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Warm temperatures and severe fire drive a range contraction of an avian old-forest specialist in the Sierra Nevada, USA

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In recent decades, climate change has exerted detrimental effects on forest ecosystems and the biodiversity they harbor, in part via the combined effects of rising temperatures and changing disturbance regimes. Old-forest species may be acutely sensitive to these changes, especially in ecosystems such as the Sierra Nevada, USA, where historical losses of old-forest habitat are now coupled with a rise in atypically large, severe fires. However, the combined effects of temperature and severe fire are relatively understudied at landscape scales. We used a four-year, landscape-scale passive acoustic monitoring program to study the Hermit Warbler (*Setophaga occidentalis*), a temperature- and fire-sensitive bird species that is closely associated with old-forest habitat. Using a dynamic occupancy model, we characterized the population dynamics in response to elevation, latitude, relative temperature, and high-severity fire. The Hermit Warbler population declined 8.3% during our study, shifting away from the warmer, lower-elevation, and southern sites and toward sites at higher latitudes. It displayed a strong extinction response to severe fire over a 1-10-year post-fire period and failed to colonize such areas over the same time span. Our results suggest that limiting the occurrence of large, severe fires will be necessary to preserve this old-forest indicator but not sufficient: rising temperatures will also lead to population declines even in the absence of habitat loss due to fire. As climate change accelerates, understanding species' responses to shifting environmental conditions will be crucial for guiding adaptive management and ensuring the persistence of biodiversity in fire-prone landscapes.

KEYWORDS
climate change, dynamic occupancy model, Hermit Warbler, megafire, range shift

Introduction

Climate change is projected to substantially alter global forest ecosystems, threatening species that inhabit them. Increases in global average temperatures—recent consensus projections estimate increases between 1.5 and 4.5°C by 2100 (IPCC, 2023)—and climate-linked increases in severe fire occurrence (Pausas and Keeley, 2021; Sayedi et al., 2024) can subject species to physiological stress and habitat loss at the population or ecosystem level. This can lead to sudden, rapid, and potentially widespread changes to biodiversity (Turner et al., 2020). Species dependent on old-forest habitat, characterized by dense canopies and old trees with high basal area, may be buffered from rising temperatures in the short-term due to the microclimatic refugia—relatively cooler pockets of habitat—created by such forests (Betts et al., 2018; Frey et al., 2016). However, they may also be acutely vulnerable to the loss of such forests as climatic warming occurs. Thus, understanding whether populations respond to spatial variation in temperature and major disturbances, like fire, is a critical first step for understanding their future response to climate change.

A species' vulnerability to climate change is comprised of its sensitivity to ongoing change, its adaptative capacity, and the magnitude and rate of exposure to change (Moritz and Agudo, 2013; Thurman et al., 2020). Species sensitivity to ongoing climate change is evident via phenological (Cohen et al., 2018) and geographic shifts (Parmesan and Yohe, 2003; Rushing et al., 2020), demographic responses to warming (Breed et al., 2013), and altered biological interactions (Alexander et al., 2015). Habitat loss may impel range shifts in sensitive species if preferred climatic conditions are neither longer locally available (e.g., a stand of old-growth forest) nor regionally prevalent, with species moving toward higher elevations and latitudes to track their thermal niche (Parmesan and Yohe, 2003). However, while rising temperature may encourage upward altitudinal and latitudinal shifts, the presence of climate refugia, physiological limitations, changes in food or moisture availability, or competition can lead to species-specific shifts that do not abide to expectations of upslope and poleward geographic shifts (Morelli et al., 2017; Tingley et al., 2012; Wood et al., 2016). At the same time, population declines and range shifts are expected to reduce genetic diversity and thus affect long-term adaptive capacity of species under threat (Pauls et al., 2013). Globally, 15% of species assemblages will experience abrupt exposure to climate change once average global temperatures exceed 4°C above pre-industrial levels (Trisos et al., 2020), making understanding species responses to climate change a widespread conservation challenge.

The complexity of species' climate responses is likely compounded by ongoing and rapid changes to habitat due to intensifying fire regimes which, in western North America, threaten the persistence of forest ecosystems (Coop et al., 2020). In California's Sierra Nevada, the legacies of colonialism, resource extraction, and fire suppression are interacting with climate change to intensify the risk of large, severe fire (Stephens et al., 2020; Taylor et al., 2016). Extensive losses of mature conifer forest have already occurred (Steel et al., 2022) and some may be quasi-permanent (Coop et al., 2020). Indeed, large, severe fires are now defining landscape structure (Cova et al., 2023). At the same time, climate-sensitive old-forest species are increasingly facing temperatures beyond their physiological limits within their range (McGinn et al., 2024), in spite of potential short-term buffering effects of old-forest microclimates. Thus, the direct effects of climate change (increasing temperatures) and the indirect effects (changing fire regimes) may combine to rapidly influence the distribution of sensitive species.

