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RESEARCH ARTICLE

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Cross-scale occupancy dynamics of a postfire specialist in response to variation across a fire regime

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Abstract

1. Fire creates challenges and opportunities for wildlife through rapid destruction, modification and creation of habitat. Fire has spatially variable effects on landscapes; however, for species that benefit from the ephemeral resource patches created by fire, it is critical to understand characteristics of fires that promote postfire colonization and persistence and the spatial scales on which they operate.
2. Using a model postfire specialist, the black-backed woodpecker (*Picoides arcticus*), we examined how colonization and persistence varied across two spatial scales as a function of four characteristics of fire regimes—fire severity, fire size, fire ignition date and number of years since fire.
3. We modelled black-backed woodpecker colonization and persistence using data from 108 recently burned forests in the Sierra Nevada and southern Cascades ecoregions of California, USA, that we monitored for up to 10 years following fire. We employed a novel, spatially hierarchical, dynamic occupancy framework which differentiates colonization and persistence at two spatial scales: across fires and within fires.
4. We found strong effects of fire characteristics on dynamic rates, with colonization and persistence declining across both spatial scales with increasing years since fire. Additionally, at sites within fires, colonization decreased with fire size and increased with fire severity and for fires with later ignition dates.
5. Our results support the notion that different aspects of a species' environment are important for population processes at different spatial scales. As habitat quality is ephemeral for any given postfire area, our results illustrate the importance of time since fire in structuring occupancy at the fire level, with other characteristics of fires playing larger roles in determining abundance within individual fires. Our results contribute to the broader understanding of how variation in fire characteristics influences the colonization and persistence of species using ephemeral habitats, which is necessary for conserving and promoting postfire biodiversity in the context of rapidly shifting fire regimes.

KEYWORDS
black-backed woodpecker, colonization, dynamic occupancy model, multiscale analysis, persistence, *Picoides arcticus*, wildfire

1 | INTRODUCTION

Fire is a key ecosystem driver that sustains biodiversity in many ecosystems by adding to habitat heterogeneity and resetting successional processes (Gill, 1975; Martin & Sapsis, 1992). No two fires are identical, with fires differing in size, severity, seasonal timing and structure. When averaged across landscapes and broad temporal windows, these characteristics define a fire regime and can be used to classify "pyromes" globally (Archibald, Lehmann, Gómez-Dans, & Bradstock, 2013). Within a landscape, variation in these characteristics creates "pyrodiversity," which has been found to correlate with biodiversity in a variety of systems and taxa (Hempson et al., 2017; Tingley, Ruiz-Gutiérrez, Wilkerson, Howell, & Siegel, 2016a). Harnessing this relationship, fire can be managed to promote or enhance biodiversity, but doing so requires knowledge of which characteristics of fires are most important for species' use of postfire landscapes (Kelly & Brotons, 2017).

Postfire biodiversity is catalysed by species that thrive in recently burned forests and which help transform the landscape following disturbance. These species include reseeding and resprouting plants (Pausas & Lavorel, 2003), detrivores such as wood-boring beetles (Costello, Jacobi, & Negrón, 2013; Schütz et al., 1999), and in many forested biomes of the world, woodpeckers—which facilitate biodiversity primarily by creating tree cavities that are used by other species (Tarbill, Manley, & White, 2015; Virkkala, 2006). Postfire succession and biodiversity growth hinges on these species finding (if initially absent), settling and reproducing within burned areas, yet little attention has been paid to identifying the drivers of these specific processes within postfire ecosystems, particularly for vertebrates. Of key interest is understanding which characteristics of fires facilitate the colonization and persistence of species within burned areas, and how these processes play out over spatial and temporal scales.

One postfire specialist, the black-backed woodpecker *(Picoides arcticus*), shows a strong affinity for standing dead trees (snags) in recently burned conifer forests in western North America (Hutto, 2008; Smucker, Hutto, & Steele, 2005). These woodpeckers typically appear in postfire forests within 1 year following disturbance. Local abundance peaks 4 or 5 years after fire and subsequently declines over the next 3–5 years (Saab, Russell, & Dudley, 2007; Saracco, Siegel, & Wilkerson, 2011). The generalized cycle of black-backed woodpecker population growth and decline tracks the abundance of snags that are created by fire and gradually deteriorate over time. Snags provide sites for foraging, nesting and roosting, and home range size tracks snag density (Nappi, Drapeau, Giroux, & Savard, 2003; Tingley, Wilkerson, Bond, Howell, & Siegel, 2014). In unburned montane forests in western North America, where snags are more sparsely distributed, black-backed woodpeckers are found sporadically or not found at all (Fogg, Roberts, & Burnett, 2014; Hutto, 2008). This leads to a patchy distribution of dense populations among spatially distinct postfire areas within a larger matrix of forest where the species is absent or occurs at much lower density. Within burned areas, which are hypothesized to host source populations (Nappi & Drapeau, 2009), habitat quality varies with environmental factors such as snag density and food availability (Seavy, Burnett, & Taille, 2012). Thus, population dynamics occur at two spatial scales: within (site-level) and between (fire-level) postfire habitats. Here, we define a "fire" as a discrete area that was burned by a single wildfire that created potential habitat for black-backed woodpeckers, and we use this term rather than "patch" when describing our system to avoid confusion caused by differences in the meaning of the term "patch" in the context of fire ecology (where a patch is typically a homogenous area within a single fire) vs. metapopulation ecology (where a patch is a discrete habitat unit surrounded by the matrix).

The ephemeral nature of black-backed woodpecker populations and their strong association with recently burned forests create conservation and management challenges for the species (Hutto & Gallo, 2006; Kotliar et al., 2002). Despite the ecological importance of black-backed woodpeckers to postfire forest ecosystems (Tarbill et al., 2015), little is known about the population dynamics that allow the species to persist in and among local populations. Unlike conventional metapopulations (sensu Hanski, 1998), extinction of local black-backed woodpecker populations is an expected outcome as food resources wane during the decade after fire and population density within occupied fires rapidly declines (Saracco et al., 2011). A dynamic process of extinction and colonization is necessary to maintain a metapopulation (Hanski, 1998), yet when patch quality is ephemeral, the metapopulation is not sustained by recolonization of the same patches over time (Etienne & Heesterbeek, 2001; Hastings, 2003). Instead, black-backed woodpecker occupancy in postfire systems depends on colonization of recent fires followed by population persistence in available habitat long enough to produce propagules for future colonization.

An ecological understanding of colonization and persistence is key to uncovering the processes behind species distributions and developing sound strategies for conservation and management of animal populations (Yackulic, Nichols, Reid, & Der, 2014). This is particularly true for species inhabiting ephemeral habitats, where long-term preservation of a particular parcel does not ensure species preservation (Thomas, 1994; Van Teeffelen, Vos, & Opdam, 2012). Linking the processes associated with population persistence to environmental variables may provide insight into the factors that regulate species' distributions and drive habitat selection in a heterogeneous landscape. Under the metapopulation paradigm, within-patch variation in habitat quality is often overlooked, but site-level variables can be important factors in population dynamics (Fleishman, Ray, Sjögren Gulve, Boggs, & Murphy, 2002). Metapopulation models should incorporate both site-level and patch-level variables to accurately identify the environmental mechanisms that drive population dynamics (Frey, Strong, & McFarland, 2012). Here, we present a novel spatially hierarchical dynamic occupancy model which allows multiscale analysis of within-fire and between-fire occupancy patterns that emerge from species living in heterogeneous habitat. The model builds from prior multiscale occupancy models (Nichols et al., 2008; Pavlacky, Blakesley, White, Hanni, & Lukacs, 2012) through its temporally dynamic formulation, assessing colonization and persistence at two distinct spatial scales.

