Black-backed woodpecker occupancy in burned and beetle-killed forests: Disturbance agent matters

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ABSTRACT

In the western United States, the black-backed woodpecker (*Picoides arcticus*) is a "snag specialist", found predominantly in burned montane forests. While fire is a key disturbance agent in this system, recently, unprecedented large tracts of drought-stressed forest in the Sierra Nevada and Southern Cascades of California have succumbed to bark beetle outbreaks. Although this tree mortality could potentially be a boon for snag-dependent species, it is unclear whether the resulting snag forests provide sufficiently high-quality habitat for black-backed woodpeckers and other wildlife that are regionally associated with burned forests. We tested for differences in black-backed woodpecker occupancy between fire- and beetle-killed forests, and whether key environmental relationships driving woodpecker occupancy differed between stands affected by the two disturbance agents. Between 2016 and 2018, we surveyed for black-backed woodpeckers during 4448 surveys at 75 burned and 113 beetle-killed forest stands throughout the black-backed woodpecker's range in California, detecting at least one black-backed woodpecker on 448 surveys (16.2%) in burned forests and 115 surveys (6.8%) in beetle-killed forests. Controlling for a suite of environmental variables that can affect habitat quality, the odds of black-backed woodpeckers occurring in burned forests were predicted to be 12.6 times higher than in beetle-killed forest. Occupancy declined with time-since-disturbance in fire-killed but not beetle-killed forests, but occupancy increased similarly with snag density resulting from either disturbance agent. Across our broad study region, black-backed woodpeckers were more likely to occur in burned forests at higher latitudes and elevations; these patterns were even stronger in beetle-killed forests, where we found woodpeckers only at the more northerly and higher elevation sites. Our results demonstrate that for this disturbed-habitat specialist, disturbance agent matters; black-backed woodpeckers do not use habitat created by bark beetle outbreaks as readily as habitat created by fire. Given the likely increased magnitude and extent of bark beetle outbreaks in the future, further work is needed to assess the role of beetle-killed forests in longer-term population dynamics of black-backed woodpeckers beyond the first decade after disturbance, and to investigate whether these results can be generalized to other fire-associated wildlife species in the region.

1. Introduction

Black-backed woodpeckers in western North America associate strongly, though not exclusively (Fogg et al., 2014), with recently burned conifer forests (Hutto, 1995; Kotliar et al., 2002; Smucker et al., 2005). The birds feed primarily on the larvae of woodboring beetles (e.g., Buprestidae and Cerambycidae; Murphy and Lehnhausen, 1998; Powell, 2000; Villard and Beninger, 1993), which colonize recently burned forests in large numbers. Woodpecker population density in the western U.S. typically peaks within about five years after fire and then

rapidly declines (Tingley et al., 2018), reflecting both concurrent declines in prey (Ray et al., 2019) and the lifespan of individual birds that colonized the burned area, or of offspring that they produced in the early postfire years (Siegel et al., 2015). In California, the southernmost extension of the species' range (Tremblay et al., 2016), the black-backed woodpecker's relatively small population and the species' association with burned forests that are often subjected to intensive postfire management has led to concerns about its conservation status (Siegel et al., 2018). The US Forest Service has designated black-backed woodpeckers a Management Indicator Species for snags in recently

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burned forest across ten National Forests in California, and explicitly analyzes effects to its habitat when planning post-fire management activities (Tarbill et al., 2018; Tingley et al., 2016).