The Hermit Warbler (*Setophaga occidentalis*) is an old forest-associated bird species in the Sierra Nevada—the southern edge of its breeding range, which extends into the Pacific Northwest—known to be especially temperature- and fire-sensitive (Betts et al., 2018; Bielski et al., 2024; Wood et al., 2024), making it an ideal candidate to examine the direct and indirect effects of climate change on vulnerable avian populations. They are strongly associated with old-forest habitat and, correspondingly, averse to high-severity fire (Bielski et al., 2024; Wood et al., 2024), and their populations decline with increased temperatures (Betts et al., 2018; Kim et al., 2022). Drawing on four years of passive acoustic monitoring data that spanned the entire western slope of the Sierra Nevada, we tested the hypothesis that Hermit Warbler occupancy dynamics are sensitive to the spatial variation in temperature and severe fire. In doing so, we predicted: (1) that site extinction rates will increase with average temperatures and the local extent of severe fire; (2) that site colonization would increase with elevation and latitude; and (3) that site colonization would decrease with increasing average temperature and with the amount of forest that recently burned at high severity. By examining the responses of a species that is sensitive to increases in temperature and severe fire, which represent direct and indirect effects of climate change, we demonstrate an analytical approach to understanding potential climate-induced avian population changes that are globally applicable to species in rapidly changing environments.

Methods

Passive acoustic surveys and audio analysis

During May-July of 2021 – 2024, we conducted passive acoustic surveys across the western slope of the Sierra Nevada (six National Forests) at 876 locations that were sampled each summer (i.e., four consecutive years) (Figure 1). Broadly, this region is characterized by mixed conifer forest, with ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*) dominating. The lower elevations in our study area (lowest elevation: 328 m a.s.l.) also have black oak (*Quercus kelloggii*), while the highest elevations in our study (highest elevation: 2528 m a.s.l.) were dominated by white fir (*Abies concolor*).

Each year, autonomous recording units (ARUs; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) were deployed for approximately five weeks each, with deployments staggered throughout the spring. Pairs of ARUs were deployed 500–900 m apart, with 1.5–3 km between pairs (see Kelly et al., 2023; Wood et al., 2019) in areas with acoustically preferable geography, such as along ridges instead of in ravines; inter-ARU spacing was initially determined to avoid overlapping survey coverage for Spotted Owls (see Wood et al., 2019) but is coincidentally sufficiently large to assume independence for small-bodied passerines with correspondingly small home ranges. ARUs recorded continuously via one omni-directional microphone at a sample rate of 32 kHz; for this analysis we focused on audio recorded between 05:00–09:00 and 18:00–20:00 local time, when Hermit Warbler vocalizations were most likely to be heard.