Our purpose was to assess which characteristics of fires influence the dynamic processes of colonization and persistence both across and within fires. Most black-backed woodpecker studies have focused on just one or a few fires, looking at changes in occupancy within fires (Murphy & Lehnhausen, 1998; Saab et al., 2007) or static determinants of occupancy across multiple fires (Latif, Saab, Hollenbeck, & Dudley, 2016; Saracco et al., 2011). We used occurrence data from 108 distinct postfire areas to examine how variation in fire regime characteristics influences subsequent population dynamics over time. Specifically, we evaluated four distinct axes of variation in fires: (a) fire severity, where we predicted that higher severity fires would facilitate colonization and persistence through habitat creation (Nappi & Drapeau, 2011; Saracco et al., 2011); (b) years since fire, where we predicted that colonization and persistence of woodpeckers would decline with increasing years since fire as a result of diminishing habitat quality (Murphy & Lehnhausen, 1998; Saab et al., 2007); (c) fire ignition date, where we predicted that fires in the first half of the fire season would facilitate colonization and persistence as these fires might be better timed for colonization by wood-boring beetles—a key food source that disperses in early to midsummer (Costello et al., 2013; Villard, 1994); and (d) fire size, where we predicted that large fires would provide more habitat and would thus have greater colonization and persistence (MacArthur & Wilson, 1967). We did not have strong a priori predictions with respect to scale but hypothesized that these four general predictions would hold at both site and fire scales. Our hierarchical approach allows us to examine why certain fires become colonized or remain occupied, while also accounting for the within-fire occupancy changes that are expected to occur as habitats change following fire.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted surveys for black-backed woodpeckers as part of a long-term project to monitor the species' occupancy and population trends in burned forests of California. Between 2009 and 2016, we sampled forested areas in National Forest System lands that had burned between 1 and 10 years prior to the sampling year. Our study area comprised ten contiguous National Forest units within the greater Sierra Nevada and southern Cascades ecoregions (Figure 1a). Each year we randomly selected 50 fires to visit that met our sampling criteria (see Supporting Information Methods S1). Our random selection included fires that were new to the survey and fires that had been sampled in previous years. Across all surveys between 2009 and 2016, we visited 111 fires ranging in burn year from 1999 to 2015 and ranging in size from 140 ha to 93,023 ha.

2.2 | Survey methods

During each of the 8 years of the study, we conducted single-visit surveys for black-backed woodpeckers at 5–24 survey sites (median = 20) in each of the 50 fire areas selected for survey that year. Within a fire, survey sites were spaced at least 250 m from one another. In general, our protocol aimed to sample 20 points within each fire, irrespective of fire size. While surveys were intended to sample a variety of conditions and habitats within fires, surveys did not exhaustively sample entire fires. We estimate that surveys sampled approximately 16% of the burned area in the average sampled fire. Given a constant definition of occupancy across spatial scales, variation in the number of sites sampled per fire may affect power to detect the true occupancy status of a given fire but should not produce bias.

We divided surveys into timed intervals and used two survey methods. Each survey included a broadcast component with three survey intervals. During each broadcast interval, electronic recordings of black-backed woodpecker vocalizations and territorial drumming (obtained from The Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology; recorded by G.A. Keller) were played for 30 seconds, followed by a 1.5-min silent observation period. We followed a removal methodology where call broadcasts were suspended after the first detection. Additionally, broadcast surveys at half the points at each fire were preceded by passive point counts with two to five survey intervals. Each passive survey started with a 3-min interval, followed by one to four 2-min intervals, depending on the year. In 2009, we used one 2-min interval, in 2010, we used four 2-min intervals, and in 2011–2016, we used two 2-min intervals. We conducted surveys in the morning hours (0530-0930) between 4 May and 18 July each year. All surveys were treated as unlimited-radius point counts. The median detection distance was 55 m, and 90% of all detections were within 200 m. For additional details on black-backed woodpecker broadcast and passive survey methods used for this analysis, see Saracco et al. (2011).

2.3 | Modelling approach

We developed a spatially hierarchical dynamic occupancy model in a Bayesian framework based on the Modelling structure of MacKenzie, Nichols, Hines, Knutson, and Franklin (2003) and Royle and Kéry (2007). Observations, y_{jkt}, for survey interval k at site j (where sites are individual survey points) in year t, are assumed to be imperfectly observed representations of the true occurrence status, z_{jt} (1 or 0), which is constant across all k survey intervals (i.e., closure is assumed within the <17-min survey period) but can change from year to year. Observed occurrence, y_{jkt}, is thus modelled as a Bernoulli-distributed random variable with a probability of $p_{jkt} \times z_{jt}$, where p_{jkt} is the probability of detection for a given survey at a site.

Dynamic occupancy models generally follow a structure where each site has an initial probability of occupancy in the time series, and then, occupancy in subsequent years is probabilistically determined based on whether sites become colonized or remain occupied through persistence (MacKenzie et al. 2003). To structure a spatially hierarchical model, we defined two different spatial scales for occupancy: a site-level true occurrence, z_{jt}, and a fire-level true occurrence, Z_{ft}, where the sampled portion of each fire f contains

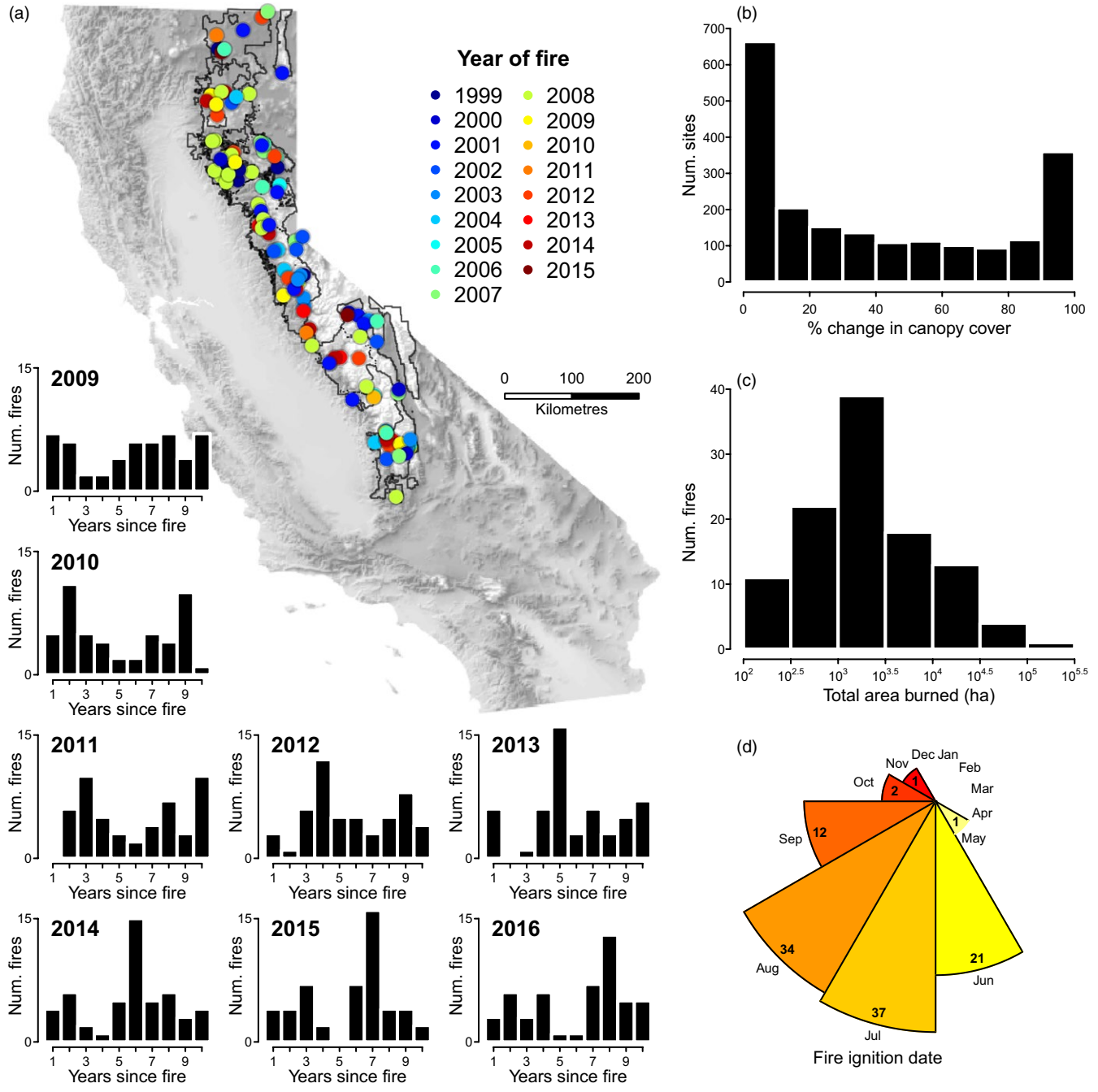

FIGURE 1 Variation in characteristics of fires sampled within a fire regime in the greater Sierra Nevada and southern Cascades ecoregions of California. (a) Locations of 108 sampled fires that burned between 1999 and 2015. Background map shows topographical relief with a black line around the 10 National Forest units that served as our study area. Inset plots show the frequency distribution of fire age classes for each year of sampling. (b) Frequency of average fire severity across all 2,052 survey sites within fires. (c) Frequency of fire size classes across the 108 fires. (d) Variation in the month in which sampled fires ignited

