Trading places: opposite colonization and extinction responses of the hermit warbler and western bluebird to the 2021 Dixie Fire

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FULL RESEARCH ARTICLE

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Abstract

Forty years of increasing fire size and severity in California's Sierra Nevada were embodied by the 2021 Dixie Fire, which burned 389,837 ha between July and October, making it one of the largest, most destructive fires in California's history. Historical fire regimes burned substantial areas annually, but primarily at low and moderate severities. Studies of the implications of fires like the Dixie Fire, which burn largely at higher severities, have focused on habitat change in the burned area; much less is known about potential edge effects. The hermit warbler (*Setophaga occidentalis*) and western bluebird (*Sialia mexicana*) have previously been characterized as species with dramatic, opposing post-wildfire responses: hermit warblers display a strongly negative response to fires while western bluebirds display a strong positive response. We conducted passive acoustic monitoring pre- and post-Dixie Fire inside and outside the burned area and analyzed the audio with the machine learning animal identification tool BirdNET. We then used a multi-season occupancy modeling framework to characterize both species' site extinction and site colonization responses as a function of fire and habitat variables. We found no influence of edge effects, though this may have been a function of the low density of our recorders relative to the home range of these species. We did, however, observe contrasting relationships between the species. Hermit warbler site extinction was elevated in burned areas, particularly those burned at higher severities, while site colonization in unburned habitat was positively associated with canopy cover. Western bluebirds displayed the exact opposite pattern (elevated colonization in areas of high-severity fire, elevated extinction in unburned areas with high canopy cover). These results suggest contrasting trajectories for fire-influenced bird species under contemporary fire regimes and could guide hypothesis generation for broader studies of biodiversity responses to fire in this ecosystem.

Key words: BACI, before-after control-impact, Dixie Fire, edge effects, fire severity, hermit warbler, megafire, occupancy, *Setophaga occidentalis*, *Sialia mexicana*, Sierra Nevada, western bluebird

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Introduction

Over the past four decades, wildfires in California’s Sierra Nevada have grown in size and severity (Westerling et al. 2006; Westerling 2016; Stevens et al. 2017; Williams et al. 2019; Taylor et al. 2022; Cova et al. 2023). While fire is a crucial part of forest ecology in the Sierra Nevada, post-colonial social-ecological changes have altered contemporary fire regimes (Taylor et al. 2016; Safford et al. 2022) such that widespread forest cover loss is occurring (Steel et al. 2022b) and some wildlife populations are declining (Jones et al. 2021). While frequent mixed-severity fires can promote biodiversity across the Sierra Nevada (Tingley et al. 2016), mounting evidence suggests that large and severe fires have acute impacts on wildlife populations (Steel et al. 2022a; Wood et al. 2024). The largest fire in contemporary Sierra Nevada history, the 2021 Dixie Fire, burned 389,837 ha, destroying several towns, and probably resulting in a short-term net decrease in avian species richness, though there is likely substantial inter-species variability (Wood et al. 2024). Over 20% of the mostly forested area affected burned at high severity (³75% canopy mortality; **Fig. 1**) potentially creating edge effects between burned and unburned areas that could have an important influence on post-fire population dynamics.

