Received: 9 August 2022 | Revised: 15 March 2023 | Accepted: 16 March 2023

DOI: 10.1002/eap.2853

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Incorporating pyrodiversity into wildlife habitat assessments for rapid post-fire management: A woodpecker case study

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Funding information
Cornell Atkinson Center for Sustainability; Joint Fire Science Program, Grant/Award Number: 19-1-01-5; USDA Forest Service

Handling Editor: Sharon M. Hood

Abstract

Spatial and temporal variation in fire characteristics—termed pyrodiversity—are increasingly recognized as important factors that structure wildlife communities in fire-prone ecosystems, yet there have been few attempts to incorporate pyrodiversity or post-fire habitat dynamics into predictive models of animal distributions and abundance to support post-fire management. We use the black-backed woodpecker—a species associated with burned forests—as a case study to demonstrate a pathway for incorporating pyrodiversity into wildlife habitat assessments for adaptive management. Employing monitoring data (2009–2019) from post-fire forests in California, we developed three competing occupancy models describing different hypotheses for habitat associations: (1) a static model representing an existing management tool, (2) a temporal model accounting for years since fire, and (3) a temporal–landscape model which additionally incorporates emerging evidence from field studies about the influence of pyrodiversity. Evaluating predictive ability, we found superior support for the temporal–landscape model, which showed a positive relationship between occupancy and pyrodiversity and interactions between habitat associations and years since fire. We incorporated the new temporal–landscape model into an RShiny application to make this decision-support tool accessible to decision-makers.

KEYWORDS

adaptive management, black-backed woodpecker, fire severity, forest management, occupancy, *Picoides arcticus*, predictive model, wildfire

INTRODUCTION

Adaptive management is a key paradigm for adjusting and updating conservation practices in the face of uncertainty during the biodiversity crisis (Walters & Holling, 1990). The necessity of adaptive management is especially apparent in fire-dominated landscapes, where management policy must track shifting baselines from global change (Kelly et al., 2020). In these systems, emerging evidence suggests that spatial and temporal variation in fire characteristics—termed pyrodiversity—plays a key role in structuring plant and animal responses to fire disturbance (Jones & Tingley, 2022; Kelly et al., 2017). The spatial configuration of different burn severities and the ways that patches change over time can greatly affect the abundance and distribution of wildlife after fire (He et al., 2019). These relationships often represent a source of uncertainty for managers tasked with making time-sensitive decisions within post-fire areas. However, there have been few attempts to incorporate pyrodiversity and post-fire habitat dynamics into predictive models of animal distributions and abundance to support post-fire management.

Decision-makers frequently rely on data from easily monitored species to evaluate and inform management planning. In California, USA, black-backed woodpecker (*Picoides arcticus*) populations are surveyed annually as part of a regional monitoring program in recently burned forests (Saracco et al., 2011). Black-backed woodpeckers colonize forests rapidly after fire (Stillman, Lorenz, et al., 2022), and they are associated with high-severity, stand-replacing burns in the western USA (Hutto, 2008; Tingley et al., 2018). This specialized habitat association makes the species sensitive to post-fire management actions that remove dense stands of dead trees after fire (Tarbill et al., 2018), leading to trade-offs between dead tree retention for post-fire wildlife, post-fire logging for risk-mitigation or economic interests, and post-fire reforestation practices which necessitate removal of deadwood before planting new trees. Because rapid post-fire decision-making is generally essential for success (Sessions et al., 2004), there is limited time to incorporate information from on-the-ground surveys of woodpecker populations.

In response to this information gap, Tingley, Wilkerson, et al. (2016) developed a predictive model—merging an occupancy model of woodpecker occurrence with a home-range scaling model—which provided the basis for a decision-support tool to estimate black-backed woodpecker densities after fire. Since then, new research has highlighted the important role of pyrodiversity in the occurrence, abundance, and behavior of black-backed woodpeckers. Specifically, the species tends to select nest sites near edges between high-severity and low-severity burns (Stillman, Siegel, Wilkerson, Johnson, Howell, & Tingley, 2019), and radiotelemetry studies demonstrate that fledglings and adults select more pyrodiverse habitats after fire (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). Juvenile woodpeckers seek cover in lower severity patches after leaving the nest, and fledgling survival is considerably higher in low-severity versus high-severity patches (Stillman et al., 2021). Pyrodiversity seems to be especially important in megafires, which can leave large expanses of homogenous, high-severity burned forest (Stephens et al., 2014). Although megafires were once thought to provide large areas of high-quality habitat for this post-fire specialist, surveys within recent megafires have found few individuals (White et al., 2019) and current management models have overpredicted woodpecker densities in these areas (Tingley, Wilkerson, et al., 2016).