a variable number of sites. The true occurrence of sampled portions of fires, Z_{ft}, is modelled as a Bernoulli outcome of the probability of fire occupancy, Ψ_{ft}, which is a deterministic combination of dynamic probabilities such that, $\Psi_{ft} = \Gamma_{ft}(1 - Z_{f,t-1}) + \Phi_{ft}Z_{f,t-1}$, where Γ_{ft} and Φ_{ft} are probabilities of fire-level colonization and persistence, respectively. Similarly, the true occurrence of surveyed sites within fires, z_{jt}, is modelled as a Bernoulli outcome of dynamic probabilities, but z_{jt} is also conditioned on the true occurrence status of the fire, which provides a hierarchical spatial dependence. Thus,

$$z_{jt} \sim \text{Bernoulli}\left(\psi_{jt}\right)$$

$$\psi_{jt} = Z_{ft}\left[\gamma_{jt}(1 - z_{j,t-1}) + \phi_{jt}z_{j,t-1}\right],$$

where ψ_{jt}, γ_{jt} and ϕ_{jt} are site-level probabilities of occupancy, colonization and persistence, respectively. We note that information on

fire-level occupancy, Z_{ft}, is solely derived from site-level observations, y_{jkt}, in our formulation, although the model could be modified to include independent data on fire-level occupancy if such were available (Nichols et al., 2008).

Because of the temporal dependence of Ψ_{ft} and ψ_{jt} on the true occurrence of fires and sites at the previous time step, the initial occupancy probability or the initial true occurrence status must be defined. In our model, we defined the initial time step (t = 1) as the year when each fire burned. Observations were only made over the following decade (t = 2–11). Given that observations were only made within fire perimeters and that fire—by its nature—is a process that excludes or removes living animals, particularly mobile ones like birds, we assumed that the true occurrence status during the fire was 0, such that $Z_{f,1}$ = 0 and $z_{j,1}$ = 0. Thus, the occurrence of fires and sites in subsequent years was a direct consequence of these areas becoming colonized and persisting (or not) through time.

We parameterized p_{jkt}, γ_{jt}, ϕ_{jt}, Γ_{ft} and Φ_{ft} as logit-linear functions of a priori selected, scale-dependent covariates. We modelled the probability of detection, p_{jkt}, as a function of survey interval duration (2 min = 0, 3 min = 1), the Julian day of the year, and the survey type (passive = 0, broadcast = 1). Given that black-backed woodpeckers exist at low densities even within ideal habitat and have primarily nonoverlapping territories (Tingley et al., 2014), we did not seek to control for the potential effect of abundance on detection probability (Royle & Nichols, 2003) which can potentially bias estimates of occupancy (Latif, Ellis, Saab, & Mellen Mclean, 2018).

Site-level colonization and persistence were each modelled as functions of seven covariates: four characteristics of fires (Figure 1) and three additional variables based on previous work (Saracco et al., 2011; Tingley, Wilkerson, Howell, & Siegel, 2016b). Fire characteristic variables included (a) % fire severity, (b) the number of years since fire, (c) fire size and (d) fire ignition season (0 = before 15 August, and 1 = after 15 August). We used 15 August as the binary cut-off for fire ignition season because dispersing wood-boring beetles available for colonizing fires typically decline after that date (Costello et al., 2013). Additional covariates of site-level colonization and persistence were as follows: (e) snag density at survey points, (f) elevation and (g) latitude. Fire-level colonization and persistence were modelled as the function of the same covariates but excluded snag density (which was unavailable at the fire level). In all cases, continuous covariates were standardized to a mean of 0 and a standard deviation of 1. See Supporting Information Methods S1 and Table S1 for further details on covariates.

Prior to analysis, we removed three fires from our dataset: Bell West (burned 22 May 1999), Azusa (burned 29 May 2000) and Soda (burned 13 Jan 2014). These fires were temporal outliers, having burned much earlier or much later than the typical fire season (June–November; Taylor & Beaty, 2005; Westerling, Hidalgo, Cayan, & Swetnam, 2006). Our final dataset therefore comprised 2,052 unique survey sites at 108 fires.

We fit the model to the data with JAGS (Plummer, 2003) using the R statistical programming language version 3.3.1 (R Core Team 2015) and the package "R2JAGS" (Su & Yajima, 2014). We used vague priors (i.e., normal with μ = 0, τ = 0.1). We ran three chains of 350,000 iterations thinned by 1,000 with a burn-in of 50,000, yielding a posterior sample of 900 across all chains. The fire-level parameters showed slow mixing, likely due to the hierarchical latent variable structure. Convergence was checked visually with traceplots and confirmed with a Gelman–Rubin statistic <1.1 (Gelman, Carlin, Stern, & Rubin, 2004). Inference on parameters was made using 95% Bayesian credible intervals (95 CI). Posterior predictive checks of model fit were conducted by calculating Bayesian p-values (Gelman, Meng, & Stern, 1996) for a series of test statistics (see Supporting Information Methods S1) derived from the observed number of woodpecker detections per fire per year. Full JAGS code and data for our model are provided in our online data archive (Tingley et al., 2018).

3 | RESULTS

We report results from black-backed woodpecker surveys at 2,052 individual sites across sampled portions of 108 fires in the greater Sierra Nevada and southern Cascades ecoregions (Figure 1). We sampled 80% (n = 1,647) of sites and 81% (n = 88) of fires in more than 1 year and 1.5% (n = 32) of sites and 1.8% (n = 2) of fires in all 8 years of the study. Our surveys recorded apparent colonization at 35% (n = 709) of sites. Of those sites, 78% (n = 555) subsequently showed apparent extinction. Fires showed different dynamics than individual sites; we recorded apparent colonization within sampled portions of 65% (n = 70) of fires, of which 47% (n = 33) showed apparent extinction.

3.1 | Detectability

Posterior estimates of the probability of detecting the species at least once at a site given multiple survey intervals (p^*; MacKenzie & Royle, 2005) indicate that on average, detectability of black-backed woodpeckers was high (p^* given six passive and broadcast intervals = 0.90–0.93; p^* given three broadcast intervals only = 0.80–0.85). The probability of detection was greater when using broadcast surveys compared to passive surveys (95 CI on slope of categorical effect = 1.07–1.39). Detectability was also higher during 3-min survey intervals instead of 2-min survey intervals (95 CI on slope of categorical effect = 0.21–0.60). The probability of detecting woodpeckers increased throughout the breeding season each year (95 CI on slope of standardized time variable = 0.003–0.19).

3.2 | Dynamics across spatial scales

Rates of colonization and persistence for black-backed woodpeckers in burned forests differed across spatial scales. Annual persistence probability at fires was generally high, averaging 0.71 (95 CI: 0.61–0.80). In contrast, when averaged across all 10 years following fire, fires were unlikely to be colonized in any given year, with a mean annual fire-level colonization probability of 0.23 (95 CI: 0.13–0.35).

Within-fire site-level dynamics demonstrated a similar trend but lower average rates. Mean annual site-level persistence probability was 0.44 (95 CI: 0.37–0.51), and mean annual site-level colonization probability was 0.17 (95 CI: 0.14–0.19).

3.3 | Colonization–persistence dynamics as a function of fire regime

Black-backed woodpeckers showed differing colonization and persistence relationships across spatial scale (fire vs. site) and among fire characteristics (Table 1, Figure 2). One characteristic that showed highly consistent responses, however, was time since fire, which had a pervasive and significant negative relationship with persistence and colonization across both spatial scales (Figure 2). This effect was stronger at the fire level, with fire colonization (95 CI: −2.41 to −1.08) and fire persistence (95 CI: −1.51 to −0.41) sharply dropping within the first few years following fire. Site-level dynamics also showed declines with time since fire (95 CI for site colonization: −0.77 to −0.50; 95 CI for site persistence: −0.57 to −0.12).