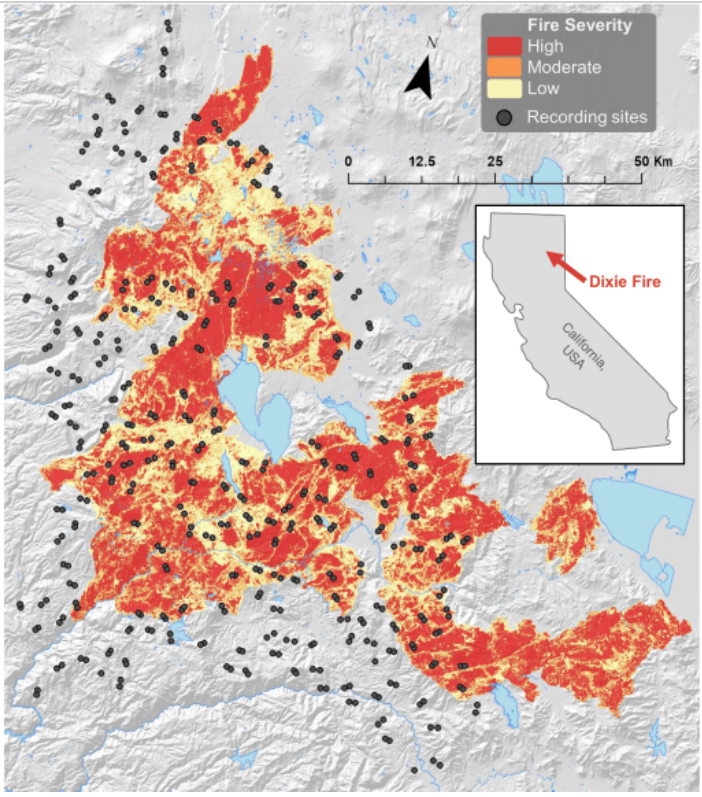


Figure 1. The Dixie Fire burned 389,837 ha between July 13 and October 26 in 2021. We conducted passive acoustic surveys at 347 locations before (May–July 2021) and after (May–July 2022) the fire, with 173 sites within the fire perimeter and 174 sites within a 14km buffer of unburned forest around the fire. Only audio recorded 1 June–26 July of each was used (103,805 total hours) so that our study focused on the breeding season of the focal species.

Edge effects are changes in species dynamics at or around the intersection of two contrasting habitat types that result from the abrupt habitat transition. Edges created by fires are known to fragment habitat, disrupting species interactions and altering food availability (Driscoll et al. 2021),. Fire-sensitive species may avoid going near the edge of the burn because of secondary changes to ecological dynamics or resource availability that the fire creates, whereas fire-attracted species might be advantaged by the new habitat features (e.g., snags). Though species' responses to large, severe fire vary, understanding the range of responses to this increasingly common disturbance type might inform broad trends in species dynamics in today's Sierra Nevada. However, beyond the finding that species richness tends to decrease toward the interior of burned areas (Steel et al. 2022a), little is known about edge effects outside of burned areas.

We combined passive acoustic surveys, a machine learning detector, and dynamic occupancy models in a Before-After, Control-Impact (BACI) design to compare the site colonization and site extinction dynamics of two bird species likely to show contrasting responses to the Dixie Fire. Among 67 diurnal Sierra Nevada birds, the hermit warbler (*Steophaga occidentalis*) had the strongest site extinction response to the 2020 North Complex Fire, a megafire that burned just south of the Dixie Fire one year earlier (Wood et al. 2024). A migratory songbird closely associated with closed-canopy forests (Bielski et al. 2024; Pearson 2020), the hermit warbler's negative responses to fire can persist for decades (Bagne and Purcell 2011; Raphael et al. 2018), though the hermit warbler appears unaffected by low- and moderate-severity fire in the Sierra Nevada (Bielski et al. 2024). In contrast, the same study of the North

Complex Fire found that western bluebirds (*Sialia mexicana*), a resident songbird generally associated with open habitat (Pearson 2020), had the strongest colonization response of the 67 bird species (Wood et al. 2024), further evidence of the bluebird's positive responses to both prescribed and naturally occurring fire (Dwyer and Block 2014; Saab et al. 2022; Dickson et al. 2009), including positive responses to mixed and high severity fire (Saab et al. 2022). Despite higher nest densities in burned areas, fire seems to have no effect on western bluebird clutch size, suggesting that fires do not negatively impact resource availability (Hurteau et al. 2010).

We examined how, one-year post-fire, fire occurrence (i.e., burned/unburned), the distance to fire perimeter (both into and away from the burned area), fire severity, fire heterogeneity, and canopy cover (in the unburned area) influenced site colonization and extinction of these two species. We hypothesized that both species' site colonization and site extinction inside and outside the Dixie Fire would be influenced by the fire. For the hermit warbler, we predicted: 1) that site extinction would be higher in burned areas than unburned areas and that it would be accentuated by higher fire severity, and 2) that site colonization rates in unburned forest would be higher closer to the fire than farther away (e.g., because individuals returned from migration to find previously occupied territories unsuitable and moved the minimum distance to alternative habitat). For the western bluebird, we predicted: 1) a positive site colonization response in burned areas, specifically that colonization would be highest in areas that experienced the greatest proportion of high-severity fire; and 2) that site extinction would be higher in the unburned areas closer to the fire (as individuals switch from lower- to higher-quality habitat). Focusing on these species allowed us to characterize two contrasting avian population responses to the Dixie fire, potentially bracketing population dynamics that may become more common given that this fire yet embodies the contemporary trend toward larger, more severe fires (Cova et al. 2023).