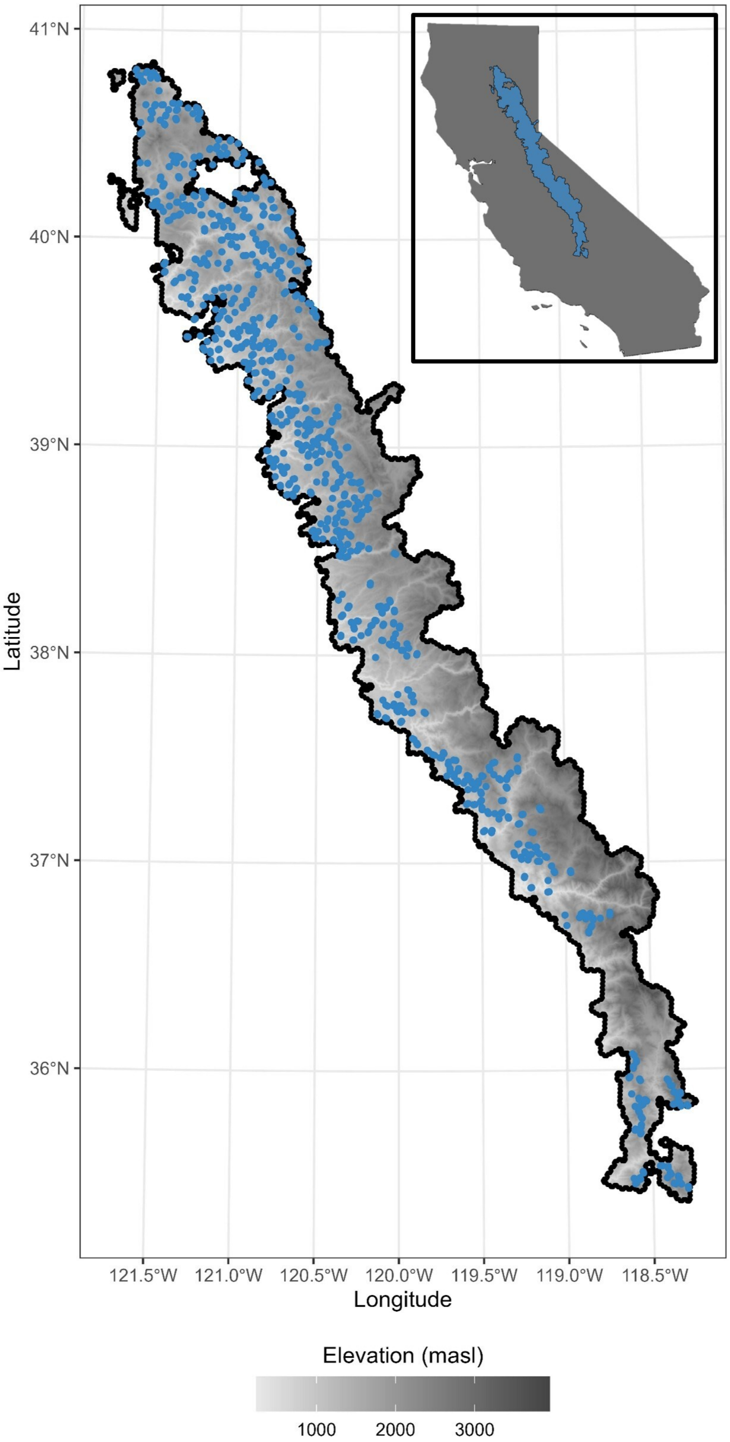

FIGURE 1
In May – July of 2021 - 2024, we deployed 876 autonomous recording units at the same locations across the Sierra Nevada, USA. For the duration of the approximately five-week annual deployments, the units recorded continuously via one omni-directional microphone at a sample rate of 32 kHz; for this analysis we focused on audio recorded between 05:00–09:00 and 18:00–20:00 local time.

We analyzed acoustic data with BirdNET, a convolutional neural network capable of identifying Hermit Warbler vocalizations and thousands of other species by sound (Kahl et al., 2021). We manually validated 200 randomly selected BirdNET predictions of Hermit Warbler vocalizations (100 from a broad score range [0.1 – 1.0]; 100 from an upper range [0.9-1.0]), and then fit a logistic regression to relate the score to prediction outcome, yielding a probabilistic relationship between prediction score and the probability that a given prediction was correct (Wood and Kahl, 2024). We treated predictions with a Pr(true positive) ≥ 0.99 as true Hermit Warbler observations. At this threshold, precision (the proportion of retained predictions that are correct) was 1.0 and recall (the proportion of target sounds that have been recorded and correctly identified as such at a given threshold) was 0.78.

Environmental data acquisition

We quantified the environmental conditions at our recording sites using remotely sensed data, using either the point value precisely overlapping an ARU's location (elevation and latitude) or a value associated with the area in a 120-m buffer around each ARU deployment location (all other variables, described below). Mean tree diameter (30-m resolution) was obtained from F3, which extrapolates local field measurements to landscape conditions via tree growth models and remotely sensed data (Huang et al., 2018). Our tree diameter data reflected the conditions in 2016, the most recent year available; this aspect of forest structure has previously been shown to be a strong predictor of Hermit Warbler occupancy in the Sierra Nevada (Bielski et al., 2024).

We represented fire severity and history using categorical 30m resolution rasters of the Composite Burn Index (CBI; Key and Benson, 2006) from 1985–2023 across our study extent. CBI maps were generated in Google Earth Engine predicting bias-corrected CBI values from random forest models parameterized with latitude, climatic water deficit, and various spectral indices 1-yr pre- and post-fire from Landsat imagery spanning 1985-2023 (Winiarski et al., 2025). We used CBI estimates for all pixels within fires ≥ 4 ha derived from CAL FIRE historical fire perimeters. CBI values ≥ 2.25 were categorized as high-severity fire (≥75% canopy mortality), and values below 2.25 were classified as low- or moderate-severity (https://burnseverity.cr.usgs.gov/ravg/background-products-applications). CBI was summarized within the 120-meter buffer of each ARU as the proportion of unburned, low-to-moderate, and high severity fire that occurred 1-5, 6-10, and 11–35 years preceding the sampling year for each ARU. After exploratory analyses indicated that differentiating 1-5- and 6-10-year-old fires did not improve model fit, we consolidated the fire data into 1-10- and 11-35-year bins.