For the three other components of fire regimes that we assessed, black-backed woodpeckers primarily showed significant relationships at the scale of site-level colonization (Figure 2). Notably, site-level colonization probability was higher for fires that burned in the latter half of the fire season, with a fire ignition date after 15 August (95 CI: 0.03–0.64). Fire-level persistence showed a response to ignition date as well, and our results suggest that black-backed woodpeckers are marginally more likely to persist from year to year in later season fires (95 CI: −0.10 to 1.66), although uncertainty around the parameter estimate overlaps zero. Additionally, site-level colonization was lower for larger fires (95 CI: −0.32 to −0.03). Site-level colonization was also higher for sites with higher fire severity (95 CI: 0.01–0.23). For all other fire regime variables at both site- and fire-level scales, covariate relationships showed substantial uncertainty (Table 1).

3.4 | Additional factors affecting dynamics

Both colonization and persistence were more likely at sites with a higher density of snags, and the parameter estimates for these two relationships had approximately equal strength (Table 1). Elevation and latitude also affected dynamic rates. The probabilities of both fire-level colonization and fire-level persistence were greater in fires that were higher in elevation and farther north (Figure 3), with the relationships stronger for persistence than colonization (Table 1). Site-level colonization also showed strong positive relationships to elevation and latitude, while site-level persistence showed a strong positive relationship to elevation but not latitude (Figure 3).

3.5 | Trends in black-backed woodpecker occupancy across sites and fires

Variation in the rates of colonization and persistence across fire characteristics produced differences in occupancy probabilities of black-backed woodpeckers across spatial and temporal scales. Mean annual probability of site-level occupancy was 0.20 (95 CI: 0.19–0.20), and the average annual fire-level occupancy was 0.57 (95 CI: 0.56–0.59) over the duration of our study. At both scales, the probability of black-backed woodpecker occupancy declined as the number of years since fire increased (Figure 4a). Our model estimated that 72% of sampled areas of fires and 29% of individual survey sites were occupied 1 year following fire (95 CI fire: 0.71–0.74; site: 0.28–0.30). Occupancy declined to 31% of fire areas and 9% of sites by 10 years following fire (95 CI fire: 0.31–0.35; site: 0.08–0.10). Fire-level occupancy peaked at 4 years following fire, before declining sharply. Site-level occupancy increased marginally between the first and second years following fire (mean change: 0.01; 95 CI: −0.01 to 0.03), after which site-level occupancy decreased monotonically until at least 7 years postfire

TABLE 1 Colonization and persistence parameter estimates for a spatially hierarchical dynamic occupancy model of black-backed woodpecker occurrence across 108 fires over 8 years

	Colonization		Persistence	
Covariate	**Fire-level**	**Site-level**	**Fire-level**	**Site-level**
Intercept	−1.24 (−1.93, −0.64)	−1.60 (−1.78, −1.44)	0.89 (0.45, 1.36)	−0.24 (−0.55, 0.05)
Fire regime variables				
Fire season	−0.04 (−1.32, 1.34)	**0.34 (0.03, 0.64)**	0.75 (−0.10, 1.66)	−0.17 (−0.58, 0.22)
Fire severity	−0.08 (−0.69, 0.45)	**0.12 (0.01, 0.23)**	−0.34 (−0.76, 0.05)	0.07 (−0.11, 0.24)
Fire size	−0.18 (−0.82, 0.40)	**−0.17 (−0.32, −0.03)**	0.10 (−0.44, 0.66)	0.12 (−0.10, 0.32)
Years since fire	**−1.66 (−2.41, −1.08)**	**−0.62 (−0.77, −0.50)**	**−0.94 (−1.51, −0.41)**	**−0.34 (−0.57, −0.12)**
Environmental and site-only variables				
Elevation	**1.14 (0.44, 1.77)**	**0.81 (0.62, 1.02)**	**1.54 (0.83, 2.27)**	**0.40 (0.08, 0.75)**
Latitude	**1.06 (0.40, 1.78)**	**0.74 (0.56, 0.91)**	**1.53 (0.91, 2.20)**	0.29 (−0.02, 0.60)
Snag density	–	**0.21 (0.10, 0.32)**	–	**0.30 (0.13, 0.49)**

Estimates show means and 95% Bayesian credible intervals. Covariate effects with 95% credible intervals that do not cross zero are highlighted in bold.

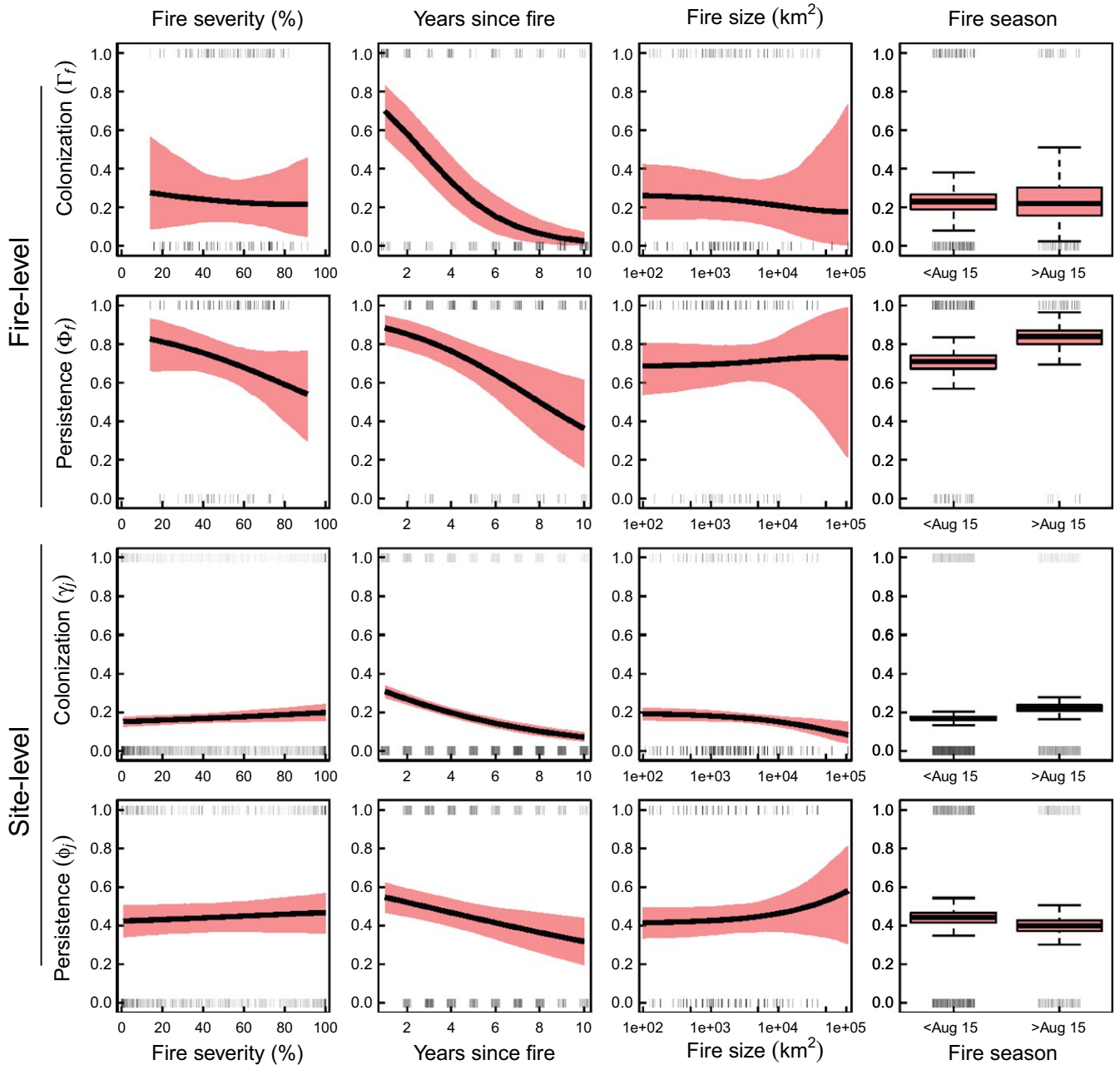

FIGURE 2 Modelled relationships of colonization and persistence by four axes of fire regimes and at two spatial scales, site-level and fire-level. Modelled relationships show mean responses (black lines) and 95% credible intervals (red). Data rugs show naïve colonization and naïve persistence as a function of covariates (jittered for noncontinuous variables)

(Figure 4a). Across the entire 10 years following fire, the model estimates that 93% of sampled fire areas were occupied in at least 1 year (95 CI: 0.880–0.972).