Methods

Passive Acoustic Surveys and Audio Analysis

During late spring and early summer (May–July) of 2021 and 2022, we conducted passive acoustic surveys across the western slope of the Sierra Nevada, predominantly on federally managed lands. The climate is Mediterranean, with hot dry summers and cold winters; most precipitation falls as snow. Elevation within the study area ranged from 300 m to >2800 m asl. It is predominantly mixed conifer forest (dominant canopy species: white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), and incense cedar (*Calocedrus decurrens*)), though California black oak (*Quercus kelloggii*) is important at lower elevations.

Autonomous recording units (ARUs; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) were deployed within randomly selected, non-contiguous 4 km^2 grid cells with two ARUs deployed per cell (minimum spacing: 500m) in areas selected to maximize acoustic survey coverage (e.g., higher points of topographic relief). Thus, any two ARUs were approximately 500–900 m apart, and 1.5–2 km from any others. Audio was recorded via one omnidirectional microphone at a sample rate of 32 kHz; ARUs were mounted to trees at chest height. For more details on study design, see (Wood et al. 2019; Kelly et al. 2023). The ARU deployment effort began in mid-May, with any given recorder deployed for approximately five weeks; we limited our analysis to audio recorded between 1 June 1 and 26 July, representing the hermit warbler breeding season (Pearson 2020) when migration is expected to have stopped, and in the hours 0500–0900 and 1800–2000. As western bluebirds are nonmigratory (Guinan et

al. 2020), they are expected to be present throughout the sampling period.

We used audio from 347 ARUs within the Dixie Fire and in a 14 km buffer around the fire (a distance that matches the maximum distance from the fire interior to the fire perimeter). All sites were surveyed in both years, and the distribution between burned and unburned was nearly equal: 173 sites in the future fire footprint/burned area and 174 outside the burned area. In the BACI framework, unburned sites were designated as 'Control,' burned as 'Impact,' with 2021 and 2022 serving as 'Before' and 'After,' respectively. Categorizing sites in this manner allows us to neatly organize comparisons to determine colonization and extinction with respect to the fire.

We recorded 103,805 hours of audio in total (56,060 and 47,745 hours in 2021 and 2022, respectively) and analyzed it with the BirdNET algorithm, a convolutional neural network able to identify > 95% of Sierra birds by sound, including the two focal species of this study (Kahl et al. 2021). BirdNET analyzes audio in 3-second snippets and makes a prediction for each species in each interval. Each prediction has a unitless confidence score on a scale of 0–1; most predictions score extremely low (e.g., when the snippet contains only silence) and are automatically discarded. Following the procedure outlined by Wood and Kahl (2024), we manually validated 200 randomly selected BirdNET predictions for each species (score range: 0.1–1.0) and used logistic regression to relate BirdNET's unitless confidence score to prediction outcome, yielding a relationship between score and the probability that any given prediction was correct.

Habitat Covariates

We generated site covariates for each of our 347 survey sites, which were quantified as either Euclidean distance or in relation to a 120 m buffer around the ARU. First, all sites were classified as either burned or unburned based on the location of the ARU. For the sites within the burned area, we calculated: 1) the distance in from the fire perimeter (m), 2) fire severity (proportion of the buffer that experienced ≥75% canopy mortality; Monitoring Trends in Burn Severity data [MTBS]; https://www.mtbs.gov/; 30 m resolution), and 3) fire heterogeneity (the number of patches with differing burn severities (canopy mortality bins of 0–25%, 25–50%, 50–75%, and 75–100%; MTBS). As a proportion, severity is a compositional metric, while heterogeneity is configurational; their relatively weak correlation ($r = 0.268$) indicates that they capture unique aspects of pyrodiversity. For sites outside the burned area, we calculated: 1) the distance out from the fire perimeter, and 2) mean canopy cover (Gradient Nearest Neighbor data from 2017; 30m resolution; https://lemma.forestry.oregonstate.edu/data/structure-maps). Importantly, all covariates were 'burn-dependent'; that is, their value was zero outside the relevant condition (burned or unburned). For instance, fire severity can only be described within a burned site, and canopy cover was only adequately measured in unburned sites. Thus, interaction terms with the categorical burned/unburned site covariate were unnecessary.