Emerging evidence on the role of pyrodiversity in structuring post-fire animal communities (Jones & Tingley, 2022) demonstrates the need to update existing management tools as we gain a more mechanistic understanding of animal responses to fire. Toward this aim, we used the black-backed woodpecker as a case study to demonstrate a pathway for incorporating pyrodiversity into wildlife habitat assessments for adaptive management. Our objective was to test whether our mechanistic hypotheses generated from local field studies (i.e., pyrodiversity effects on habitat use and survival) would “scale up” to region-wide occupancy patterns and improve the fit, and thus utility, of management-oriented models. We accomplished this by developing three occupancy models representing different hypotheses about responses to post-fire habitat. First, we fitted a year-independent “static” model, mirroring Tingley, Wilkerson, et al. (2016), to represent the previous state of knowledge. Second, we updated this model to create a “temporal” model that accounted for the nonlinear relationship of woodpecker occupancy to time since fire (Tingley et al., 2018). Third, we extended the temporal model to include additional covariates for post-fire habitat dynamics and pyrodiversity to create a “temporal–landscape” model based on hypotheses generated from local field studies. Thus, differences in predictive performance between the static and temporal models represent the added value of including time since fire and multiyear surveys in our decision-support model, and further differences between the temporal and temporal–landscape models show the added value of including information on spatial pyrodiversity and habitat dynamics over time. We used our results to update a predictive model which can be used to predict black-backed woodpecker density in burned areas, and we present an online RShiny application to make this decision-support tool fast and easy for managers to implement in the months or years following forest fire.

METHODS

Occupancy surveys

We conducted surveys as part of a long-term effort to monitor black-backed woodpecker occupancy and population dynamics in burned, montane forests in California. Between 2009 and 2019, and again in 2021, we sampled forested areas within 10 contiguous National Forests that had burned in the 10 years previous to the survey year. Our study area fell within the Sierra Nevada and southern Cascades ecoregions located between 470 and 3060 m elevation. Dominant forest types within surveyed fires included Sierran mixed-conifer, eastside pine, ponderosa pine (*Pinus ponderosa*), and white/red fir (*Abies concolor*, *Abies magnifica*; CAL FIRE Fire and Resource Assessment Program, 2020). The study region is characterized by low- to mixed-severity fire regimes where wildfires have historically produced patches of low-, medium-, and high-severity burn depending on a variety of environmental, vegetation, and climatic factors (Perry et al., 2011).

Our survey effort followed the protocol of a long-term monitoring program for black-backed woodpeckers in burned forests of California (Tingley et al., 2018). Each year we randomly selected up to 50 fires to visit that met our established sampling criteria, visiting 140 total fires ranging in burn year from 1999 to 2020. We conducted single-visit surveys for black-backed woodpeckers at 2–24 survey sites (median = 20) in each of the ~50 burned areas selected each year. Survey points were spaced at least 250 m from each other and at least 50 m from the nearest road. We divided surveys into timed intervals which we treated as repeat visits (i.e., closure assumed within the <17-min survey period). Each survey included three 2-min "playback" intervals in which we broadcast recordings of black-backed woodpecker vocalizations for 30 s followed by a 1.5-min observation period. Our survey protocol followed a removal design where playbacks were suspended after the first detection. We preceded ~50% of surveys with a series of passive point counts which began with a 3-min interval followed by one to four 2-min intervals, depending on the year. We conducted surveys in the morning hours (05:30–09:30) between 4 May and 18 July each year. Prior to data analysis, we applied stringent filtering to remove surveys that occurred within or adjacent to areas with post-fire logging and sites which experienced more than one fire event in the last 10 years. For additional information on study design and data collection following the same protocol, see Saracco et al. (2011) and Tingley et al. (2018, 2020).

Modeling approach

We developed three competing occupancy models of differing complexity to test our hypotheses about the effects of post-fire habitat dynamics on black-backed woodpecker occupancy. The "static" model follows a classic single-season formulation (MacKenzie et al., 2002), and the "temporal" and "temporal–landscape" models explicitly account for temporal dependence among sites with multiple visits in consecutive years. The temporal model used a similar covariate set to the static model while also testing the effect of years since fire, and the temporal–landscape model included five additional covariates based on our updated information on the potential effects of pyrodiversity and fire dynamics. Each model is described in greater detail in the sections below. We fit models to data from 2009 to 2019 and held-out data from 2021 for validation. Our ultimate goal was to select the model with the highest predictive power to update decision-support tools for adaptive management and provide insight into the species' habitat associations after fire.

We employed identical approaches to account for imperfect detection in all three occupancy models. Using previous work in this system as a baseline (Saracco et al., 2011; Tingley et al., 2018, 2020), we modeled the probability of detection as a logit–linear function of three covariates: survey interval duration (2 min, 0; 3 min = 1), the ordinal day of the year, and the survey type (passive, 0; broadcast, 1). We fit models to the data in R version 4.1.0 using JAGS version 4.3.0 and the package *R2JAGS* (Plummer, 2003; R Core Team, 2021; Su & Yajima, 2021). We used agnostic priors with slight regularization, Normal ($\mu = 0$, $\tau = 0.2$), on all fixed effects and a uniform prior (0.1, 3) on the standard deviation of random effects. We used a uniform prior (0.01, 0.99) to constrain the detection model intercept between 0 and 1 on the probability scale. We ran three chains in parallel with 50,000 iterations after a burn-in of 30,000 and a thin rate of 100, yielding a posterior sample of 1500 across all chains. We confirmed that the Gelman–Rubin statistic was <1.1 for every estimate and visually inspected traceplots to assess convergence (Gelman et al., 2004). We made inference on parameters using 95% Bayesian credible intervals (95% CI).