Elsewhere in western North America, black-backed woodpeckers are also known to colonize forests with elevated tree mortality due to disturbance agents other than fire (Bonnot et al., 2008; Goggans et al., 1989; Rota et al., 2014a,b), especially outbreaks of native bark beetles (Coleoptera: Scolytinae). Compared to other parts of western North America, bark beetle outbreaks in California's forests have historically been comparatively limited in scope (Fettig et al., 2019; Stephens et al., 2018), rarely yielding the extensive tracts of snags preferred by black-backed woodpeckers (Tingley et al., 2014). However, severe drought and increasing temperatures during the past decade have stressed trees throughout the region, making California forests more susceptible to bark beetle outbreaks (Bentz et al., 2010; Marini et al., 2017; Williams et al., 2013), which have increased dramatically in severity and extent (Preisler et al., 2017; Young et al., 2017). Between 2012 and 2015, tree mortality in California increased by an order of magnitude – from tens to hundreds of dead trees per km^2 – with especially heavy mortality during 2015, concentrated at low latitudes and elevations (Asner et al., 2016; Young et al., 2017). The resulting large and numerous patches of forest with highly elevated tree mortality have been described as 'unparalleled' in the modern history of the region (Preisler et al., 2017), and thus provide a somewhat novel environment for local populations of disturbance-adapted wildlife species like the black-backed woodpecker.

Black-backed woodpeckers have sometimes been observed to forage on bark beetle larvae (Goggans et al., 1989; Lester, 1980), but these larvae are much smaller-bodied (typically < 6 mm long) than the woodpeckers' preferred diet of woodboring beetle larvae (up to 50 mm long; Powell, 2000). Even if bark beetles are not a preferred food item for black-backed woodpeckers, the beetles likely create habitat by killing or weakening trees and thus facilitating colonization by woodboring beetles. Unlike bark beetles, most woodborers are unable to attack otherwise healthy trees, and instead concentrate in dead or dying trees (Hanks, 1999). Some woodborer genera are able to find appropriate fire-damaged trees by sensing smoke or heat emanating from actively burning forest fires (Álvarez et al., 2015; Schmitz et al., 1997; Schütz et al., 1999). While recent evidence indicates that populations of smoke- or fire-sensing woodborers may be higher in burned forests than in forests affected by bark beetle outbreaks, other less specialized woodborers can also colonize beetle-killed forests in large numbers (Ray et al., 2019). It is unclear whether California's unburned forest stands that have been disturbed by bark beetle outbreak may provide sufficient food for black-backed woodpeckers, and if they do, whether populations in California have the behavioral plasticity to identify and colonize such areas in large numbers.

Differences in ecological effects of specific forest disturbance agents on opportunistic species are relatively poorly studied. In boreal and temperate forests, vastly more information is available about the ecological effects of fire than the effects of bark beetles (Thom and Seidl, 2016). Nevertheless, the existing data generally support contrasting effects of the two agents on ecosystem services, but a lack of clear differences in effects on overall biodiversity (Thom and Seidl, 2016). Systematic comparisons of the effects of fire versus bark beetles on particular forest taxa (rather than overall biodiversity) are generally rare, but in the Black Hills region of South Dakota, Rota et al. (2014b) found that post-disturbance growth rates of black-backed woodpecker populations were positive only in habitat created by summer wildfire. In their study region, black-backed woodpeckers in forest disturbed by mountain pine beetle (*Dentroctonus ponderosae*) outbreaks had negative population growth rates and larger home ranges than in early post-fire forests (Rota et al., 2014a,b).