Occupancy Modeling

We used dynamic, or "multi-season" occupancy models to assess the response of both species to the Dixie Fire (MacKenzie et al. 2003, 2009). Each year of data (2021 and 2022) was treated as a season and was divided into eight, 7-day secondary sampling periods in June and July. The Dixie Fire burned after our 2021 field season (our sampling period ended 26 July, and the fire began on 13 July), such that support for fire-related covariates of site colonization and extinction could be evaluated.

We treated BirdNET predictions with a pr(true positive) ≥ 0.99 as true bird observations and discarded all other predictions. This yielded 14,086 and 7,090 predictions for the hermit warbler and western bluebird, respectively. To further mitigate the possibility of false positives (either due to misclassifications or the correct identification of individuals displaying vagrant or non-resident behavior), we only considered a site occupied in a given season if it had an observation on at least two different days. After applying the two data filters, we treated the occurrence of one or more bird observations during a secondary sampling period as a detection.

To test our hypotheses concerning colonization and extinction for both species, we compared competing models created using the R package unmarked (Fiske and Chandler 2011) in program R (R Core Development Team 2020) based on Akaike's Information Criterion (AIC), considering models with DAIC 2 to be supported by the data (Burnham and Anderson 2010). All models included survey effort (hours of audio recorded per secondary sampling period) as a detection covariate (Julian date of each secondary sampling period was considered as a detection covariate but was not supported). For each species, we compared the support for univariate models representing different hypotheses for one state variable (colonization or extinction) while the other state variable was held constant (i.e., null, or uniform).

For the hermit warbler, we compared models in which site colonization (1) was uniform (i.e., a null model), or varied with (2) categorical burned vs. unburned status, (3) distance of an unburned site out from the fire perimeter, or (4) canopy cover of unburned sites. Separately, we compared models in which site extinction (1) was uniform, or varied with (2) burn status, (3) distance of a burned site in from the fire perimeter, (4) fire heterogeneity (number of patches of differing severity), or (5) fire severity (proportion of a patch burned at high severity).

For the western bluebird, we compared models in which site colonization (1) was uniform, or varied with (2) burn status, (3) distance in from the fire perimeter, (4) fire heterogeneity, or (5) fire severity. Again separately, we then compared models in which site extinction (1) was uniform, or varied with (2) burn status, (3) distance out from the burned area from fire perimeter, or (4) canopy cover in unburned areas.

Finally, we calculated estimated occupancy ( ) for both species Before (t = 1) and After (t = 2) for the Control (unburned areas) and Impact (burned areas) conditions, based upon a global model in which colonization (γ) and extinction (ε) both varied with burn status. Initial occupancy ( ) was estimated directly; year two occupancy ( ) is a derived parameter based on initial occupancy and applicable (burned or unburned) site colonization and extinction rates:

$\psi_2 = \psi_1 + (\gamma * (1 - \psi_1)) - (\varepsilon * \psi_1)$

Results

Both species displayed the expected responses to the Dixie Fire overall, with hermit warblers declining in the burned area (positive extinction response) and western bluebirds increasing (positive colonization response). However, there was no evidence of edge effects on either species' colonization or extinction dynamics; distance from fire perimeter was never an informative parameter (i.e., it received less support than a relevant nested model; Arnold 2010). hermit warblers were not displaced into unburned areas as a function of distance from the fire and even did not preferentially colonize unburned areas ($\Delta AIC_{\gamma_unburned}$ = 19.69; **Table 1**); within the burned area their extinction was not determined by how close a burned site

was to the fire perimeter ($\Delta AIC_{\varepsilon_distance\ in}$ = 31.32; Table 1). Similarly, the western bluebird did not "drain" from unburned forest close to the fire to colonize the burned area ($\Delta AIC_{\varepsilon_distance\ out}$ = 6.37; Table 1) and they colonized the interior of the fire just as readily as sites near the perimeter ($\Delta AIC_{\gamma_distance\ in}$ = 4.57; Table 1).