Static occupancy model

We built a single-season occupancy model to generate a baseline for model comparisons based on previous work. The static model used the same fixed effects as Tingley, Wilkerson, et al. (2016) and represented the state of our knowledge prior to incorporating new information from recent field studies (Table 1). As in Tingley, Wilkerson, et al. (2016), we only used data from the first visit to each fire to avoid pseudoreplication at the site level, yielding a total of 2384 sites and visits. The observed detection/nondetection data, y_{jk}, are assumed to be imperfectly observed representations of the true occupancy state for survey interval k at site j and year t. The true occupancy status for each site, z_j, is assumed to be closed among all k survey intervals within the <12-min survey period. Observed occurrence is modeled as a Bernoulli-distributed random variable:

TABLE 1 Description and data sources for covariates on occupancy.

Variable	Models	Description and source
Years since fire	T, LT	No. years between fire ignition and each survey.
Burn severity	S, T, LT	Average burn severity within 500-m or 100-m of survey points using the % change in canopy cover from before to immediately after fire (USDA Forest Service, 2020).
Diversity in burn severity	LT	Inverse Simpsons diversity of all burn severity pixels within 500-m or 100-m of survey points.
Distance to edge	LT	Distance from the survey point to the nearest area classified as low severity based on a threshold of ≤25% change in canopy cover.
Fir basal area	LT	The summed pre-fire basal area of live red fir and white fir within 100 m of a survey point using GNN structure maps (Landscape Ecology Modeling, Mapping, and Analysis, 2020).
Pre-fire canopy cover	S, T, LT	Forest canopy cover within 100 m of the survey site, derived from LandTrendr data that preceded the fire by 1–4 years (Landsat-based Detection of Trends in Disturbance and Recovery; Hooper & Kennedy, 2018).
Tree size class	S	Habitat classification for dominant tree size (CAL FIRE Fire and Resource Assessment Program, 2020), included as a binary indicator for the presence of large trees using the threshold WHR_size >3.
Elevation	S, T, LT	Elevation at the survey location (m).
Latitude	T, LT	Latitude at the survey location.
Residual latitude	S	The residuals from a simple linear model of elevation as a function of latitude. The static occupancy model used this variable to remain consistent with previous approaches (Saracco et al., 2011).
Habitat classification	S, T, LT	Habitat classification based on dominant habitat type (CAL FIRE Fire and Resource Assessment Program, 2020).
Ignition season	LT	Binary variable indicating the time of year for fire ignition date (0, before 15 August; 1, after 15 August).
Fire size	LT	Size of the fire area (log ha).

Note: Each of the three competing models in this study used a different combination of these variables to model black-backed woodpecker occupancy: LT, landscape-temporal model; T, temporal model; and S, static model.
Abbreviations: GNN, gradient nearest neighbor; USDA, United States Department of Agriculture; WHR, Wildlife Habitat Relationships.

$$y_{jk} \sim \text{Bernoulli}(z_j p_{jk}),$$

where p_{jk} is the probability of detection for a given site and survey interval. The true occurrence status, z_j, is a latent variable, modeled as:

$$z_j \sim \text{Bernoulli}(\psi_j),$$

where ψ_j is the probability of occupancy of site j. The state process of the model included a random intercept for habitat type and a random intercept for each fire area.

Temporal occupancy model

Next, we developed a temporal model to account for the effect of years since fire on occupancy. This model included a temporal autologistic component designed to examine the factors affecting occupancy rates while accounting for temporal dependence between sites with surveys over multiple years (Tingley, Ruiz-Gutiérrez, et al., 2016). Thus, we were able to leverage our entire multiyear dataset which included 8484 surveys at the same 2384 sites used by the static model. We modeled the probability of occupancy in year 1 after fire as:

$$\text{logit}(\psi_{j,t=1}) = \beta X,$$

where ψ_{jt} is the probability of occupancy of site j in year t, β represents a vector of intercept and slope coefficients, and X represents a design matrix including observed covariates. For subsequent years after fire, $t = 2, ..., 10$, we modeled the probability of occupancy as:

$$\text{logit}(\psi_{j,t>1}) = \beta X + \phi z_{jt},$$

where ϕ is a site-specific temporal autologistic parameter which is modified by z_{jt}, the true occupancy status for each site-year combination.

We modeled the probability of occupancy as a function of eight covariates based on previous studies (Saracco et al., 2011; Tingley et al., 2018, 2020), including a quadratic effect of time since fire, a quadratic effect of elevation, and the linear interaction between elevation and latitude (Table 1). We used the same random effects structure as the static model.