To quantify the thermal environment, we used 30-m resolution remotely sensed mean relative summer temperature derived from the Landsat8 Thermal Infrared Sensor (TIRS) (Elsen et al., 2020, 2021). Relative temperature values were calculated from 2013–2018 as the mean value within an 11x11 pixel moving window for each year and then collapsed to a single image using the median pixel value across the 6-year time-series (Elsen et al., 2020). We chose to use *in situ* measurements of thermal conditions (i.e., TIRS) to capitalize on finer spatial resolution (30-m) in complex terrain and more "proximal" conditions (Klinges et al., 2024) rather than contemporaneous but coarser, gridded temperature data (e.g., Daymet; Thornton et al., 2022) derived from sparse weather stations across the Sierra. For each ARU location we summarized relative temperature measurements as the mean value of the time span considered within our 120 m buffer. Thus, our thermal data had high spatial resolution that reflected important local conditions (e.g., slope and aspect) over a recent but longer-term average, rather than annual thermal conditions of a site in any given year. Correspondingly, in subsequent analyses relative temperature was treated as a static site covariate (akin to elevation or latitude) rather than a time-varying covariate (like our annually updated fire data). Therefore, we interpreted significant temperature-linked parameters as indicative of a response to local, medium-term average thermal conditions.

Importantly, relative temperature and mean tree diameter had a strong negative correlation (r = -0.77), so we fit a linear model of the relative temperature as a function of tree diameter (β = -0.768; R^2 = 0.59, p<0.001). Positive residuals are indicative of a site that is warmer than expected given the mean tree diameter; negative residuals are indicative of a site that is cooler than expected given the tree diameter. Thus, the relative temperature~tree diameter residuals provide a forest structure-corrected measure of the thermal environment and, critically, are uncorrelated with tree diameter (r = 0.00).

For all raster data we performed spatial operations and extractions in R Version 4.4.1 (R Core Development Team, 2020) using R packages 'terra' (Hijmans et al., 2025), 'sf' (Pebesma and Bivand, 2025), and 'exactextractr' (Baston, 2024). We estimated the proportion of fire classes within our buffer using the 'landscapemetrics' package (Hesselbarth et al., 2019). Elevation data was accessed via Google Earth Engine (Gorelick et al., 2017).

We scaled all site covariates and conducted pairwise correlational analyses of all covariates. The strongest correlation was a strong negative relationship between temperature and tree diameter (r = -0.77); all other correlations were weak (r< 0.3). The distribution of each variable in their original units and scaled values are available in Supplementary Table 1.

Occupancy modeling

We used a dynamic occupancy modeling approach to test our predictions about Hermit Warbler population dynamics (MacKenzie et al., 2003). Our model contained four primary sampling periods representing the breeding seasons of 2021, 2022, 2023, and 2024, each of which was divided into eight six-day secondary sampling periods. We applied two filters to our Hermit Warbler observations to create encounter histories for each site. First, we defined our primary seasons as June 1 through July 18 in each year because observations before June could reflect seasonal migration rather than stable breeding behavior, while observations after July 18 could increasingly reflect post-breeding movement (and were comparatively scarce in our dataset). Second, we considered any site with only one observation—one Hermit Warbler vocalization above our Pr(tp) ≥ 0.99 inclusion threshold —in June as unoccupied, to account for occasional transient behaviors (violations of the closure assumption) or high-scoring false positives. After applying these criteria, if one or more observations occurred during a secondary sampling period, we treated that as a detection. As noted above, precision for our detector was extremely high (1.0) and our two-prediction threshold provided further insurance against false positives. The high recall ensured that false negatives would have a minimal effect on detection probability.

We tested our hypothesis about the direct and indirect effects of climate change on Hermit Warblers in the Sierra Nevada by interpreting parameter estimates in a single global model. This approach was best suited to directly test our hypotheses, allowing us to compare the relative effects of each covariate. Detection (p), the probability of observing the species given that it was present, was modeled as a function of survey effort (total number of hours of audio recorded *per* sampling period) and ordinal date. Initial occupancy (ψ) was modeled as a function of elevation (linear and quadratic terms), latitude (linear and quadratic terms), mean tree diameter, temperature~tree diameter residuals, and the amount of high-severity fire during the prior 10 years. Mean tree diameter, though not directly relevant to this investigation's hypotheses, is predictive of Hermit Warbler occupancy (Bielski et al., 2024) and was included to improve model fit. Colonization (γ) and extinction (ε) were modeled as a function of elevation (linear and quadratic terms), latitude, mean tree diameter, temperature~tree diameter residuals, and high-severity fire in the previous 10 years. The amount of high-severity fire in the previous 11–35 years was included as a colonization covariate but not an extinction covariate because we expected fire-related site extinction responses to be more temporally proximate to the fire.