Table 1. Dynamic occupancy models for the hermit warbler and western bluebird were evaluated with Akaike's Information Criterion (AIC), which was calculated for univariate models of each state variable (colonization or extinction) while the other state variable was held constant. *w* denotes AIC model weight; β denotes the parameter estimate for a given covariate (all were standardized to allow for direct comparisons); SE is the standard error associated with an estimate.

Species	State Variable	Covariate	ΔAIC	*w*	Intercept	β	SE
Hermit warbler	Colonization	Canopy Cover	0.00	0.500	0.805	0.827	0.559
Hermit warbler	Colonization	Null	0.69	0.355	0.407	N/A	N/A
Hermit warbler	Colonization	Unburned	2.48	0.145	0.284	0.325	0.712
Hermit warbler	Colonization	Distance Out	19.41	0.000	0.379	–0.207	0.373
Hermit warbler	Extinction	Fire Severity	0.00	1.0	–2.64	0.892	0.175
Hermit warbler	Extinction	Burned	15.58	0.0	–3.18	1.40	0.486
Hermit warbler	Extinction	Distance In	23.29	0.0	–2.35	0.289	0.199
Hermit warbler	Extinction	Null	23.47	0.0	–2.33	N/A	N/A
Hermit warbler	Extinction	Heterogeneity	25.26	0.0	–2.33	0.0903	0.199
Western bluebird	Colonization	Severity	0.000	0.527	0.535	0.596	0.345
Western bluebird	Colonization	Burn	1.70	0.225	0.0634	0.913	0.574
Western bluebird	Colonization	Null	2.62	0.142	0.537	N/A	N/A
Western bluebird	Colonization	Distance In	4.57	0.054	0.540	0.060	0.277
Western bluebird	Colonization	Heterogeneity	4.62	0.052	0.537	0.010	0.26
Western bluebird	Extinction	Canopy Cover	0.000	0.813	–0.688	0.672	0.262
Western bluebird	Extinction	Unburned	4.30	0.095	–1.092	0.805	0.484
Western bluebird	Extinction	Null	5.27	0.058	–0.631	N/A	N/A
Western bluebird	Extinction	Distance Out	6.37	0.034	–0.633	0.205	0.212

Hermit warbler site colonization was best explained by canopy cover of unburned sites (*w* = 0.5; Table 1), where the probability of site colonization increased with canopy cover (= 0.827, 85% Confidence Interval [0.022, 1.632]). However, the null model, which assumed uniform colonization across all sites, also received support (ΔAIC_{γ_null} = 0.69, *w* = 0.355; Table 1). The fire severity within a burned site (i.e.,

the proportion of a site that burned at high severity [³ 75% canopy mortality]) was most influential factor for hermit warbler extinction (w = 1.0; Table 1), with the probability of extinction increasing with the proportion of a site that burned at high severity (= 0.892, 85% CI [0.64, 1.144]; **Table 1**). No other models were competitive.

Western bluebird site colonization was most influenced by fire severity within the burned area (w = 0.527; **Table 1**): birds preferentially colonized sites where a higher proportion of the 120m buffer area burned at high severity (= 0.596, 85% CI [0.099, 1.093]). The categorical burned vs. unburned covariate, a generalized case of the "fire severity" covariate, was competitive ($\Delta AIC_{\gamma\text{–burned}}$ = 1.70, w = 0.225), with fire overall positively influencing colonization (= 0.913, 85% CI [0.159, 1.735]). Burned sites were 1.99 times more likely to be colonized than unburned sites. Western bluebird site extinction was best explained by canopy cover in unburned sites, with higher extinction rates at sites with more canopy cover (w = 0.813, = 0.672, 85% CI [0.295, 1.049]). No other models were competitive.