We sought to compare black-backed woodpecker occupancy in California forests disturbed by different agents – fire versus bark beetle outbreak. Previous work has already demonstrated key patterns of black-backed woodpecker occupancy in burned forests of California (e.g., Saracco et al., 2011; Tingley et al., 2016, 2018). In this study, we sought to examine whether the birds were as likely to occur in beetle-killed forests and whether the key covariates that affect occupancy in burned forests – including time since fire, snag density, elevation, and latitude – also exhibit similar relationships to occupancy in beetle-killed forests. Snag density is a particularly key variable, as it represents a common metric for assessing the severity of disturbance across both disturbance types. Addressing these questions is necessary to predict population responses to disturbance, model suitable habitat across the ecoregion, and assess the effects of post-disturbance management such as logging on available habitat. Thus, our results will be directly relevant to management and conservation efforts for this species in the Sierra Nevada and Southern Cascade ecoregions, where large-scale bark beetle outbreaks are a relatively new phenomenon, leading to questions about the potential value of vast quantities of newly disturbed habitat to species like the black-backed woodpecker.
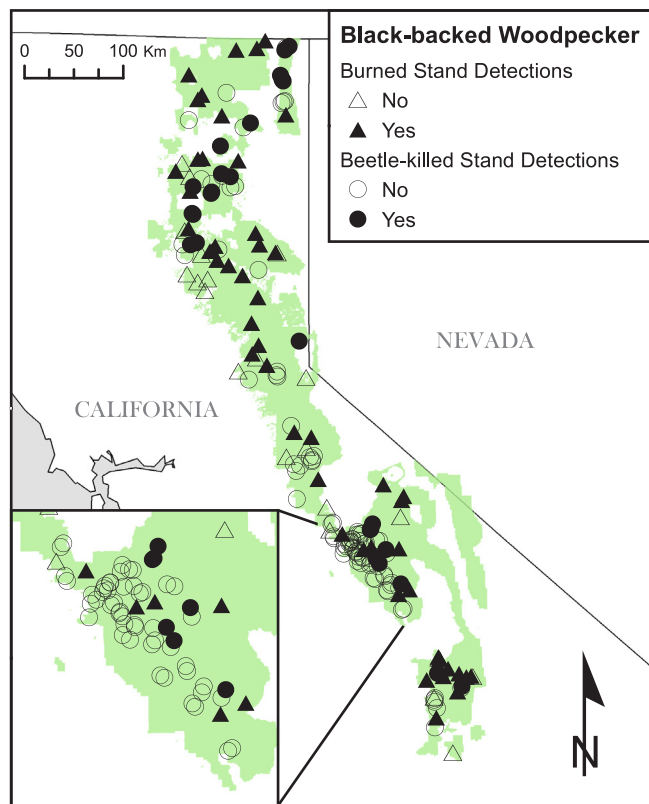
2. Methods

2.1. Study area and survey locations

We conducted surveys for black-backed woodpeckers as part of a long-term project to monitor the species' occupancy and population trends in montane forests of California. This ongoing study (Saracco et al., 2011; Tingley et al., 2018) began in 2009 and has primarily focused on surveying black-backed woodpeckers in National Forest System lands that burned between 1 and 10 years prior to the sampling year. Our study area comprised ten contiguous National Forest units within the Sierra Nevada and Southern Cascades ecoregions of California (Fig. 1), where we randomly selected 50 fires to visit each year that met our sampling criteria. Each year, 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.

Starting in 2016 and continuing through 2018, we additionally surveyed for black-backed woodpeckers in forests subject to non-fire tree mortality (Fig. 1). We used Forest Service Region 5 Aerial Detection Survey (ADS) data (https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid = fseprd506712) to identify forest stands with elevated tree mortality, presumably due to a combination of the recent drought (Young et al., 2017) and bark beetle outbreaks (hereafter 'beetle-killed' stands). Although we did not sample or identify bark beetles in these stands, other research (Ray et al. 2019) has indicated that abundant species include the fire engraver beetle (*Scolytus ventralis*), western pine beetle (*Dendroctonus brevicomus*), and Jeffrey pine beetle (*Dedocronus jeffreyi*). Portions of ADS polygons that overlapped with recent fire areas (less than ten years old) were removed from consideration, as were polygons with total area < 250 ha. We drew a random sample of the remaining polygons and then assessed road length and vegetation coverage in each selected polygon to ensure that it contained enough road length within coniferous forest to accommodate a survey transect comprising at least ten sampling points. Smaller polygons that could not fit two complete survey transects in conifer forest were paired with a second polygon by selecting the closest neighboring polygon that met all of the above criteria. Selected polygons were visited in a random priority order (while allowing slight modifications due to access), and survey points were laid out with the same methods and restrictions as for burned areas, above. The number of points per beetle-killed stand varied from 5 to 20, with a median of 10.