All covariates were scaled to allow effect size comparisons on colonization and extinction dynamics. We considered a covariate as influential on the population if the 85% confidence interval around its point estimate did not overlap zero (Arnold, 2010). We derived annual occupancy estimates and calculated associated standard errors with nonparametric bootstrapping (100 samples). We fit the model using package 'unmarked' (Fiske and Chandler, 2011) in Program R v4.4.1 (R Core Development Team, 2020).

Results

Consistent with our hypothesis, Hermit Warbler population dynamics across the Sierra Nevada were responsive to temperature and fire, among other influences, with the direction of effects broadly consistent with our predictions. Importantly, we observed an 8.3% decline in site occupancy rates during our study period, from 0.658 (85% CI: 0.633-0.682) in 2021 to 0.603 (85% CI: 0.579-0.627) in 2024 (Figure 2). While derived occupancy estimates were statistically unchanged between successive years, the overall occupancy change suggests that an ecosystem-scale decline may be occurring in this old-forest, climate-sensitive species. The complete model summary (intercepts, parameter estimates, and standard errors) is available in Supplementary Table 1.

Detection probabilities were high, indicating that our results are minimally affected by missed observations. Detection increased with survey effort ($\beta = 0.0925$, $SE = 0.00163$), though there was not substantial variation in effort (among secondary sampling periods with any survey effort, almost 70% had the full 42 hours), and decreased from the beginning of the season to the end ($\beta = -0.633$, $SE = 0.0134$). There were eight possible secondary sampling periods per year, though any given location only received five (due to the limits of battery life and overall project logistics). A site surveyed for the first five secondary sampling periods had a cumulative detection probability (p^*) of 1.0; a site surveyed for the last five secondary sampling periods had a p^* of 0.936.

As expected, initial occupancy was positively associated with mean tree diameter ($\beta = 1.608$, $SE = 0.147$) and more strongly influenced by this aspect of forest structure than by any other environmental covariate we considered. Sites with larger-diameter trees were cooler overall (r = -0.77) but after controlling for this relationship, Hermit Warblers were still more likely to occupy sites that were cooler than expected given the tree diameter (i.e., negative temperature~diameter residuals) ($\beta = -0.624$, $SE = 0.177$). After tree diameter, the next most influential driver of initial occupancy was latitude ($\beta_{latitude} = 0.716$, $SE = 0.132$; $\beta_{latitude^2} = -0.298$, $SE = 0.115$; Figure 3). Initial site occupancy rates were higher in the north than in the south, but the relationship was non-linear (Figure 3) such that occupancy at the southern end of our study area was approximately 0.1, climbed to 0.78 slightly north of the midpoint (approximately the South Fork of the American River), and only increased to 0.84 by the northernmost extent of the study area. Initial occupancy displayed a negative quadratic relationship with elevation such that it peaked at intermediate elevations ($\beta_{elevation} = 0.476$, $SE = 0.118$; $\beta_{elevation^2} = -0.157$, $SE = 0.0878$; Figure 3). As expected, the amount of high-severity fire in the past ten years had a strong negative effect on occupancy ($\beta_{fire} = -0.509$, $SE = 0.101$; Figure 3).

The influence of elevation on population dynamics (i.e., colonization and extinction) was only partially consistent with our prediction. Colonization increased with elevation ($\beta_{elevation} = 0.165$, $SE = 0.0873$; $\beta_{elevation^2} = -0.0227$, $SE = 0.0711$; Figure 3) while elevation had a positive quadratic effect on extinction ($\beta_{elevation} = 0.248$, $SE = 0.0110$; $\beta_{elevation^2} = 0.225$, $SE = 0.0958$; Figure 3). In other words, the lower elevational bound of Hermit Warbler's distribution in the Sierra Nevada during our study period shifted upslope, but the upper elevational bound did not display an unambiguous corresponding upslope shift because both colonization and extinction were higher there than at intermediate elevations.