Temporal–landscape occupancy model

Building on the temporal model structure above, we developed a temporal–landscape model to explicitly test for added value from incorporating post-fire habitat dynamics and pyrodiversity. This model included an additional five covariates based on our updated information on black-backed woodpecker responses to fire (Table 1). These included: (1) diversity in burn severity, (2) the interaction between burn severity and years since fire, (3) distance to low-severity edge, (4) basal area of fir trees within 100 m, and (5) the interaction between fir basal area and years since fire. We calculated diversity in burn severity to represent a fine-scale index of spatial pyrodiversity around each survey point. To calculate this metric, we first divided the percent change in canopy cover into 11 bins (0%, 1%–10%, ... 91%–100%). Next, we calculated the inverse Simpsons diversity of all burn severity pixels within a 100-m and 500-m buffer of survey points. Values range continuously from 1 (all pixels equal) to 11 (pixels equally distributed between different severity classes). This metric conveys information about the representation and evenness of severity classes, providing a single metric of variation that may be useful to land managers (Ponisio et al., 2016). To calculate the distance to low-severity or unburned edge, we measured the distance from survey points to the nearest area with ≤25% change in canopy cover (e.g., low-severity burn or unburned). We were only interested in the effect of edges for sites surveyed within high- or medium-severity burn, so we multiplied this covariate by an indicator variable within the model (1 if the site falls within a pixel with >25% change in canopy cover, 0 if otherwise). This covariate represents the effect of distance to low-severity burn or unburned areas for sites located within patches burned at medium to high severity. Last, we measured fir basal area as the summed pre-fire basal area of live red fir (*A. magnifica*) and white fir (*A. concolor*) within 100 m of a survey point. Pre-fire measurements were drawn between 1–4 years before fire.

Given that previous studies have documented strong relationships between black-backed woodpecker habitat selection and burn severity at multiple spatial scales (Campos et al., 2020; Hutto, 2008; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019), we used an indicator variable approach to select an appropriate scale (100-m or 500-m radius buffer) for the burn severity and diversity in burn severity variables. Indicator variables came from a Bernoulli distribution Bernoulli($\iota_{j,t}$), where $\iota_{j,t}$ is given a prior distribution of $Beta(\alpha = 1, \beta = 1)$. We retained the scale with the highest posterior probability to use as a covariate in the final model.

In addition, we allowed a fire-specific random effect to arise from a hyperdistribution modeled as a linear function of fire size and ignition season. We included ignition season as a binary variable (0, before 15 August; 1, after 15 August). The August 15 cutoff represents the date that dispersing wood-boring beetles available for colonizing new fires typically decline (Costello et al., 2013), potentially leading to lower food availability for black-backed woodpeckers. The temporal–landscape model also included a random intercept for habitat type.

Evaluating model predictions

We evaluated all three occupancy models using held-out survey data from 2021. Although some sites in the evaluation data were also visited in 2009–2019, all sites had a minimum 2-year gap between surveys used for model fitting and surveys used for model evaluation. For each model, we assessed whether continuous probability predictions for ψ could discriminate between detections and nondetections using two metrics: the area under the receiver operator characteristic curve (ROC-AUC; Fielding & Bell, 1997), and the area under the precision-recall curve (PR-AUC; Sofaer et al., 2019). ROC-AUC summarizes the false-positive rate (i.e., $1 - \text{specificity}$) versus sensitivity across thresholds: a value of 0 indicates that a model discriminates correctly 0% of the time, 0.5 approximates random discrimination, and 1 indicates perfect discrimination. In contrast, PR-AUC focuses on the ability to predict presences across thresholds. Values that are higher than the proportion of positive detections in the observed data (in our case, 0.21) indicate discrimination better than random. We propagated model uncertainty through the validation procedure by calculating AUC metrics from model predictions at every posterior draw.

RESULTS

The temporal–landscape model had the highest values for both ROC-AUC (mean 0.783; 95% CI 0.752, 0.797) and PR-AUC (mean 0.472; 95% CI 0.409, 0.508), while the static model had the lowest (mean ROC-AUC: 0.711;

95% CI 0.659, 0.755; mean PR-AUC: 0.398; 95% CI 0.350, 0.443, Figure 1, Appendix S1: Table S1). The inclusion of multiyear surveys and temporal fire dynamics through temporally autoregressive models substantially increased predictive power, and the distribution of AUC values showed limited overlap between the static and temporal models. The addition of habitat and pyrodiversity covariates in the temporal–landscape model generally improved continuous presence/absence discrimination over the temporal model, although both models showed high overlap in the ability to discriminate presences (Figure 1).