Despite consistent declines in site- and fire-level occupancy with the number of years since fire, we did not find persistent temporal trends across the eight survey years (Figure 4b). Annual site-level occupancy varied little on average from year to year, with a year-to-year mean standard deviation in occupancy of 2.4% (95 CI = 2.0%–2.8%). In contrast, fire-level occupancy varied more, with a year-to-year mean standard deviation in occupancy of 7.0% (95 CI = 5.8%–8.3%).

3.6 | Model fit

We tested overall model fit with a posterior predictive test on the average number of detections per fire across all years. The observed value of this test statistic ($T = 1.56$) was very closely approximated by the model, with a Bayesian p-value of 0.487, indicating no lack of fit (see Supporting Information Methods S1). Posterior predictive tests also indicated no lack of fit for 8 of the 10 years following fire (Supporting Information Figure S1). Potential lack of fit was indicated for the first year after fire, when the model underestimated the average number of detections per

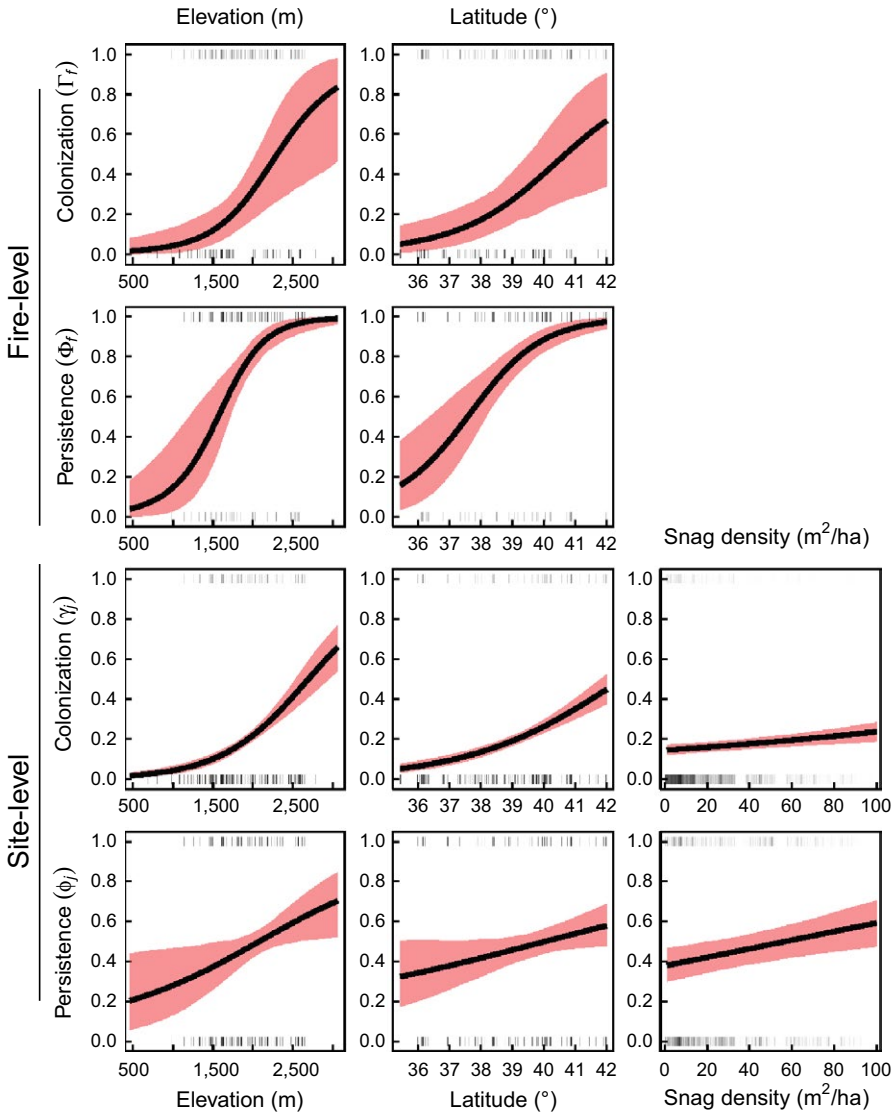

FIGURE 3 Modelled relationships of colonization and persistence by elevation, latitude and snag density at two spatial scales. Modelled relationships show mean responses (black lines) and 95% credible intervals (red). Rugs show naïve colonization and naïve persistence as a function of covariates

fire (Bayesian *p*-value = 0.96), and 8 years after fire, when the model overestimated the average number of detections per fire (Bayesian *p*-value = 0.05).

4 | DISCUSSION

Principal questions in fire ecology include how fire-associated species colonize and populate ephemeral habitats that appear on the landscape in a stochastic manner, and how these dynamic processes change as a function of fire characteristics. Here, we presented a novel hierarchical modelling approach to estimate the probabilities of colonization and persistence of black-backed woodpeckers within burned forests at two spatial scales in response to variation in fire characteristics across the larger fire regime. We found effects of each fire characteristic on at least one aspect of fire or site dynamics, indicating that when, where and how fires burn can have important impacts on wildlife in the years to decades that follow. The multiple axes of variation in fire regimes have only recently been quantified for many systems (Archibald et al., 2013), and our results provide novel evidence that these different axes may all be relevant for postfire biodiversity.

Of the fire characteristics investigated, perhaps the most intriguing is the impact of the season in which a fire burns. "Natural" fire seasons vary globally but generally have defined seasonal bounds; yet, empirical fire seasons can deviate extensively from these bounds through human intervention, particularly in grassland ecosystems (Le Page, Oom, Silva, Jönsson, & Pereira, 2010). Throughout our study region in the inland mountains of California, fires tend to burn during a fire season that extends from early summer to November—fires outside of this time window (i.e., in December or January) are infrequent. Our a priori hypothesis was that late-season fires might create lower quality habitat for black-backed woodpeckers due to limited food availability. In the western United States, wood-boring beetles of the families Cerambycidae and Buprestidae—which are the primary food for black-backed woodpeckers (Rota, Rumble, Lehman, Kesler, & Millspaugh, 2015)—disperse via a winged adult stage that peaks in abundance in early to midsummer before sharply decreasing in August

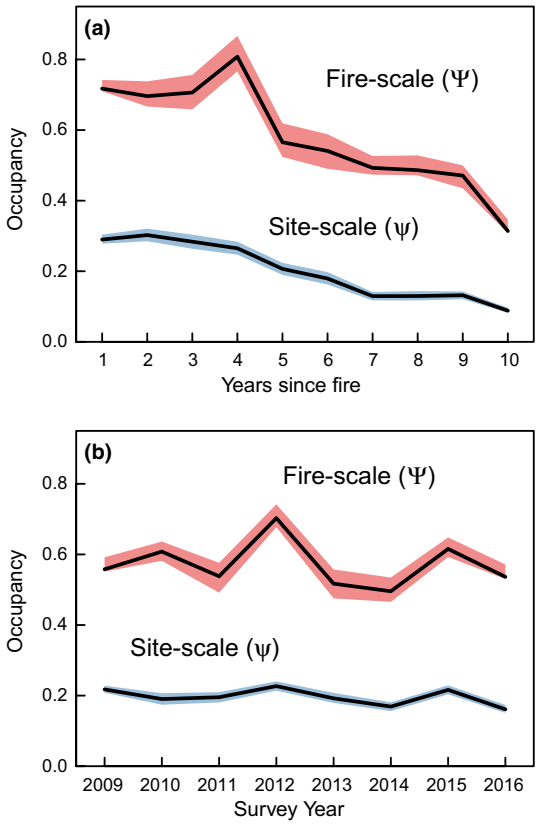

FIGURE 4 Model-derived changes in black-backed woodpecker occupancy across burned forests over time. The proportion of occupied fires and the proportion of occupied points (a) decreased strongly over the first 10 years following fire, even while occupancy at both scales (b) remained relatively constant across the 8-year time interval of the study

and September (Costello et al., 2013). Our hypothesis was grounded in the idea that late-season fires may miss large-scale colonization events by beetles attracted by the chemical and infrared stimuli of fire.