Changes in occupancy between years for both species were consistent with our predictions. The categorical 'burn' effects enabled fire-level estimates of change in occupancy and generally had more support than the relevant null models even if they were not the most supported by the data (**Table 1**). Hermit warbler occupancy declined in the burned area (After–Impact) and increased slightly outside the burned area (After–Control) (ψ_1 = 0.88; ψ_{2_burned} = 0.82; $\psi_{2_unburned}$ = 0.92; **Fig. 2**). However, if a site burned entirely at high severity, the probability of hermit warbler site occupancy in the second season was just 0.663. Western bluebird occupancy increased substantially in the burned area and was stable in the unburned areas (ψ_1 = 0.54; ψ_{2_burned} = 0.72; $\psi_{2_unburned}$ = 0.56; **Fig. 2**).

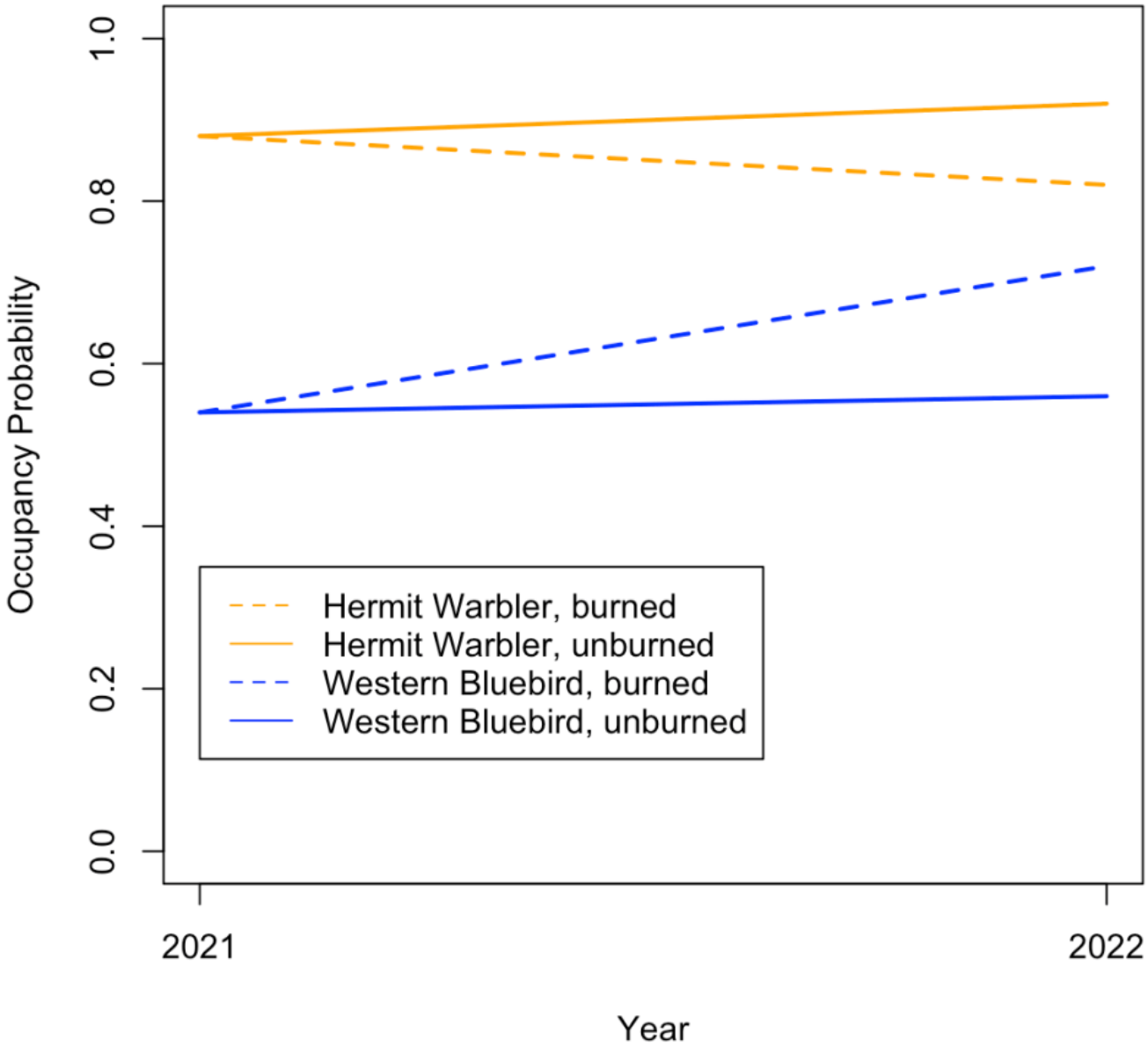


Figure 2. Occupancy estimates for hermit warbler and western bluebird before the 2021 Dixie Fire and in burned and unburned habitat one year after the fire (n = 347 recording units) based on models in which site colonization and extinction varied with a categorical 'burn' variable—a model structure that allows fire-level estimates and is broadly supported by our model selection process (see **Table 1**).

Discussion

As expected, the 2021 Dixie Fire had a negative effect on the hermit warbler population and a positive

effect on the western bluebird population one-year post-fire. Strikingly, the same environmental factors explained both species' colonization and extinction dynamics, but in opposite directions. However, we found no evidence to support our hypothesis that this historic fire caused edge effects evident in the colonization or extinction dynamics of either species. The spatial resolution of our survey coverage may have influenced these results. Broad-scale acoustic survey coverage is prioritized over high ARU density, which allows sampling of nearly the entire Sierra Nevada at a spatial resolution corresponding with the biological resolution of spotted and barred owls (*Strix occidentalis* and *S. varia*, respectively). However, the resulting spacing of our ARUs (500–900+ m) is large compared to the home ranges of our two focal species; hermit warblers and western bluebirds defend roughly 35 m (Frey et al. 2016) and 40 m (Hurteau et al. 2010) radii around their nest sites, respectively. Thus, a relatively small proportion of available territories are actually surveyed, so fine-scale displacements of individuals may be invisible.