Assigning the exact year when a disturbance occurred was straightforward where the disturbance agent was fire, although we note that fire-damaged trees that survived the initial fire may continue to die during the early post-fire years (Hood and Cluck, 2007). However, assigning a year to bark beetle outbreaks was more complicated. Droughts

Fig. 1. Map of study region within California, highlighting sampling transects with and without black-backed woodpecker detections in forest stands disturbed by two different agents, fire and bark beetle outbreaks. Green polygons represent the sampling frame for disturbed forests across 10 National Forest units in the Sierra Nevada and Southern Cascades of California. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

weaken trees gradually over multiple years as a drought strengthens, and tree mortality from bark beetle outbreaks can accelerate or slow accordingly. Even within ADS-identified mortality patches, patch boundaries can change annually as additional trees succumb each year. For this reason, we defined a unique "disturbance year" for each survey point transect in beetle-killed stands, attempting to identify the specific year when widespread tree mortality was first identified in an area. To accomplish this, we placed a 500-m buffer around each survey point, merging this buffer across all points in a single transect. We then used annual ADS data to calculate the percentage area of a survey buffer that was overlapped by at least one ADS polygon in a given year, with a transect's main disturbance year defined as the first year when ADS polygons covered at least 40% of a transect's buffered area. If the threshold was never met (i.e., 40% of the buffer never overlapped ADS layers), we assigned disturbance year as the year with the greatest amount of overlap. We experimented with basing year of disturbance on other overlap thresholds (e.g., 20–75%) and found them to provide largely consistent results (mean correlation of year of disturbance based on 40% threshold to thresholds at 20%, 30%, 50%, 60%, and 75% = 0.71).

To test our hypotheses, we combined data collected from burned and beetle-killed forests into a single database. In doing so, we restricted the burned forest dataset to only those surveys conducted from 2016 to 2018, to temporally match the survey period within beetle-killed forest. In total, our analysis included 75 burned areas and 113 beetle-killed stands (when combined, "disturbance units"), comprising 2764 and 1679 surveys conducted over the three years at 1436 and 1379 unique survey points, respectively.

2.2. Survey methods

We divided surveys into timed intervals and used two detection methods within an unlimited-radius point-count framework. 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 s, followed by a 1.5-minute silent observation period. We followed a removal methodology where call broadcasts were suspended after the first detection. Additionally, broadcast surveys at half the points were preceded by passive point counts divided into an initial 3-minute interval and two subsequent 2-minute intervals. We conducted surveys in the morning hours (0530-0930) between 17 May and 14 July each year. For additional details on black-backed woodpecker survey methods used for this analysis, see Tingley et al. (2018).

2.3. Modeling approach

We developed a static occupancy model (MacKenzie et al., 2002) in a Bayesian framework that was designed to evaluate differences in woodpecker occurrence and test how covariate effects differ by disturbance agent. Observations, y_{jk}, for survey interval k at site j (where sites are individual survey points), are assumed to be imperfectly observed representations of the true occurrence status, z_j (1 or 0), which is constant across all k survey intervals (i.e., closure is assumed within the < 17-minute survey period) but can change from year to year. Observed occurrence, y_{jk}, is thus modeled as

$$y_{jk} \sim \text{Bernoulli}(z_j p_{jk}) \tag{1}$$

where p_{jk} is the probability of detection for a given survey at a site. Similarly, the true occurrence status of a site, z_j, is modeled as

$$z_j \sim \text{Bernoulli}(\psi_j) \tag{2}$$

where ψ_j is the probability of occurrence at a site.