The influence of latitude on population dynamics was consistent with our prediction: Hermit Warblers displayed a northward shift in their relative density of site occupancy across the Sierra Nevada during our study. Although occupancy rates were already high in the northern Sierra Nevada, colonization rates are nonetheless higher in the north than in the south ($\beta = 0.263$, $SE = 0.0989$; Figure 3) whereas extinction rates are higher in the south than in the north ($\beta = -0.384$, $SE = 0.115$; Figure 3).

The influence of relative temperature after controlling for tree diameter was mixed. It had no effect on colonization ($\beta = -0.0394$, $SE = 0.149$; Figure 3), but site extinction rates were higher at sites that were warmer than expected given the tree diameter ($\beta = 0.225$, $SE = 0.152$; Figure 3).

Finally, the effect of high-severity fire on population dynamics was also consistent with our predictions, with colonization negatively ($\beta = -0.623$, $SE = 0.0989$; Figure 3) and extinction positively ($\beta = 0.852$, $SE = 0.0907$; Figure 3) related the amount of fire in the previous 10 years. Most sites were completely unburned (within a 120-m buffer around an ARU) but most of the sites that experienced fire burned extensively (~10% of the site*year observations). At an unburned site, the probability of extinction was 0.106 while the probability of colonization was 0.383; at a fully burned site, probability of extinction was 0.883 while the probability of colonization was 0.0292. Site colonization was unaffected by high-severity fire occurring 11–35 years before the study period ($\beta = -0.00516$, $SE = 0.0728$). Thus, the occurrence of locally extensive high severity fire represented a decadal loss of habitat.

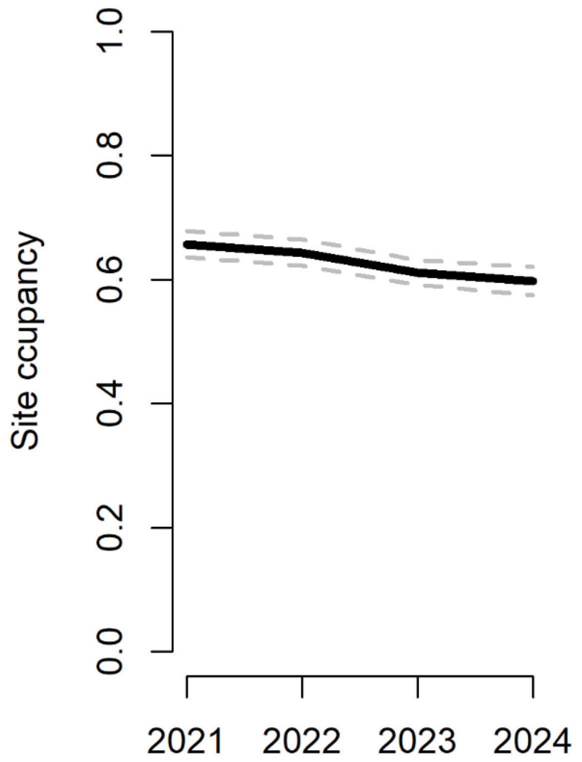

FIGURE 2
Derived site occupancy estimates for the Hermit Warbler (*Setophaga occidentalis*) across the Sierra Nevada, USA for May-July, 2021–2024 sampled at 876 locations across ~25,000km^2 (Figure 1). Dashed gray lines represent the 85% confidence interval. The population experienced an 8.3% decline, from 0.658 (85% CI: 0. 633-0.682) to 0.603 (85% CI: 0. 579-0.627).

Discussion

Our results demonstrate the multifaceted climate-sensitivity of an old-forest-associated species at the southern edge of its breeding range. Over our four-year study period, breeding seasons 2021 – 2024, we observed a significant decline in the Hermit Warbler site occupancy rate across the Sierra Nevada (Figure 2). The regional-scale decline corresponds with shifts toward higher latitudes, away from lower elevation sites, away from sites that had warmer than expected average temperatures given the tree diameter, and away from sites that had burned at high severity in the last ten years. Sensitivity to temperature was clear: the warbler preferred sites with large-diameter trees, which tended to be cooler than other areas (r = -0.77 based on the five-year average summer temperatures at a given site) and sites that were cooler than expected given the tree diameter. Critically, we saw mixed evidence for an upslope distributional shift – a broadly posited potential response to climate change (Parmesan and Yohe, 2003) – with range contraction at lower elevations not clearly accompanied by range expansion at higher elevations. Collectively, these patterns solidify the Hermit Warbler as emblematic of the challenges facing old-forest specialists in the era of climate change. As such, the insights here may be applicable to other similarly situated species.