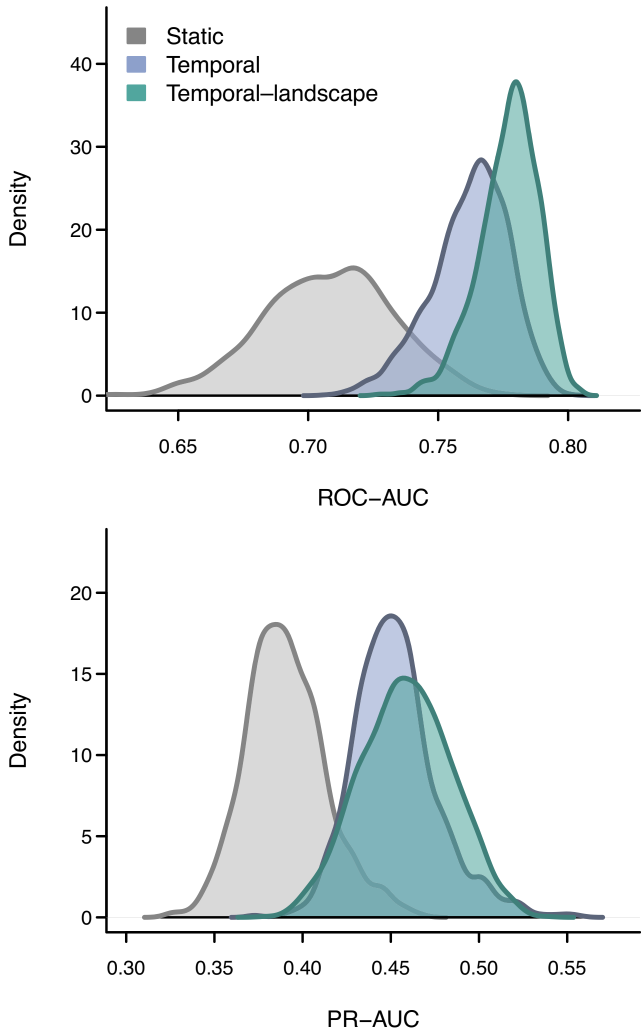

FIGURE 1 Updating prior models based on new evidence increased the ability of occupancy models to discriminate detections and nondetections according to the area under the receiver operator characteristic curve (ROC-AUC; upper) and the precision-recall curve (PR-AUC; lower). Distributions show Bayesian posterior uncertainty around AUC estimates for three models of black-backed woodpecker occupancy in burned forests. ROC-AUC summarizes the false-positive rate versus sensitivity across thresholds, and PR-AUC focuses on the ability to predict presences across thresholds (PR-AUC > 0.21 indicates discrimination better than random).

Habitat relationships

The temporal–landscape model identified multiple important relationships between black-backed woodpecker occupancy, pyrodiversity, and associated fire dynamics (Figure 2). Although occupancy probability increased with burn severity in recent fires, the positive effect of burn severity decreased in later post-fire years (Figure 2b). Occupancy probability was also higher in areas with greater diversity in burn severity, indicating that woodpeckers were more likely to occupy a habitat with higher spatial pyrodiversity (Figure 2c). The pre-fire basal area of fir trees within 100 m of survey points also showed a positive relationship with occupancy, and the magnitude of this effect increased each year following fire (Figure 2d). Contrary to previous findings, we did not detect an effect of distance to low-severity/unburned edge on occupancy for survey points in high severity (Appendix S1: Figure S1). In addition, there were no strong relationships between occupancy and fire size (β_{season}: −0.09, 95% CI: −0.35, 0.18) or ignition season (β_{size}: 0.22, 95% CI: −0.30, 0.77), although the sign of mean hyperparameters did agree with hypothesized directions. Across all three models, occupancy probability increased with increasing elevation and latitude, and occupancy showed weak relationships to pre-fire canopy cover (Appendix S1: Figure S1). Covariate estimates for all models are included in Appendix S1: Table S2.

DISCUSSION

Our case study highlights a pathway for incorporating pyrodiversity into management decisions. Mounting evidence associating pyrodiversity with increased biodiversity after fire demonstrates a critical need to update management objectives to account for pyrodiversity (Jones & Tingley, 2022). Studies have provided empirical evidence for this "pyrodiversity–biodiversity" hypothesis in a variety of ecosystems including African savannas (birds and mammals: Beale et al., 2018), the coastal plain of the southeastern USA (pollinators: Ulyshen et al., 2021), and mixed-conifer forests of western North America (birds: Tingley, Ruiz-Gutiérrez, et al., 2016; bats: Steel et al., 2019; pollinators: Ponisio et al., 2016). Even a flagship late-seral species, the California spotted owl (*Strix occidentalis occidentalis*), may selectively forage in post-fire areas with high pyrodiversity when surrounding forests are fire suppressed (Jones et al., 2020). Pyrodiversity–biodiversity patterns