The probabilities of detection and occurrence are both modeled as logit-linear functions of *a priori* hypothesized covariates. Following previous work studying black-backed woodpeckers with this survey methodology (Saracco et al., 2011; Tingley et al., 2018), we expected detection, p_{jk}, to vary as a function of an intercept and the linear additive combination of three covariates: the survey interval duration ("effort": 2-minutes = 0, 3-minutes = 1), the ordinal day of the year, and the survey type (passive = 0, broadcast = 1), giving

$$\text{logit}(p_{jk}) = \alpha_0 + \alpha_{ef}\text{effort}_k + \alpha_{day}\text{day}_j + \alpha_{type}\text{type}_k \tag{3}$$

The probability of occupancy of a survey point was modeled as a function of six covariates: (1) disturbance agent (fire = 0, beetle-killed = 1), (2) elevation, (3) latitude, (4) the interaction of elevation and latitude, (5) snag density, and (6) disturbance age (number of years since disturbance, see above). Previous research restricted to burned forests of California indicates that the overall abundance of snags, rather than the presence of any particular tree species, is among the more important predictors of black-backed woodpecker occupancy (Saracco et al., 2011; Tingley et al., 2018) and home-range size (Tingley et al., 2014). Additionally, we use snag counts here as a mechanistic metric of disturbance severity that is common to both burned and beetle-killed forests. Snag counts were conducted immediately after completing woodpecker surveys and consisted of counting all snags of different size classes (10–30, 30–60, and > 60 cm dbh) within 50 m of each survey point. Size-specific snag counts were aggregated in the field into count categories (≤5, 6–15, 16–30, 31–50, 51–100, > 100), which were converted to numerical quantities (1, 6, 16, 31, 51, 101, respectively) for analysis. Counts across all three size classes were summed in order to calculate snag density (snags per ha). We additionally controlled for

spatial autocorrelation within sampling units and any year effects by adding a random effect for disturbance unit and a random effect for year, both drawn from normal random distributions with a mean of 0 and a precision of τ_{unit} and τ_{year}.

We constructed a linear model to simultaneously estimate occupancy of black-backed woodpeckers in forests of both disturbance types, while also explicitly testing for whether covariate effects differed between burned versus beetle-killed site. Thus, for covariates 2–6 we additionally added interactions with disturbance type, so as to provide a within-model hypothesis test of whether a covariate relationship in beetle-killed forest was significantly different than in burned forest. The linear additive model for occupancy can be described as

$$\text{logit}(\psi_j)$$

$$= \beta_0 + \delta_{disturb}\text{disturb}_j + \text{elev}_j(\beta_{elev} + \delta_{elev}\text{disturb}_j) + \text{lat}_j$$

$$(\beta_{lat} + \delta_{lat}\text{disturb}_j) + \text{elev}_j\text{lat}_j(\beta_{elevlat} + \delta_{elevlat}\text{disturb}_j) + \text{snag}_j$$

$$(\beta_{snag} + \delta_{snag}\text{disturb}_j) + \text{age}_j(\beta_{age} + \delta_{age}\text{disturb}_j) + \text{unit}_j + \text{year}_j$$

$$(4)$$

where β represents fire-specific parameters and δ represents the difference in parameters between fire sites and beetle-killed sites. Note that the interpretation of β is fundamentally different than that of δ; β is a slope parameter for burned-forest covariates, whereas δ is a hypothesis test of whether the covariate effect in beetle-killed forest differs from that in burned forest. As such, in order to calculate the slope effect of a covariate on occupancy of woodpeckers in beetle-killed forests, one would additively combine the two parameters, for example $\beta_{elev} + \delta_{elev}$.

We fit the model to the data with JAGS (Plummer, 2003) using the R statistical programming language version 3.5.3 (R Core Team, 2019) and the package 'R2jags' (Su and Yajima, 2014). We used vague priors (i.e., normal with $\mu = 0$, $\tau = 0.1$). We ran three chains of 10,000 iterations thinned by 10 with a burn-in of 5000, yielding a posterior sample of 3000 across all chains. Convergence was checked visually with traceplots and confirmed with a Gelman-Rubin statistic < 1.1 (Gelman et al., 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 et al., 1996) for two test statistics representing the mean and standard deviation of the observed number of survey points with woodpecker detections per disturbance unit. Full JAGS code and data for our model are provided in our online Research data archive via Mendeley.