We did not measure climate change *per se* in our study, relying instead on longer-term mean temperatures measured at comparatively high spatial resolution (30m). Thus, we cannot make inferences about the direct thermal effects of climate change on the Hermit Warbler with our data. Nonetheless, their substantial sensitivity to temperature, as indicated by their initial occupancy associations (noted above) and their elevated extinction rates at warmer-than-expected sites, corroborates other work in suggesting that rising temperatures will have negative consequences for Hermit Warblers (Betts et al., 2018; Kim et al., 2022). Two macrogeographic proxies for temperature, elevation and latitude, were only weakly correlated with relative temperature in our study (r = -0.12 and -0.24, respectively). The lack of a strong correlation between temperature and elevation may stem from fine-scale temperature responses to topographic heterogeneity that weakened expected macro-climatological gradients (e.g., cold air inversions in low elevation valleys; Ashcroft, 2010; Mahrt, 2006). The mixed evidence for upslope shifts (i.e., greater extinction rates accompanying greater colonization rates at high elevations) may reflect constraints to the Hermit Warbler's niche. Elevated site extinction rates at the lowest elevations may reflect thermal limits, while elevated extinction rates at the highest elevations may reflect the transition from mixed conifer forest to subalpine habitat that lacks the structural features the species needs. Individuals may colonize high-elevation sites for thermal reasons but abandon them after one or a few seasons due to a lack of structural elements. The latitudinal shift, however, was striking, and suggested a landscape-scale manifestation of the localized temperature data. We found steady attrition of the Hermit Warbler population in the southern Sierra Nevada – the southern edge of their breeding range – and a movement into the already comparatively high-density population stronghold in the northern Sierra Nevada. This ecosystem-scale pattern may explain the surprisingly muted response of the Hermit Warbler to the catastrophic Dixie Fire in fall 2021, which burned almost 3,900 km^2 of the northern Sierra Nevada, >20% at high severity. A before-after, control-impact study found a negative effect of the fire on Hermit Warbler site extinction and colonization, though site occupancy rates remained high given the extent of habitat loss (Bielski and Wood, 2024). The apparent northward shift of Hermit Warblers in the Sierra Nevada may have partially offset the effects of the Dixie Fire, and underscores the importance of regional context when interpreting local studies.

The negative effect of high-severity fire on initial occupancy and site colonization, and its positive effect on site extinction, over a ten-year period post-fire was unsurprising given extensive prior research showing this species' sensitivity to fire (Bagne and Purcell, 2011; Bielski et al., 2024; Bielski and Wood, 2024; Furnas et al., 2020). Indeed, our results suggest that the observed population decline could be attributed to the several large, severe fires that occurred during our study (e.g., Dixie, Caldor, and KNP Complex Fires). The absence of a colonization response to high-severity fire (≥75% canopy mortality) 11–35 years post-fire suggests a capacity for resilience to this increasingly prevalent disturbance type (Cova et al., 2023; Westerling, 2016). If forest managers can successfully reduce the frequency of large, severe fires in the Sierra Nevada on decadal time scales while enough unburned habitat remains to support acutely fire-sensitive species like the Hermit Warbler, it and other species may at least retain the structural

