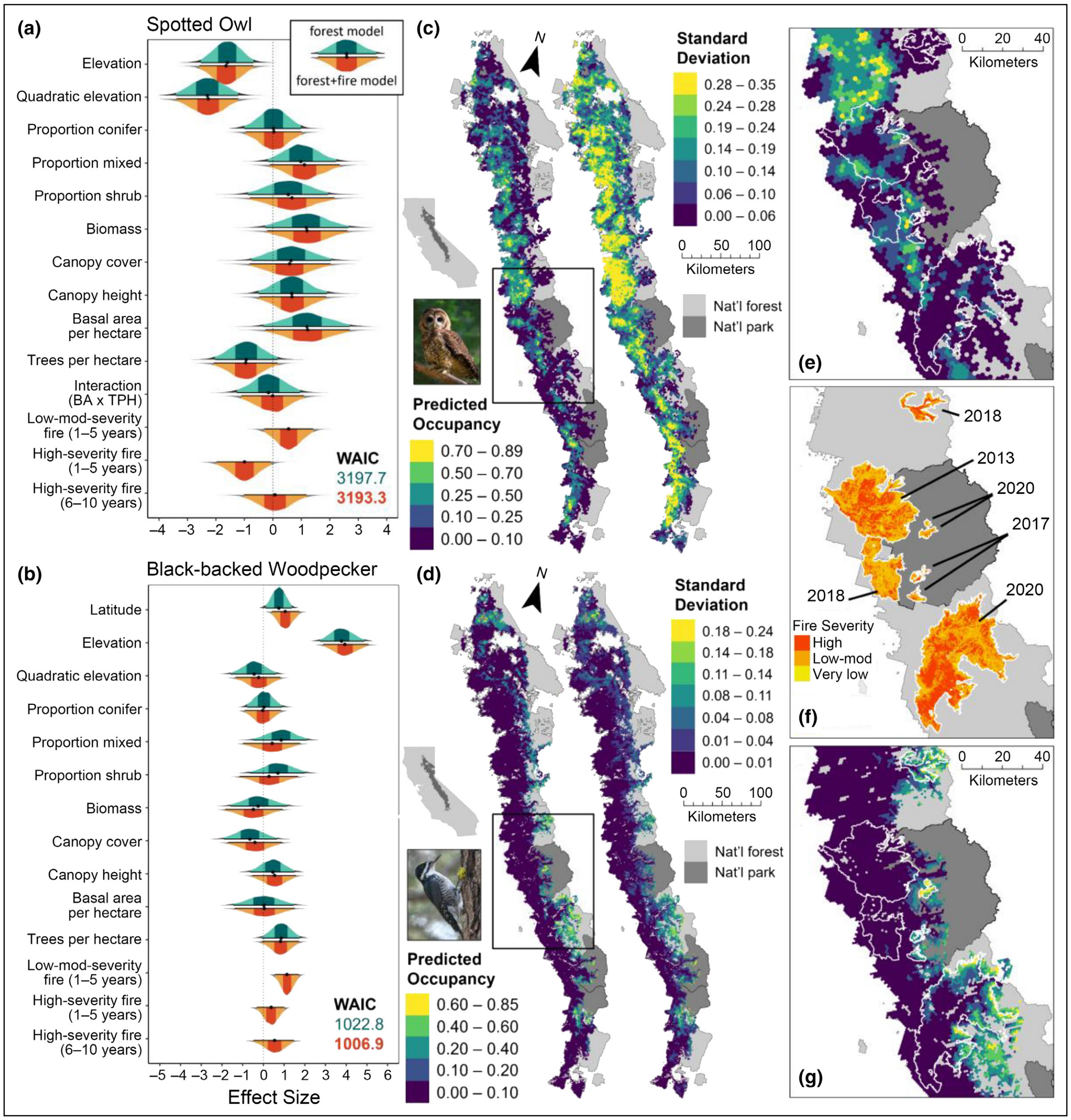

Figure 2. Full results for California spotted owl and black-backed woodpecker across the Sierra Nevada bioregion. (a and b) Comparison of posterior distributions of scaled covariate estimates and widely applicable information criterion (WAIC) for the forest model (top distributions) and the forest+fire model (bottom distributions) for (a) California spotted owl and (b) black-backed woodpecker; 95% credible intervals (CIs) are denoted by the light-colored sections and 50% CIs by the dark-colored sections. (c and d) Maps of predicted occupancy (left) and standard deviation (right) for both species across the bioregion. (f) Examples of large fires in the Sierra Nevada bioregion over the past 10 years and estimated occupancy of (e) California spotted owl and (g) black-backed woodpecker in relation to fire footprints. Image credits are the same as in Figure 1.