3. Results

We conducted 4448 surveys over three years in 75 burned and 113 beetle-killed forest stands in the Sierra Nevada and Southern Cascades of California. We detected at least one black-backed woodpecker during 448 of the 2764 surveys (16.2%) in burned forests, and during 115 of the 1679 surveys (6.8%) in beetle-killed forests.

This apparent difference in woodpecker occurrence was strongly confirmed by our Bayesian occupancy model which directly compared woodpecker occupancy in fire-killed and beetle-killed forests (Table 1). Average woodpecker occupancy in fire-killed forest, holding all other factors constant at average values, was 10.4% (95 CI: 3.9%, 25.8%), whereas average occupancy in beetle-killed forest was 1.1% (95 CI: 0.2%, 3.4%). Correcting for imperfect detection, the odds of a black-backed woodpecker occurring in a fire-killed forest were 12.6 times higher than the odds of one occurring in a beetle-killed forest.

In both beetle-killed and fire-killed forests, black-backed woodpeckers showed positive relationships to snag density. Woodpecker occupancy increased with snag density approximately equally in both burned (Fig. 2; β_{snag}, mean = 0.36, 95 CI: 0.20, 0.53) and beetle-killed forests ($\beta_{snag} + \delta_{snag}$, mean = 0.74, 95 CI: 0.01, 1.43).

Posterior parameter estimates showed several strong contrasts between the factors that determine woodpecker occupancy patterns in

burned versus beetle-killed forest (Table 1). Primarily, woodpeckers in fire-killed forest showed a strong relationship to time since fire (Fig. 2), with occupancy declining with increasing years (β_{age}, mean = –1.12, 95 CI: −1.56, −0.68). In beetle-killed forest, however, we found no temporal relationship to disturbance ($\beta_{age} + \delta_{age}$, mean = 0.19, 95 CI: −0.61, 1.05).

Black-backed woodpeckers additionally showed complex and disturbance-dependent responses to elevation and latitude. In general, woodpecker occurrence in burned forests increased with both elevation and latitude (Table 1, Fig. 3), with no strong interactive effect between elevation and latitude ($\beta_{elevlat}$, mean = –0.41, 95 CI: −0.93, 0.15). Woodpecker occupancy in beetle-killed forest stands showed very similar responses to elevation and latitude (Table 1), but also showed a strong negative interaction between the two ($\beta_{elevlat} + \delta_{elevlat}$, mean = −1.33, 95 CI: −2.30, −0.39); at low latitudes (at the southern extent of the species' range) woodpeckers only occurred in beetle-killed stands at the highest elevations, but at higher latitudes near the California-Oregon border, no relationship to elevation was evident (Fig. 3).

We tested overall model fit with posterior predictive checks on two metrics that characterize the mean and variability, respectively, of the observed raw data. The number of survey points with detections per disturbance unit averaged 2.99 with a standard deviation of 6.10. Posterior predictions from our model broadly overlapped these metrics (Supplemental Fig. S1), with Bayesian *p*-values indicating no lack of fit for either metric ($p_b = 0.30$ for the mean, $p_b = 0.23$ for the standard deviation).

4. Discussion

Black-backed woodpecker occupancy was over 12 times greater in burned forests than in beetle-killed forests, controlling for measured differences in habitat, disturbance age, and severity (measured as snag density). In California forests, the species thus appears to be not merely a forest disturbance associate, but specifically a burned-forest associate. The five covariates we assessed – elevation, latitude, the interaction of elevation and latitude, snag density, and time since disturbance – do not in themselves explain the importance of disturbance agent to the woodpeckers, but nevertheless do reveal some interesting patterns.