Contrary to our predictions, however, we found that woodpeckers were more likely to colonize fires that burned later in the fire season (August–November) than in earlier months (May–July), and later fires may also have higher woodpecker persistence. This finding suggests that seasonal constraints on beetle dispersal into postfire forests likely do not regulate which burned areas are ultimately colonized by woodpeckers. Rather, these trends may arise from temporal constraints on woodpecker dispersal between postfire areas. How black-backed woodpeckers (and other mobile species associated with postfire conditions) find newly burned habitat remains mostly unknown, but presumably colonization occurs either by long-distance dispersal from other burned areas (Nappi & Drapeau, 2009; Pierson, Allendorf, Drapeau, & Schwartz, 2013) or recruitment from surrounding unburned forest (Fogg et al., 2014). Analysis of black-backed woodpecker age distributions in burned forests has revealed high proportions of younger birds in newly burned forest (Siegel et al., 2015), suggesting both that natal dispersal is the primary means of patch colonization for this species and that black-backed woodpecker offspring from older fire areas may disperse to surrounding habitat patches instead of settling in the natal fire. If natal dispersal occurs primarily after 15 August—in the second half of the fire season—then late-season fires may be more likely to recruit individuals that are dispersing through the landscape, which could explain the increased rate of colonization for these areas in our results. While fire season has been studied extensively in relation to plant phenology and seed dispersal (Whelan, 1986), we know of no studies directly relating fire season to animal dispersal.

A second novel result from our analysis was the impact of fire size. Our expectation, grounded in island biogeographical theory (MacArthur & Wilson, 1967), was that larger fires should show increased colonization and persistence. To the contrary, sites in larger fires were less likely to be colonized. We interpret this result as indicating that while larger fires become colonized at equal rates to smaller fires, they have lower woodpecker densities. While large patches of burned habitat are clearly important for black-backed woodpeckers (Hutto, 2008; Odion & Hanson, 2013), it has been unclear whether larger fires per se necessarily yield larger populations. While not settling this debate, our finding supports the assumption that black-backed woodpeckers (presumably like other volant vertebrates) are excluded from forests as their habitat burns and have to recolonize afterwards; that is, within the lexicon of plant functional types, woodpeckers are "reseeders" not "resprouters" (Pausas & Lavorel, 2003). In this view, abundance within a postfire system is a function of external propagule pressure and internal recruitment and survival. Larger fires have smaller ratios of fire perimeter to fire area, which, given equal propagule pressure, means fewer colonizers for equal amounts of area. Our results indicate that larger fires do not necessarily produce better or worse habitats for post-fire-associated woodpeckers; instead, larger fires likely have lower densities due to an increased reliance on internal recruitment. Black-backed woodpeckers may therefore be at odds with a variety of other species—including plants and herbivorous mammals—which largely do not show relationships between postfire density and burned patch size, primarily because postfire dispersal from nearby refugia is not limiting (Turner, Romme, Gardner, & Hargrove, 1997).

Given that black-backed woodpeckers generally occur at low density in unburned landscapes in the Sierra Nevada (Fogg et al., 2014), we subsequently hypothesize that larger fires may tend to be underutilized and have unfilled potential territories, particularly in the first 1–2 years following fire. This hypothesis would fail, however, if larger fires differed structurally in important ways that made them less suitable. There is evidence—for example, with the 2013 Rim fire which burned over 1,000 km^2 (Lydersen, North, & Collins, 2014)—that larger fires in California also burn more homogeneously, leading to lower pyrodiversity and also lower biodiversity (Tingley et al., 2016a). Further study is required to investigate the extent to which this hypothesis is supported, particularly given the current trend towards increasing fire size in the Sierra Nevada and throughout the western United States (Cansler & McKenzie, 2014; Westerling et al., 2006).

Of the two remaining fire regime axes investigated, both fire severity and years since fire also showed strong relationships

to woodpecker dynamics, with site-level colonization increasing with fire severity, and multiscale colonization and persistence decreasing with the number of years since fire (Figure 2, Table 1). For site-level colonization, the number of years since fire had the strongest relative impact of the four fire characteristics, and years since fire was the only fire characteristic strongly influencing fire-level colonization and both site- and fire-level persistence (Table 1). Both fire age and fire severity have similarly been found to have strong influences on black-backed woodpecker occurrence in previous studies (Saracco et al., 2011; Smucker et al., 2005), and in general are the two factors that have the strongest effects on postfire bird communities (Smucker et al., 2005), but have not previously been investigated with respect to dynamic rates. Here, we demonstrate that time since fire affects both colonization and persistence, indicating that older postfire areas both become less attractive to colonizing woodpeckers and less capable of retaining populations.

Finally, although not a fire characteristic but rather a site-level property that arises from fire severity and prefire tree density, snag density had a strong positive effect on site-level probabilities of colonization and persistence. Snags are a key resource for black-backed woodpeckers, and snag density is known to correlate with population density (Tingley et al., 2014), survivorship (Rota, Millspaugh, Rumble, Lehman, & Kesler, 2014) and reproductive success (Nappi & Drapeau, 2009). While multiple characteristics of fires can potentially be influenced through prefire forest management, snag density was the only factor investigated that can be directly manipulated by postfire management and therefore could provide an opportunity for managers to increase overall population persistence—presumably through the retention of postfire stands with high snag densities.

Considered together, our results demonstrate the critical role of local or site-level colonization in driving occurrence dynamics within this population. Unlike conventional metapopulations, which consist of relatively constant patches of suitable habitat (Hanski, 1998), black-backed woodpeckers use ephemeral habitat that forms suddenly and declines gradually. Under these circumstances, local extinction is a common and predictable occurrence as habitat quality for the species declines over time, and rapid colonization of newly created habitat may be necessary to sustain populations (Etienne & Heesterbeek, 2001; Johnson, 2000). The importance of colonization highlights the key role of dispersal in maintaining and establishing local populations in a patchy postfire environment (Johst, Brandl, & Eber, 2002; Pierson et al., 2013); not just for black-backed woodpeckers, but for any metapopulation-structured species living in ephemeral habitats (Amarasekare & Possingham, 2001).

We caution that the lack of strong fire-level effects compared to site-level effects in our study does not necessarily mean that fire-level colonization and persistence are random for black-backed woodpeckers. Because our model formulation makes inference on fire-level processes solely through the hierarchical structure, the model necessarily has less power to estimate fire-level processes than site-level ones. For other applications, inferential power could be increased if supplemental data on the higher order occupancy status (e.g., via remote sensing or environmental DNA) were integrated into the model, as in the case of Nichols et al. (2008). Alternatively, mechanistic knowledge of patch-scale colonization or persistence probabilities could be used to create informed priors for parameters (McCarthy & Masters, 2005).

Another potential limitation to our inference on fire-level effects is that we did not exhaustively survey all portions of fires. With a median of 20 survey points per fire, our inference on fire-level colonization and persistence is restricted to the portion of the fire in which our surveys were located. Partial sampling of large spatial units is a common limitation in monitoring efforts (Legendre et al., 2002). With random sampling across 108 fires, this should not bias estimates of dynamic parameters, but partial sampling does change the interpretation of results. In particular, derived estimates of fire-level occupancy (Figure 4) must be interpreted only as occupancy within the sampled portion and not as absolute occupancy within an entire fire perimeter. Researchers interested in absolute occupancy of large areas could potentially use model-based simulations of the unsampled areas—for example, with a site-based type of data augmentation (Kéry, Royle, Plattner, & Dorazio, 2009)—to estimate those quantities.