(Figure 2 c, e, and f), while the black-backed woodpecker's preference for burned forest with access to unburned or low-severity burned areas for breeding (Stillman *et al.* 2019) was demonstrated by higher predicted occupancy in small fire footprints and around the edges of larger fires (Figure 2, d, f, and g). The bioacoustic framework that we utilized here enabled the creation of high-resolution habitat suitability maps for an entire suite of complementary indicator species (Figure 3), which provide more complete information about how these species are associated with current forest conditions. Although the challenge of balancing the short-term and long-term costs and benefits of management intervention for biodiversity remains unresolved (Stephens *et al.* 2020), our study lays the groundwork to better understand these trade-offs for a wider range of species and to more rapidly detect changes in species occurrence and adapt management strategies when necessary.

Our work also highlights the importance of fire history in shaping species occurrence. The forest+fire models had a lower WAIC score for eight species, and eight species had at least one well-supported fire history covariate (Figure 2; Appendix S1: Figure S1). In many cases, the forest model remained competitive with the forest+fire model (eg acorn woodpecker and American goshawk), suggesting that forest structure and cover information is useful, especially if disturbance information is not readily available. However, frequent support for the forest+fire models suggests that many species are not merely responding to the relatively few dimensions of vegetation used in many forest management plans, such as canopy cover or biomass, but to other ecological changes induced by fire disturbance as well. All of the species we considered responded either positively or neutrally to recent low-to-moderate severity fire, which was historically more common in this ecosystem (and typically leaves large trees unscathed). With respect to recent high-severity fire, the spotted owl and hermit warbler had negative associations, while the acorn woodpecker and olive-sided flycatcher had positive associations. In addition, with respect to older high-severity fire, the fox sparrow, mountain quail, and yellow warbler had positive associations. Collectively, our findings affirm the importance of specific combinations of severity and time-since-fire as drivers of biodiversity (Jones and Tingley 2022).