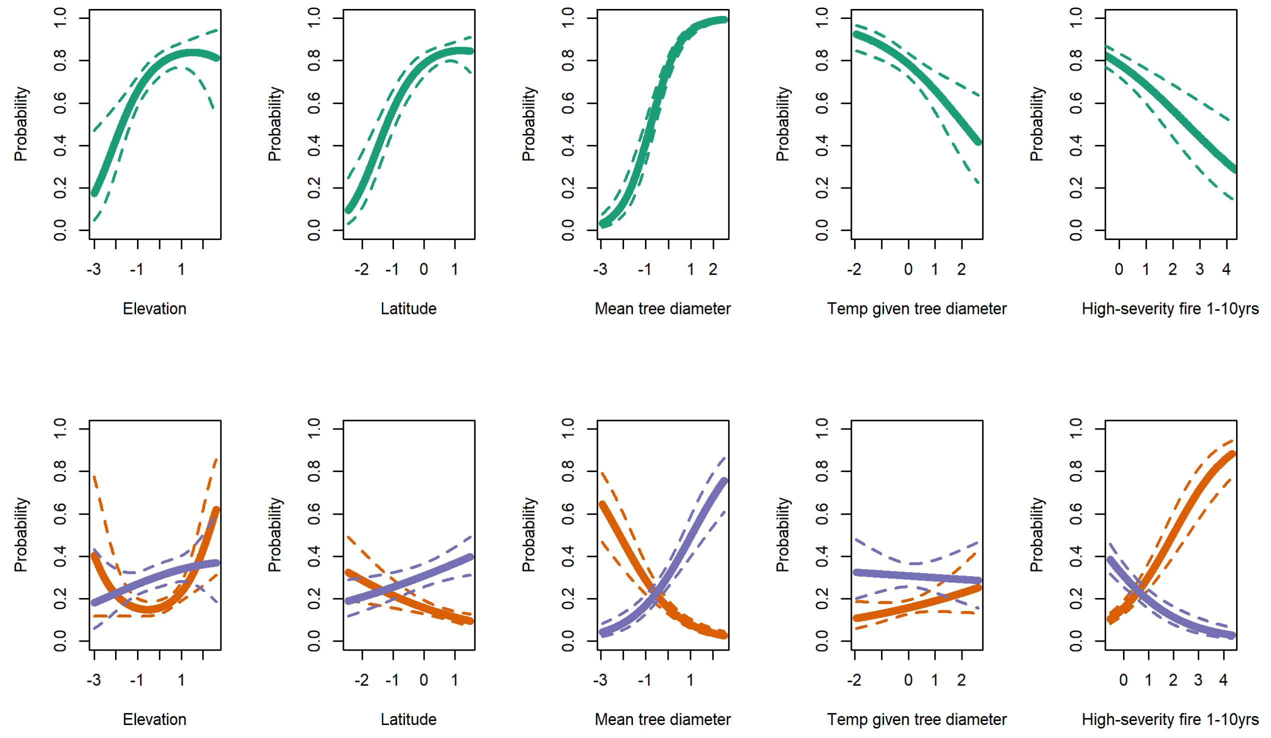

FIGURE 3
Species-habitat relationships estimated for the Hermit Warbler (*Setophaga occidentalis*) across the Sierra Nevada, USA, summers 2021-2024. Initial site occupancy rates (top row, green lines) and (bottom row) the site extinction (orange) and site colonization (violet lines). All covariates have been standardized. Dashed lines represent 85% confidence intervals. Mean tree diameter was highly correlated with relative temperature (2013–2018 mean, 30-m resolution; r= -0.77) but uncorrelated (r = 0.00) with the residuals of the temperature ~ diameter relationship (R^2 = 0.59); positive residuals represent sites that were warmer than expected given the mean tree diameter, negative residuals are cooler-than-expected sites.

aspects of their habitat – if not the climatic conditions – necessary to endure current disequilibrium conditions.

The Hermit Warbler may indeed be an important barometer of old-forest, temperature-sensitive species in the Sierra Nevada. Previous work has suggested that the Hermit Warbler can serve as proxy for the Spotted Owl (*Strix occidentalis occidentalis*) in the Sierra Nevada (Bielski et al., 2024), and of >60 other Sierra Nevada bird species, 13 are co-associated with the Spotted Owl and none more so than the Hermit Warbler (Brunk et al., 2025). Critically, the Hermit Warbler's much smaller body size results in a much smaller home range; thus, it can be monitored with much greater sample sizes, yielding greater statistical power to detect responses to change that will be relevant to Spotted Owls and the other associated species (Wood, 2022). Interestingly, while Spotted Owls are facing temperature-driven extirpation at the southern extent of their range in California (McGinn et al., 2024), high-elevation forests of the Sierra Nevada are not expected to provide short- to intermediate-term climate refugia due to complex interactions between canopy cover, microclimate, and prey (Jones et al., 2016). Thus, for the owl, the warbler, and a suite of co-associated species upslope shifts in response to rising temperatures may not be a viable climate adaptation strategy in the absence of concurrent changes to forest structure and forest management that allow for the recovery of old-forest habitat.

Without proactive conservation strategies that move away from strict fire-suppression and incorporate key principles of pre-colonial fire stewardship, continued intensification of contemporary fire regimes could lead to further population declines for the Hermit Warbler and other species. However, we have shown that addressing the risk of fire may be necessary but not sufficient to conserve the Hermit Warbler and similarly climate-sensitive species. Rising temperatures will lead to population declines even in the absence of habitat loss due to fire. As climate change accelerates, understanding species' responses to shifting environmental conditions will be crucial for guiding adaptive management and ensuring the persistence of biodiversity in fire-prone landscapes.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5281/zenodo.18225029.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because all vertebrate research was passive, no animals were handled or even influenced behaviorally by this work.

Author contributions

LB: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. SK: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Investigation. MP: Writing – review & editing, Funding acquisition, Project administration. CW: Funding acquisition, Project administration, Writing – review & editing, Conceptualization, Data curation, Methodology, Supervision, Visualization, Writing – original draft, Formal Analysis.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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