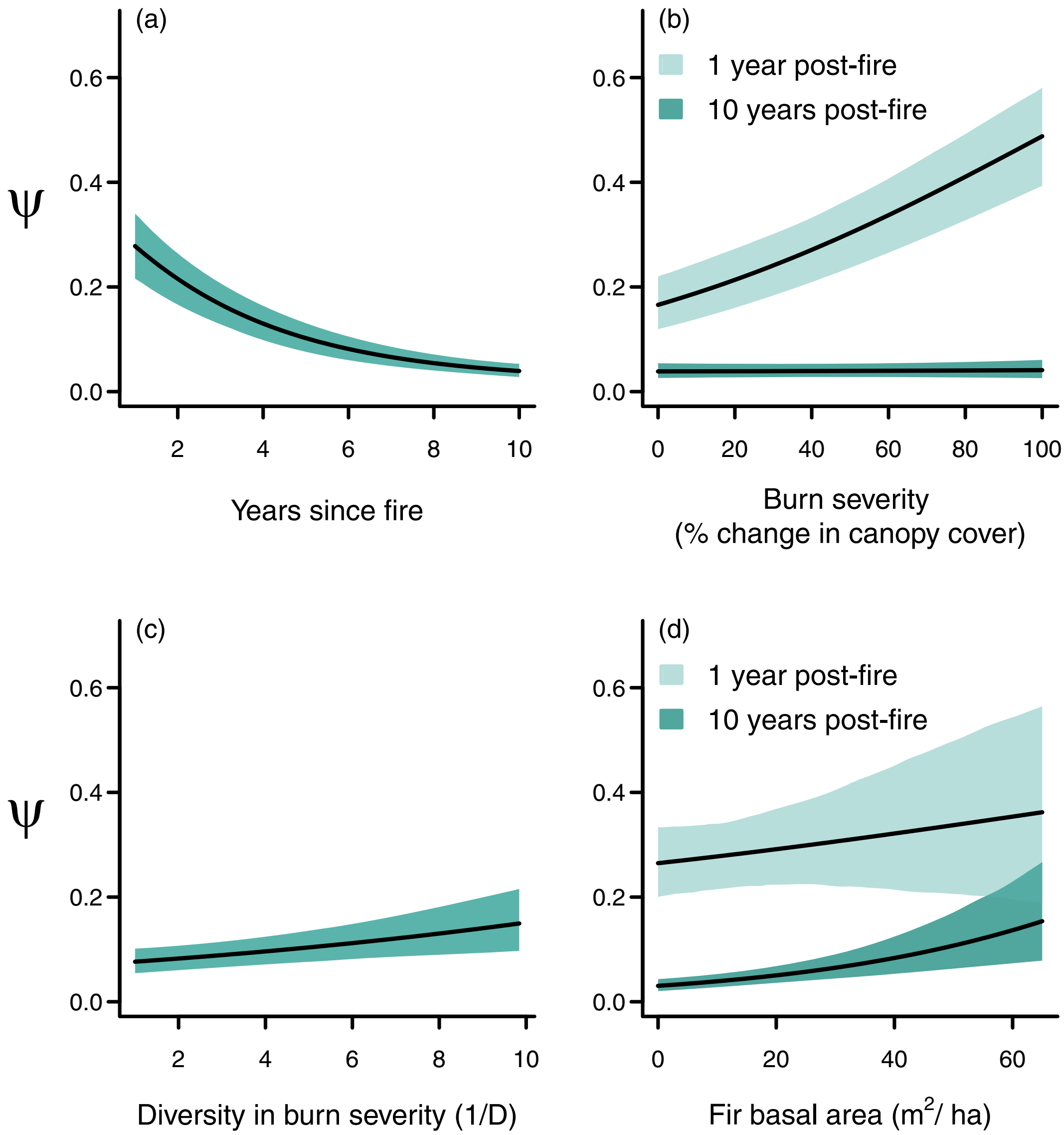

FIGURE 2 Occupancy relationships in the temporal–landscape model supported mechanistic hypotheses about the importance of pyrodiversity and fire dynamics for black-backed woodpeckers. Black lines show mean predictions and shaded regions show 95% credible intervals for the relationship between occupancy and (a) years since fire, (b) burn severity, (c) diversity in burn severity, and (d) fir basal area. For predictions, other predictors are held at their average value and interactions with years since fire are shown by plotting effects at 1 and 10 years post-fire.

stem from multiple mechanisms including niche partitioning (driven by habitat diversity) and habitat complementation (driven by resource availability; Jones & Tingley, 2022). Although black-backed woodpeckers are often treated as quintessential specialists on forests burned at high severity, recent evidence indicates a need to update management priorities for this species to account for the importance of pyrodiversity to vital rates and habitat selection (Stillman et al., 2021; Stillman, Siegel, Wilkerson, Johnson, Howell, & Tingley, 2019).

However, disturbance regimes worldwide are experiencing shifting baselines from climate change and fire suppression over the past century (Kelly et al., 2020). In western North America, fire regimes are increasingly characterized by large, severe megafires that depart from the historic range of disturbance conditions (Hagmann et al., 2021). These changes often result in large, uniform high-severity patches, leading to decreased pyrodiversity after fire (Stevens et al., 2017), and potentially threatening the persistence of post-fire wildlife (Steel et al., 2022; Stillman et al., 2021). Our results emphasize the importance of accounting for pyrodiversity when planning management to promote wildlife conservation after fire. Pyrodiversity is a complex element of post-fire landscapes, and its effects on wildlife depend on the context of underlying fire regimes and animal adaptations

(Jones & Tingley, 2022). Moving forward, adaptive management will likely need to incorporate a better understanding of nonstationary relationships between wildlife and fire characteristics across space and time; effects of pyrodiversity, for example, may differ among ecoregions (Jones & Tingley, 2022; Steel et al., 2021).