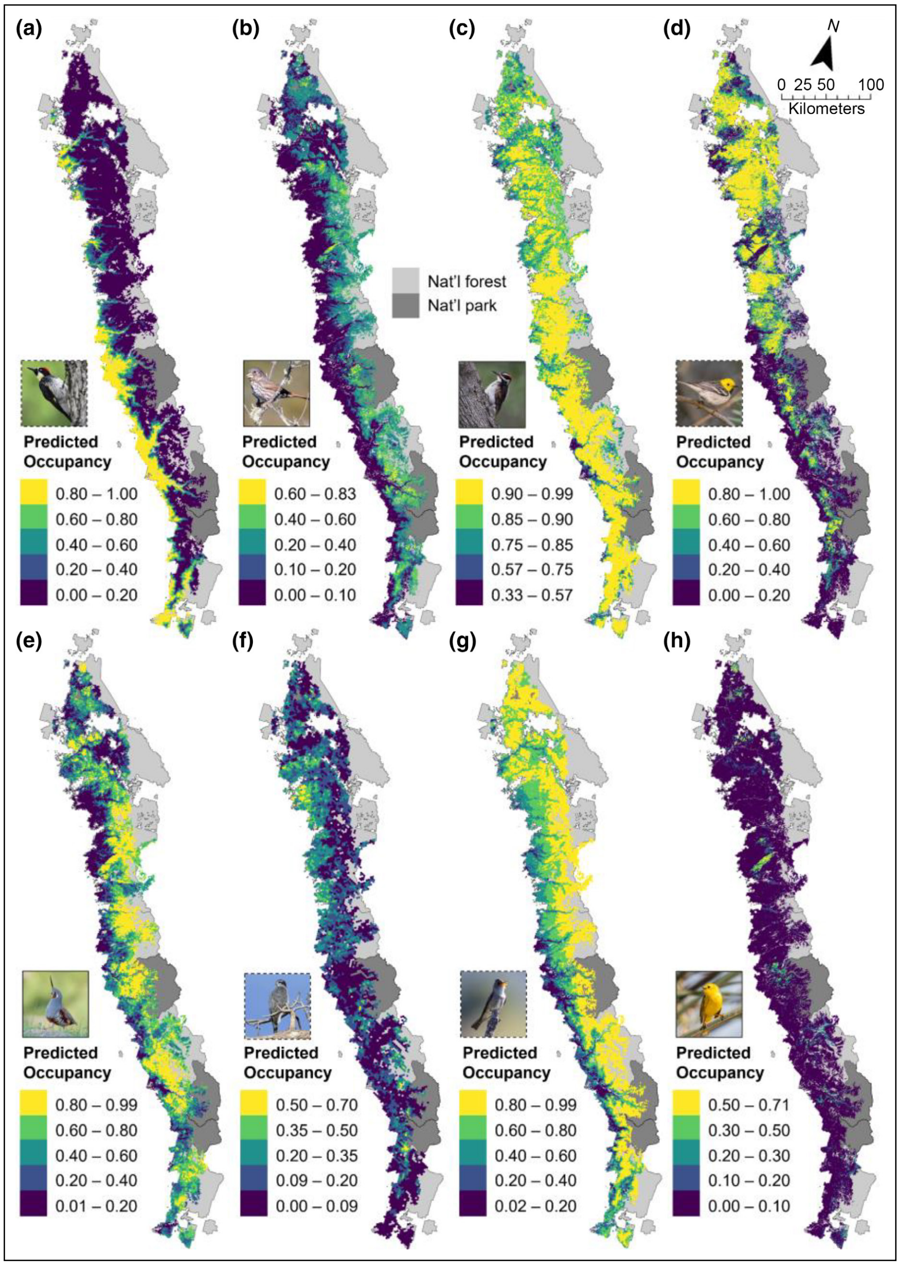

Figure 3. Interpolated occupancy estimates across the Sierra Nevada bioregion for (a) acorn woodpecker, (b) fox sparrow, (c) hairy woodpecker, (d) hermit warbler, (e) mountain quail, (f) American goshawk, (g) olive-sided flycatcher, and (h) yellow warbler. Posterior distributions of occupancy parameter estimates and maps of error for interpolated occupancy can be found in Appendix S1: Figure S1. Image credits are the same as in Figure 1.

We envision several applications for these results and, more broadly, our bioacoustic framework. First, our habitat suitability maps—and others like them generated for other ecosystems—can be used to prioritize areas for restoration treatments. For example, because hermit warblers are negatively associated with high-severity fire, areas of high habitat suitability for the hermit warbler could be prioritized for fuels reduction treatments that promote low-to-moderate severity fire and limit the extent of high-severity fire (eg prescribed burns). Second, results generated by our bioacoustic framework provide real-world information about how species respond to management actions in practice, a key step in planning within an adaptive management framework. In our case, fuels reduction treatments typically reduce canopy cover and biomass; thus, in the short term, species like the spotted owl would be expected to have reduced occupancy after such treatments (Figure 2a), while other species, like the mountain quail, could benefit (Appendix S1: Figure S1). Third, the habitat associations we established here are currently being used to generate forward projections of indicator species occupancy through mid-century under different climate and forest restoration scenarios. Synthesizing species and climate models with plausible restoration scenarios will better characterize the potential short-term and long-term trade-offs of alternative management scenarios for indicator species directly in the context of climate change in this ecosystem or any for which the requisite data can be collected. Lastly, we emphasize that the habitat associations we found in our first year of Sierra-wide acoustic monitoring, while useful, may not be static. Continual data collection, as is currently underway, will allow models to be re-fit to better characterize habitat associations of indicator species, the variability around relationships, and the population dynamics (eg colonization and local extinction) that lead to observed patterns. In the Sierra Nevada, altered disturbance regimes are likely to transform forests unless management can strengthen forest resilience through restoration (Hoecker *et al.* 2023). Using passive acoustic monitoring to map species occurrence cost-effectively and iteratively in relation to management-relevant forest characteristics can facilitate better restoration planning and enable more efficient adaptive management.

Implications

When implementing ecosystem restoration, managers globally face critical and time-sensitive trade-offs. In the Sierra Nevada, managers must balance the need for restoration with the impacts of restoration on the species they hope to protect (Jones *et al.* 2022). Our monitoring framework improves understanding of restoration treatment impacts across a broader range of species, and enables managers to adapt restoration implementation (eg location, intensity, or technique) more rapidly if adverse outcomes become apparent for species of interest. The use of management-ready habitat variables is critical: in some cases, it is more important to understand how a species distribution may shift in response to the features of the landscape used to define restoration goals, rather than to rely on boutique habitat variables that enable excellent predictions but fail to align with how restoration is implemented. As acoustic monitoring continues in the Sierra Nevada and elsewhere globally, it enables increasingly powerful experimental designs, such as before–after control–impact studies, that can help elucidate causal effects of both natural disturbances and restoration treatments on indicator species and biodiversity more broadly (Wood *et al.* 2024). Thus, bioregional-scale passive acoustic monitoring, when combined with machine-learning tools and policy-ready habitat information, can be part of the solution to the challenge of conserving biodiversity in a rapidly changing world.

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Data Availability Statement

Data and code (Brunk 2024) are available on Zenodo at https://doi.org/10.5281/zenodo.14365019. Additionally, raw acoustic data can be accessed via the Sierra Nevada Bioacoustic Monitoring Data Hub, accessible here: https://acousticdownload.russell.wisc.edu.

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Supporting Information

Additional material can be found online at http://onlinelibrary.wiley.com/doi/10.1002/fee.2843/suppinfo