There may also be biological causes of an absence of edge effects. The hermit warbler's migratory behavior may have obviated a need for local-scale responses fire edge effects. The Dixie Fire began near the end of the hermit warbler's breeding season (mid-July), after which they migrated to Central America returning to Sierra Nevada shortly before our survey effort after the fire. In spring 2022, having travelled >3000 km, it may be comparatively easy for them to move several more kilometers upon returning to their breeding grounds in order to avoid areas that experienced extensive high-severity fire in favor of vacant sites with high canopy—as opposed to preferentially colonizing or avoiding sites close to the fire perimeter (plausible manifestations of edge effects). Western bluebirds do not display continental-scale migration like hermit warblers but may undergo an elevational migration to avoid deep Sierra Nevada snows. Nonetheless, we expected edge effects to be evident for western bluebirds in: (1) the extinction dynamics of unburned areas (After–Control sites) because birds close to but outside of the fire's perimeter would be more exposed to stimuli (smoke, sight of fire or burned trees) indicative of favorable habitat, making them more likely to abandon their previous habitat and (2) the colonization dynamics of burned (After–Impact) sites given the sheer size of the fire, as edge effects tend to increase with burned area. The absence of the latter effect suggests that individuals were willing to travel substantial distances—up to 14 km to the center of the burned area—in order to colonize their most preferred habitat (areas that experienced the most extensive high-severity fire). It is also possible that the creation of large areas of suitable habitat allowed for higher than usual survival among first-year birds by means of more available habitat, either via direct colonization of the burned area or by backfilling territories vacated by older adults in unburned areas. In short, the fire could have resulted in extensive recruitment for this species. Thus, it is possible that even further population growth of western bluebirds could be observable in the second-year post-fire (i.e., 2023), both because an initial pulse of high recruitment and because breeding habitat could become even more suitable as the burned area ages (Keyser et al. 2004).