In general, our model adequately fits the data and captured complex temporal and spatial patterns. Posterior predictive checks, however, suggested that occurrence was underestimated in the first year following fire and overestimated in the eighth year following fire. Our model formulation assumed that all individuals were eliminated from the area during the fire and that all occurrences detected 1 year following fire were due to new colonizations. The underestimation at 1-year postfire could indicate two nonexclusive unmodelled mechanisms: that the colonization process in the first year following fire is fundamentally different from the colonization process in subsequent years; or, that a certain percentage of black-backed woodpeckers existing in unburned forest prior to fire are able to persist in situ during and immediately after the fire. Although the difficulty of predicting when and where fires will occur inhibits the study of this topic, this question should not be ignored, as some of the most fascinating questions in fire ecology currently revolve around how species respond during and immediately after fire (Kelly & Brotons, 2017).

Spatial scale can exert considerable influence on ecological patterns and processes (Wiens, 1989). When local populations are connected through dispersal, overall population dynamics are shaped by the patterns that arise within patches and the patterns of interaction between patches (Le Corre, Johnson, Smith, & Guichard, 2015; Runge, Runge, & Nichols, 2006). We treated colonization and persistence as scale-dependent processes that operate within and between ephemeral habitat patches to maintain populations across landscapes. This approach allowed us to determine the effects of different aspects of a fire regime on occurrence dynamics at two spatial scales. Colonization–extinction dynamics are conventionally viewed as arising at the patch level, providing limited means for understanding the impacts of site-level heterogeneity. However, conservation

and management actions are typically aimed at improving habitat quality or availability at the site level. A cross-scale examination of these processes could allow managers to identify and target specific characteristics at the right scale to improve landscape-level population persistence.

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AUTHOR'S CONTRIBUTIONS

M.W.T., B.W. and R.B.S. conceived the ideas and designed methodology; B.W. and R.B.S. oversaw data collection with help of S.C.S. and C.A.H.; M.W.T. and A.N.S. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Input data and model code in JAGS language are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jt38tj9 (Tingley et al., 2018).

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REFERENCES

Amarasekare, P., & Possingham, H. (2001). Patch dynamics and metapopulation theory: The case of successional species. *Journal of Theoretical Biology*, *209*, 333–344. https://doi.org/10.1006/jtbi.2001.2269

Archibald, S., Lehmann, C. E. R., Gómez-Dans, J. L., & Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 6442–6447. https://doi.org/10.1073/pnas.1211466110

Cansler, C. A., & McKenzie, D. (2014). Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. *Ecological Applications*, *24*, 1037–1056. https://doi.org/10.1890/13-1077.1

Costello, S. L., Jacobi, W. R., & Negrón, J. F. (2013). Emergence of buprestidae, cerambycidae, and scolytinae (Coleoptera) from mountain Pine beetle-killed and fire-killed ponderosa pines in the Black Hills, South Dakota, USA. *Coleopterists Bulletin*, *67*, 149–154. https://doi.org/10.1649/0010-065X-67.2.149

Etienne, R. S., & Heesterbeek, J. A. P. (2001). Rules of thumb for conservation of metapopulations based on a stochastic winking-patch model. *The American Naturalist*, *158*, 389–407.

Fleishman, E., Ray, C., Sjögren Gulve, P., Boggs, C. L., & Murphy, D. D. (2002). Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology*, *16*, 706–716. https://doi.org/10.1046/j.1523-1739.2002.00539.x

Fogg, A. M., Roberts, L. J., & Burnett, R. D. (2014). Occurrence patterns of Black-backed Woodpeckers in green forest of the Sierra Nevada Mountains, California, USA. *Avian Conservation and Ecology - Écologie et conservation des oiseaux*, *9*, 3. https://doi.org/10.5751/ACE-00671-090203

Frey, S. J. K., Strong, A. M., & McFarland, K. P. (2012). The relative contribution of local habitat and landscape context to metapopulation processes: A dynamic occupancy modeling approach. *Ecography*, *35*, 581–589. https://doi.org/10.1111/j.1600-0587.2011.06936.x

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2004). *Bayesian data analysis*, 2nd ed. Boca Raton, FL: CRC/Chapman & Hall.

Gelman, A., Meng, X.-L., & Stern, H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*, *6*, 733–760.

Gill, A. M. (1975). Fire and the Australian flora: A review. *Australian Forestry*, *38*, 4–25. https://doi.org/10.1080/00049158.1975.10675618

Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*, 41–49. https://doi.org/10.1038/23876

Hastings, A. (2003). Metapopulation persistence with age-dependent disturbance or succession. *Science*, *301*, 1525–1526. https://doi.org/10.1126/science.1087570

Hempson, G. P., Parr, C. L., Archibald, S., Anderson, T. M., Mustaphi, C. J. C., Dobson, A. P., … Beale, C. M. (2017). Continent-level drivers of African pyrodiversity. *Ecography*, *40*, 1–10.

Hutto, R. L. (2008). The ecological importance of severe wildfires: Some like it hot. *Ecological Applications*, *18*, 1827–1834. https://doi.org/10.1890/08-0895.1

Hutto, R. L., & Gallo, S. M. (2006). The effects of postfire salvage logging on cavity-nesting birds. *The Condor*, *108*, 817–831. https://doi.org/10.1650/0010-5422(2006)108[817:TEOPSL]2.0.CO;2

Johnson, M. P. (2000). The influence of patch demographics on metapopulations, with particular reference to successional landscapes. *Oikos*, *88*, 67–74. https://doi.org/10.1034/j.1600-0706.2000.880108.x

Johst, K., Brandl, R., & Eber, S. (2002). Metapopulation persistence in dynamic landscapes: The role of dispersal distance. *Oikos*, *98*, 263–270. https://doi.org/10.1034/j.1600-0706.2002.980208.x

Kelly, L. T., & Brotons, L. (2017). Using fire to promote biodiversity. *Science*, *355*, 1264–1265. https://doi.org/10.1126/science.aam7672

Kéry, M., Royle, J. A., Plattner, M., & Dorazio, R. M. (2009). Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, *90*, 1279–1290. https://doi.org/10.1890/07-1794.1

Kotliar, N. B., Hejl, S. J., Hutto, R. L., Saab, V. A., Melcher, C. P., & McFadzen, M. E. (2002). Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology*, *25*, 49–64.

Latif, Q. S., Ellis, M. M., Saab, V. A., & Mellen Mclean, K. (2018). Simulations inform design of regional occupancy-based monitoring for a sparsely distributed, territorial species. *Ecology and Evolution*, *8*, 1171–1185. https://doi.org/10.1002/ece3.3725

Latif, Q. S., Saab, V. A., Hollenbeck, J. P., & Dudley, J. G. (2016). Transferability of habitat suitability models for nesting woodpeckers associated with wildfire. *The Condor*, *118*, 766–790. https://doi.org/10.1650/CONDOR-16-86.1

Le Corre, N., Johnson, L. E., Smith, G. K., & Guichard, F. (2015). Patterns and scales of connectivity: Temporal stability and variation within a marine metapopulation. *Ecology*, *96*, 2245–2256. https://doi.org/10.1890/14-2126.1

Le Page, Y., Oom, D., Silva, J. M. N., Jönsson, P., & Pereira, J. M. C. (2010). Seasonality of vegetation fires as modified by human action: Observing the deviation from eco-climatic fire regimes. *Global Ecology and Biogeography*, *19*, 575–588.

Legendre, P., Dale, M. R. T., Fortin, M.-J., Gurevitch, J., Hohn, M., & Myers, D. (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, *25*, 601–615. https://doi.org/10.1034/j.1600-0587.2002.250508.x

Lydersen, J. M., North, M. P., & Collins, B. M. (2014). Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management*, *328*, 326–334. https://doi.org/10.1016/j.foreco.2014.06.005

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of Island biogeography*. Princeton, NJ: Princeton University Press.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, *84*, 2200–2207. https://doi.org/10.1890/02-3090

MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, *42*, 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

Martin, R. E., & Sapsis, D. B. (1992). *Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Symposium on Biodiversity in Northwestern California*.