We found evidence that black-backed woodpecker habitat relationships in California change as the number of years since fire increases, indicating a dynamic process of habitat selection that responds to changes in food availability and habitat structure over time. Importantly, this interaction effect was especially strong for burn severity, which is often highlighted as the key element of "high-quality" black-backed woodpecker habitat. In addition, we found that the positive effect of pre-fire fir basal area increased over time. Burned fir trees tend to remain standing longer than pines (Grayson et al., 2019), and our field observations suggest that fir trees are also better able to retain wood-boring beetle larvae—a key food source (Stillman, Caiafa, et al., 2022)—in later post-fire years. Together, these results suggest that fir-dominated forests may retain black-backed woodpecker populations at higher densities 5–10 years after fire relative to pine-dominated forests in California. Individual birds may shift habitat selection patterns to match areas with higher wood-boring beetle abundance as the number of years since fire increases.

Decision-support tool for post-fire management

Information about wildlife responses to pyrodiversity and fire dynamics must be gathered rapidly to guide time-sensitive decisions about where and how to manage burned areas. Many hurdles may impede this process, and gathering the necessary information (e.g., species occurrence) can require immense field effort (Hessburg et al., 2021). Predictive models based on remotely sensed data can fill these information gaps, and several models have been developed to incorporate woodpecker habitat suitability into post-fire management (Campos et al., 2020; Tingley, Wilkerson, et al., 2016). In the black-backed woodpecker case study, we employed an adaptive management framework to demonstrate how several components of spatial pyrodiversity can be integrated into existing models and decision-support tools to inform planning in the context of shifting fire regimes. Our results suggest that using our best-supported occupancy model to update the occupancy component of the integrated model by Tingley, Wilkerson, et al. (2016), which provides an externally validated management tool to predict animal abundance and density at fine spatial resolution, will improve utility for effective conservation decision-making. Here, employing adaptive management meant updating the existing model as new field data on pyrodiversity and temporally varying fire characteristics became available. Adaptive management is an iterative process meant to reduce uncertainty over time, and we expect that management tools for post-fire biodiversity will benefit from continued updates. In the context of our case study, additional efforts to study black-backed woodpecker colonization and the use of anomalously large, severe fires will be particularly useful (White et al., 2019).

To make the predictions from the updated model more accessible to decision-makers, we developed an RShiny App in partnership with the United States Department of Agriculture (USDA) Forest Service to generate results with a point-and-click interface available at https://birdpop.org/pages/bbwoPredPostFireDist.php. To generate model predictions, users simply upload two required files: (1) a shapefile giving the outline of the fire boundary or a subset of its area, and (2) remotely sensed data on burn severity. Both files are available within months of a fire burning in California and are freely obtainable from the Rapid Assessment of Vegetation Condition After Wildfire program (https://burnseverity.cr.usgs.gov/ravg/). Other covariate values, such as elevation and forest type, are stored internally within the App. After initiation, the App uses the integrated occupancy and space use model to produce spatially explicit predictions of potential pair density at ~30 × 30 m resolution (Figure 3). These predictions account for the effects of pyrodiversity and fire dynamics based on the temporal–landscape model, and users have options to further account for temporal dynamics by generating predictions specific to a selected post-fire year. Given these spatially explicit density predictions, the App will also sum predictions across a specified area to estimate potential abundance while propagating posterior uncertainty from all component models (Figure 3). The expected users for this tool include land managers, conservation scientists, and other natural resource practitioners operating within the black-backed woodpecker's range in California. Conducting on-the-ground surveys for black-backed woodpeckers may require multiple years of fieldwork, especially when information is needed over a large area and surveys are constrained to the breeding season. The RShiny App provides a way to easily predict potential woodpecker abundance and density when time-sensitive management decisions cannot wait for—or when limited budgets cannot provide for—professional field surveys. An additional benefit of the App is the speed of generating predictions: the full suite of analysis outputs can be calculated in <10 min, even for large fires.

Multispecies assessments of post-fire wildlife habitat represent an important pathway forward in adaptive