The significant effect of canopy cover on hermit warbler colonization is consistent with their preference for old-forest habitat, often marked by high canopy cover, among other characteristics (Bielski et al. 2024). Site extinction within burned sites was driven by burn severity, adding to the evidence that hermit warblers are likely specifically negatively affected by high-severity fire, and are minimally or not affected by moderate- and low-severity fire (i.e., canopy mortality <75%; Bielski et al. 2024). Net change in occupancy of unburned sites was slightly positive from 2021 to 2022 (**Fig. 2**), suggesting broad-scale use of unburned areas as alternative habitat or simply minor annual variation in the overall population (they breed across the Sierra Nevada). Further, though the population did decline in the burned area, high initial occupancy and preservation of some useful habitat allowed the bird to remain widely distributed, with a final occupancy still well above 80% (**Fig. 2**). Abandonment of the burned area by adult birds

could have masked by recruitment of first-year birds (a possible driver of western bluebird population growth in the burned area noted above), albeit into suboptimal habitat. Alternatively, the response of adult birds to the fire may be lagged, with high site fidelity but poor reproductive success in the first-year post-fire (i.e., our 2022 survey season), followed by widespread territory abandonment (i.e., site extinctions) in year two. In either case, further years of data are required to understand the long-term implications of the fire, Overall, the hermit warbler's clear negative response to high severity fire, coupled with a large population size, and wide distribution make it a potentially useful species to model other avian post-fire responses, particularly for other old-forest species with smaller populations like the spotted owl (Wood 2022; Bielski et al. 2024). Despite its strong negative response to extensive patches of high-severity fire, which are increasing in the Sierra Nevada, the high baseline prevalence of the hermit warbler may insulate it from near-term conservation concern, allowing it to serve as a model species to better understand species that are at greater risk.

Western bluebird colonization depended on burn severity, which may be explained by the creation of favorable post-fire habitat specifically by extensive (>75%) canopy mortality. Combined with the finding that categorical "burn" was competitive for bluebird colonization but not for hermit warbler extinction (ΔAIC = 1.70 and 15.58, respectively; **Table 1**), we can infer that western bluebirds display a more generalized post-fire response, notwithstanding their preference for the open habitat created by high-severity burns in particular. High-severity fire in the Sierra Nevada produces a distinct landscape with much of the basal area dominated by snags (Fontaine et al. 2009), a habitat feature known to be favored by western bluebirds (Kozma 2014), providing a potential explanation for their preference, despite the species' generally high nest site fidelity (Keyser et al. 2004). Western bluebird extinction parallels their colonization. High canopy cover, the structural inverse of severe fire, best explained western bluebird site extinction (outside the burned area), with the categorical "burn" model supported as well (western bluebirds were more likely to go extinct from unburned sites). As with colonization, it seems that western bluebirds flee unburned sites, and those with high canopy cover are particularly unsuitable (though baseline site extinction of high-canopy cover sites may also be possible). This may support the supposition that western bluebirds moved directly from unburned to burned areas while hermit warblers did the opposite as they abandoned comparatively inhospitable burned areas. Given the decreasing pace of forest restoration designed to limit the occurrence of large, severe fires (Knight et al. 2022), substantial population increases of the western bluebird and similar species may be likely. However, sustained increases in the frequency of large, severe fire across the Sierra Nevada will make recently severely burned forest more prevalent, possibly resulting in a reduction in avian diversity (Taillie et al. 2018; Steel et al. 2022a; Wood et al. 2024), with new landscapes dominated by comparatively few fire-adapted species like the western bluebird.

Collectively, avian responses to large fires vary widely in the Sierra Nevada (Tingley et al. 2016; Steel et al. 2022a; Wood et al. 2024), and responses to one fire may not generalize to 'megafires' overall because of variation in finer-scale burn severity and heterogeneity factors, as well as pre-fire context and inter-species dynamics. Nonetheless, these results can serve several roles. First, in predicting post-fire changes for hermit warblers, western bluebirds, and species with similar habitat associations, our results may be used for hypothesis generation, particularly when studying fires of similar sizes and proportion burned at high severity. Second, since the two species had directly opposed responses to the Dixie Fire in terms of colonization and extinction, and they have been previously theorized to represent the extremes of positive and negative response to wildfires (Wood et al. 2024), these results might be used to 'bracket' the range of likely responses of any species to a similar fire. Finally, our work illustrates both the power and limitations of regional-scale monitoring efforts. Broad-scale survey coverage precludes extremely

high survey density, making fine-scale movements of populations difficult to detect, but long-running and broad-scale monitoring efforts are uniquely capable of supporting powerful BACI analyses. The insights afforded by broad-scale, long-term bioacoustic monitoring efforts can help managers better prepare for no-analog futures threatened by changing fire regimes in the Sierra Nevada and globally.

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