McCarthy, M. A., & Masters, P. (2005). Profiting from prior information in Bayesian analyses of ecological data. *Journal of Applied Ecology*, *42*, 1012–1019. https://doi.org/10.1111/j.1365-2664.2005.01101.x

Murphy, E. C., & Lehnhausen, W. A. (1998). Density and foraging ecology of woodpeckers following a stand-replacement fire. *Journal of Wildlife Management*, *62*, 1359–1372. https://doi.org/10.2307/3802002

Nappi, A., & Drapeau, P. (2009). Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: Are burns source habitats? *Biological Conservation*, *142*, 1381–1391. https://doi.org/10.1016/j.biocon.2009.01.022

Nappi, A., & Drapeau, P. (2011). Pre-fire forest conditions and fire severity as determinants of the quality of burned forests for deadwood-dependent species: The case of the black-backed woodpecker. *Canadian Journal of Forest Research*, *41*, 994–1003. https://doi.org/10.1139/x11-028

Nappi, A., Drapeau, P., Giroux, J.-F., & Savard, J.-P. L. (2003). Snag use by foraging black-backed woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. *The Auk*, *120*, 505–511. https://doi.org/10.1642/0004-8038(2003)120[0505:SUBFBW]2.0.CO;2

Nichols, J. D., Bailey, L. L., O'Connell, A. F., Talancy, N. W., Grant, E. H. C., Gilbert, A. T., … Hines, J. E. (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, *45*, 1321–1329. https://doi.org/10.1111/j.1365-2664.2008.01509.x

Odion, D. C., & Hanson, C. T. (2013). Projecting impacts of fire management on a biodiversity indicator in the Sierra Nevada and Cascades, USA: The black-backed woodpecker. *The Open Forest Science Journal*, *6*, 14–23. https://doi.org/10.2174/1874398620130508001

Pausas, J. G., & Lavorel, S. (2003). A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science*, *14*, 409–416. https://doi.org/10.1111/j.1654-1103.2003.tb02166.x

Pavlacky, D. C., Blakesley, J. A., White, G. C., Hanni, D. J., & Lukacs, P. M. (2012). Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. *The Journal of Wildlife Management*, *76*, 154–162. https://doi.org/10.1002/jwmg.245

Pierson, J. C., Allendorf, F. W., Drapeau, P., & Schwartz, M. K. (2013). Breed locally, disperse globally: Fine-scale genetic structure despite landscape-scale panmixia in a fire-specialist. *PLoS ONE*, *8*, e67248. https://doi.org/10.1371/journal.pone.0067248

Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*.

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Core Team.

Rota, C. T., Millspaugh, J. J., Rumble, M. A., Lehman, C. P., & Kesler, D. C. (2014). The role of wildfire, prescribed fire, and mountain pine beetle infestations on the population dynamics of black-backed woodpeckers in the black hills, South Dakota. *PLoS ONE*, *9*, e94700. https://doi.org/10.1371/journal.pone.0094700

Rota, C. T., Rumble, M. A., Lehman, C. P., Kesler, D. C., & Millspaugh, J. J. (2015). Apparent foraging success reflects habitat quality in an irruptive species, the Black-backed Woodpecker. *The Condor*, *117*, 178–191. https://doi.org/10.1650/CONDOR-14-112.1

Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, *88*, 1813–1823. https://doi.org/10.1890/06-0669.1

Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, *84*, 777–790. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

Runge, J. P., Runge, M. C., & Nichols, J. D. (2006). The role of local populations within a landscape context: Defining and classifying sources and sinks. *The American Naturalist*, *167*, 925–938. https://doi.org/10.1086/503531

Saab, V. A., Russell, R. E., & Dudley, J. G. (2007). Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *The Condor*, *109*, 97–108. https://doi.org/10.1650/0010-5422(2007)109[97:NDOCBI]2.0.CO;2

Saracco, J. F., Siegel, R. B., & Wilkerson, R. L. (2011). Occupancy modeling of Black-backed Woodpeckers on burned Sierra Nevada forests. *Ecosphere*, *2*, 1–17.

Schütz, S., Weissbecker, B., Hummel, H. E., Apel, K.-H., Schmitz, H., & Bleckmann, H. (1999). Insect antenna as a smoke detector. *Nature*, *398*, 298–299. https://doi.org/10.1038/18585

Seavy, N. E., Burnett, R. D., & Taille, P. J. (2012). Black-backed woodpecker nest-tree preference in burned forests of the Sierra Nevada, California. *Wildlife Society Bulletin*, *36*, 722–728. https://doi.org/10.1002/wsb.210

Siegel, R. B., Tingley, M. W., Wilkerson, R. L., Howell, C. A., Johnson, M., & Pyle, P. (2015). Age structure of Black-backed Woodpecker populations in burned forests. *The Auk*, *133*, 69–78.

Smucker, K. M., Hutto, R. L., & Steele, B. M. (2005). Changes in bird abundance after wildfire: Importance of fire severity and time since fire. *Ecological Applications*, *15*, 1535–1549. https://doi.org/10.1890/04-1353

Su, Y.-S., & Yajima, M. (2014). *R2jags: A package for running JAGS from R*.

Tarbill, G. L., Manley, P. N., & White, A. M. (2015). Drill, baby, drill: The influence of woodpeckers on post-fire vertebrate communities through cavity excavation. *Journal of Zoology*, *296*, 95–103. https://doi.org/10.1111/jzo.12220

Taylor, A. H., & Beaty, R. M. (2005). Climatic influences on fire regimes in the northern Sierra Nevada mountains, Lake Tahoe Basin, Nevada, USA. *Journal of Biogeography*, *32*, 425–438. https://doi.org/10.1111/j.1365-2699.2004.01208.x

Thomas, C. D. (1994). Extinction, colonization, and metapopulations: Environmental tracking by rare species. *Conservation Biology*, *8*, 373–378. https://doi.org/10.1046/j.1523-1739.1994.08020373.x

Tingley, M. W., Ruiz-Gutiérrez, V., Wilkerson, R. L., Howell, C. A., & Siegel, R. B. (2016a). Pyrodiversity promotes avian diversity over the decade following forest fire. *Proceedings of the Royal Society B*, *283*, 20161703. https://doi.org/10.1098/rspb.2016.1703

Tingley, M. W., Stillman, A. N., Wilkerson, R. L., Howell, C. A., Sawyer, S. C., & Siegel, R. B. (2018). Data from: Cross-scale occupancy dynamics of a post-fire specialist in response to variation across a fire regime. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.jt38tj9

Tingley, M. W., Wilkerson, R. L., Bond, M. L., Howell, C. A., & Siegel, R. B. (2014). Variation in home-range size of Black-backed Woodpeckers. *The Condor*, *116*, 325–340. https://doi.org/10.1650/CONDOR-13-140.1

Tingley, M. W., Wilkerson, R. L., Howell, C. A., & Siegel, R. B. (2016b). An integrated occupancy and space-use model to predict abundance of imperfectly detected, territorial vertebrates. *Methods in Ecology and Evolution*, *7*, 508–517. https://doi.org/10.1111/2041-210X.12500

Turner, M. G., Romme, W. H., Gardner, R. H., & Hargrove, W. W. (1997). Effects of fire size and pattern on early succession in Yellowstone national park. *Ecological Monographs*, *67*, 411–433. https://doi.org/10.1890/0012-9615(1997)067[0411:EOFSAP]2.0.CO;2

Van Teeffelen, A. J. A., Vos, C. C., & Opdam, P. (2012). Species in a dynamic world: Consequences of habitat network dynamics on conservation planning. *Biological Conservation*, *153*, 239–253. https://doi.org/10.1016/j.biocon.2012.05.001

Villard, P. (1994). Foraging behavior of Black-backed and Hairy Woodpeckers during spring and summer in a Canadian boreal forest. *Canadian Journal of Zoology*, *72*, 1957–1959. https://doi.org/10.1139/z94-266

Virkkala, R. (2006). Why study woodpeckers? The significance of woodpeckers in forest ecosystems. *Annales Zoologici Fennici*, *43*, 82–85.

Westerling, A. L., Hidalgo, H. G., Cayan, D. R., & Swetnam, T. W. (2006). Warming and earlier spring increase western U.S. forest wildfire activity. *Science*, *313*, 940–943. https://doi.org/10.1126/science.1128834

Whelan, R. J. (1986). Seed dispersal in relation to fire. In D. R. Murray (Ed.), *Seed dispersal* (pp. 237–272). Sydney, NSW: Academic Press. https://doi.org/10.1016/B978-0-12-511900-9.50011-5

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*, 385–397. https://doi.org/10.2307/2389612

Yackulic, C. B., Nichols, J. D., Reid, J., & Der, R. (2014). To predict the niche, model colonization and extinction. *Ecology*, *96*, 16–23.

SUPPORTING INFORMATION

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

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