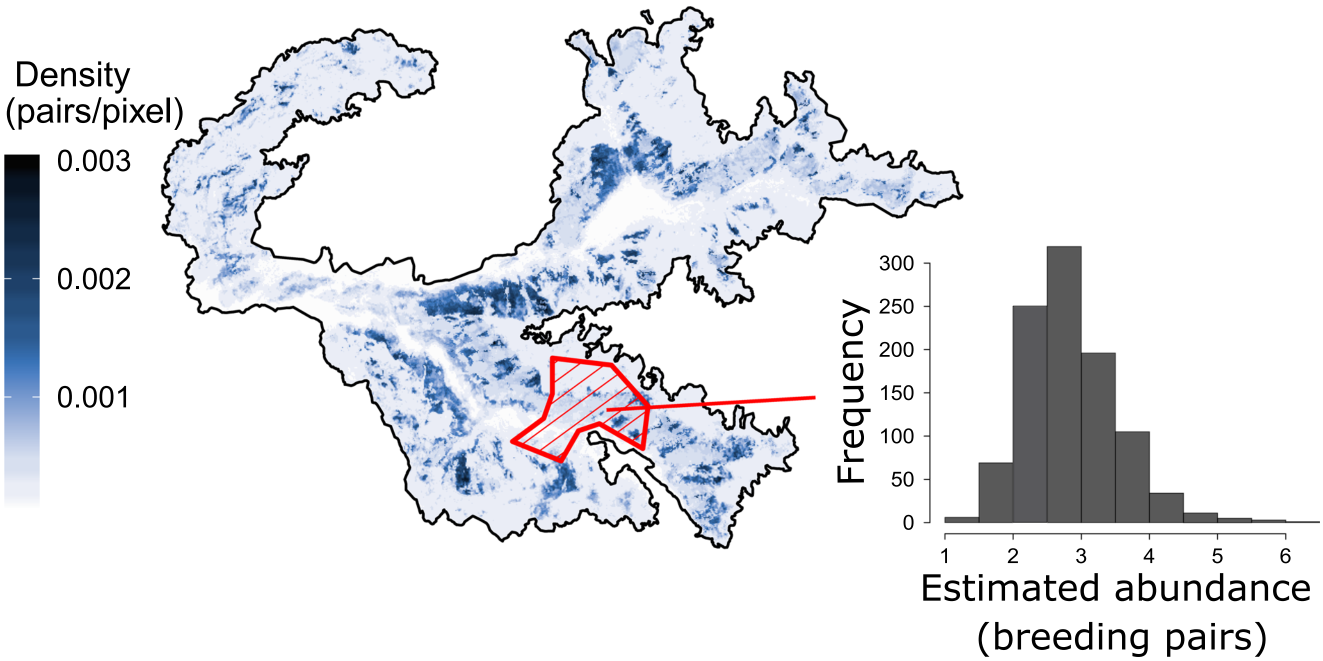

FIGURE 3 We used a temporal–landscape model of black-backed woodpecker occupancy to update a decision-support tool in an adaptive management framework. The online tool produces spatiotemporal predictions of black-backed woodpecker density and abundance potentially supported by a post-fire landscape. Here, density predictions are shown at approximately 30 × 30 m resolution across the 146 km^2 Donnell fire which burned in 2018. Potential densities within a specific area of interest (e.g., red polygon in this example) can be summed to predict potential abundance along with posterior uncertainty.

management. The integrated occupancy and space use model employed in our case study can be extended to other species given the availability of two data sources: (1) detection/nondetection surveys (e.g., occupancy), and (2) quantitative relationships between environmental features and home-range size (Tingley, Wilkerson, et al., 2016). These data sources are already available for several species relevant to forest management in California, including fishers (*Pekania pennanti*; Spencer et al., 2015) and California spotted owls (Blakey et al., 2019; Jones et al., 2021). Other woodpecker species are used to guide management decisions in North American forests, and existing decision-support tools (e.g., nest suitability; Campos et al., 2020) may provide a platform to incorporate pyrodiversity into management. In addition, recent technological advances to monitor animals, such as large-scale camera trap networks and automated recording units, provide an opportunity to estimate region-wide occupancy patterns for species where data are otherwise lacking (Wood et al., 2019).

The combination of biodiversity loss and shifting fire regimes point to the need for adaptive management practices that reduce uncertainty over time and proactively anticipate environmental change. Our case study demonstrates the value of ongoing efforts to incorporate pyrodiversity into wildlife habitat assessments. Adaptive management requires continuous updating of decision frameworks for biodiversity conservation before and after fires burn, particularly as new data become available on wildlife responses to altered fire regimes (Hessburg et al., 2021). For example, targeted surveys in fires with exceptionally large high-severity patches may show stronger associations with pyrodiversity or patch metrics compared to studies that cover a wider range of fire conditions. Future work would benefit from additionally incorporating the post-fire colonization process and more detailed pyrodiversity metrics (e.g., Steel et al., 2021) into model predictions for wildlife responses to fire.

AUTHOR CONTRIBUTIONS

All authors contributed to conceptualization, Rodney B. Siegel and Robert L. Wilkerson supervised data collection with support from Sarah C. Sawyer, and Andrew N. Stillman and Morgan W. Tingley led the formal analysis. Andrew N. Stillman wrote the initial draft and all authors reviewed and edited the manuscript. The manuscript benefited from feedback from three anonymous reviewers.

ACKNOWLEDGMENTS

This study was funded by the Pacific Southwest Region of the USDA Forest Service. Andrew N. Stillman was supported by the Joint Fire Science Program Graduate Research Innovation Award 19-1-01-5 and the Cornell

Atkinson Center for Sustainability. We are grateful to the many field technicians who conducted woodpecker surveys. This is Contribution No. 750 of The Institute for Bird Populations.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Stillman et al., 2023) are available in Dryad at https://doi.org/10.5061/dryad.3tx95x6jx.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Stillman, Andrew N., Robert L. Wilkerson, Danielle R. Kaschube, Rodney B. Siegel, Sarah C. Sawyer, and Morgan W. Tingley. 2023. "Incorporating Pyrodiversity into Wildlife Habitat Assessments for Rapid Post-Fire Management: A Woodpecker Case Study." *Ecological Applications* e2853. https://doi.org/10.1002/eap.2853