4.1. Snag density

Snag density is a metric of disturbance severity common to both burned and beetle-killed forests. The overall difference in occupancy – while controlling for snag density – between burned and beetle-killed forest suggests that a fire-killed snag may be fundamentally more valuable to black-backed woodpeckers than a beetle-killed snag during the first 10 years following disturbance. Although there are additional, untested hypotheses that could also explain this difference, other research also suggests that fire-killed snags may provide more food resources than beetle-killed snags, at least in areas of high burn severity (Ray et al., 2019). Our model additionally tested whether the additive value of each snag differed by disturbance type, and found no significant difference (Table 1), indicating that sites with more snags were proportionally more likely to be occupied, regardless of disturbance. Though we controlled for variation in snag density in our analysis, we also found that snag density was significantly greater around survey points in burned-forest plots compared to beetle-killed plots (Table 2), as fire often kills patches of trees all at once, rather than gradually over time as in beetle-killed stands. Consequently, not only may each fire-killed snag provide greater resources for black-backed woodpeckers than a beetle-killed snag, but the average fire-killed site also contains a greater density of snags – two independent factors that may explain why the species was much more abundant in burned forest stands. This dual finding highlights the importance of variation in the ecological outcomes of different disturbance processes, and the cascading effects of such variation.

Table 1
Posterior means (and 95% credible intervals) for all parameters included in a model of black-backed woodpecker occupancy in areas disturbed by fire or bark beetle outbreaks across ten National Forests in California, separated out between detection and occupancy covariates. Items in bold indicate 95% CI that do not overlap zero. Effects in beetle-killed forests were modeled through interactions, such that slopes represent the additive difference from the main effects in burned forests and therefore represent hypothesis tests of whether the effect is different in beetle-killed than in burned forests. To calculate the absolute slope of a covariate in beetle-killed forest, one would sum the two effects ($\beta + \delta$).
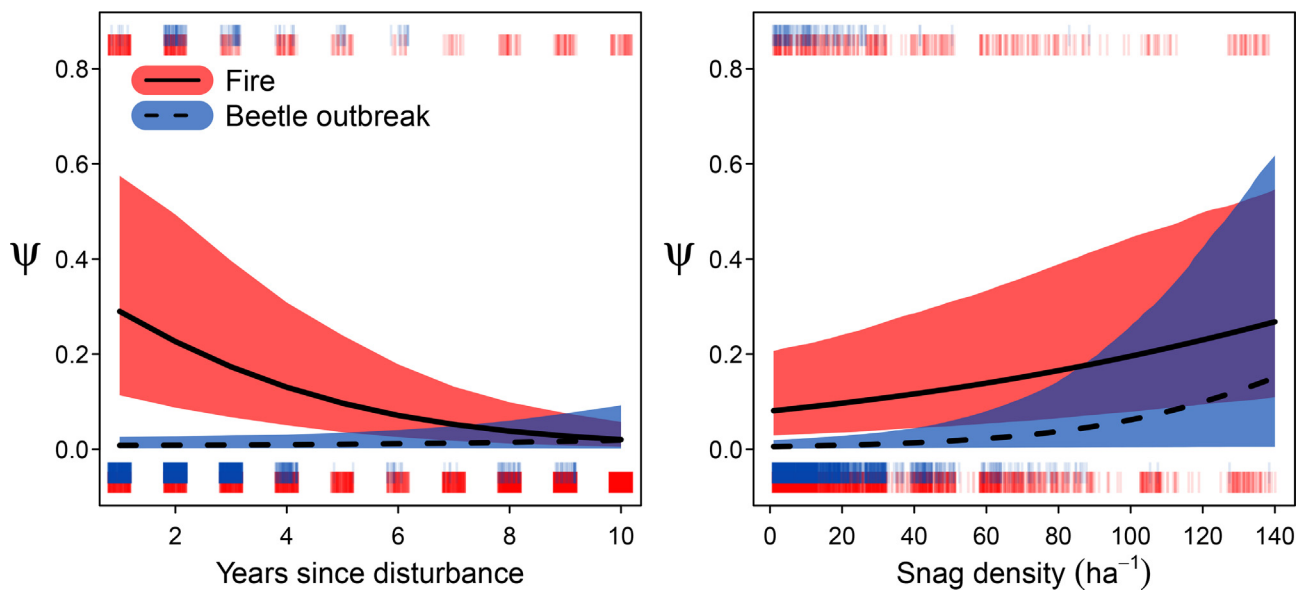
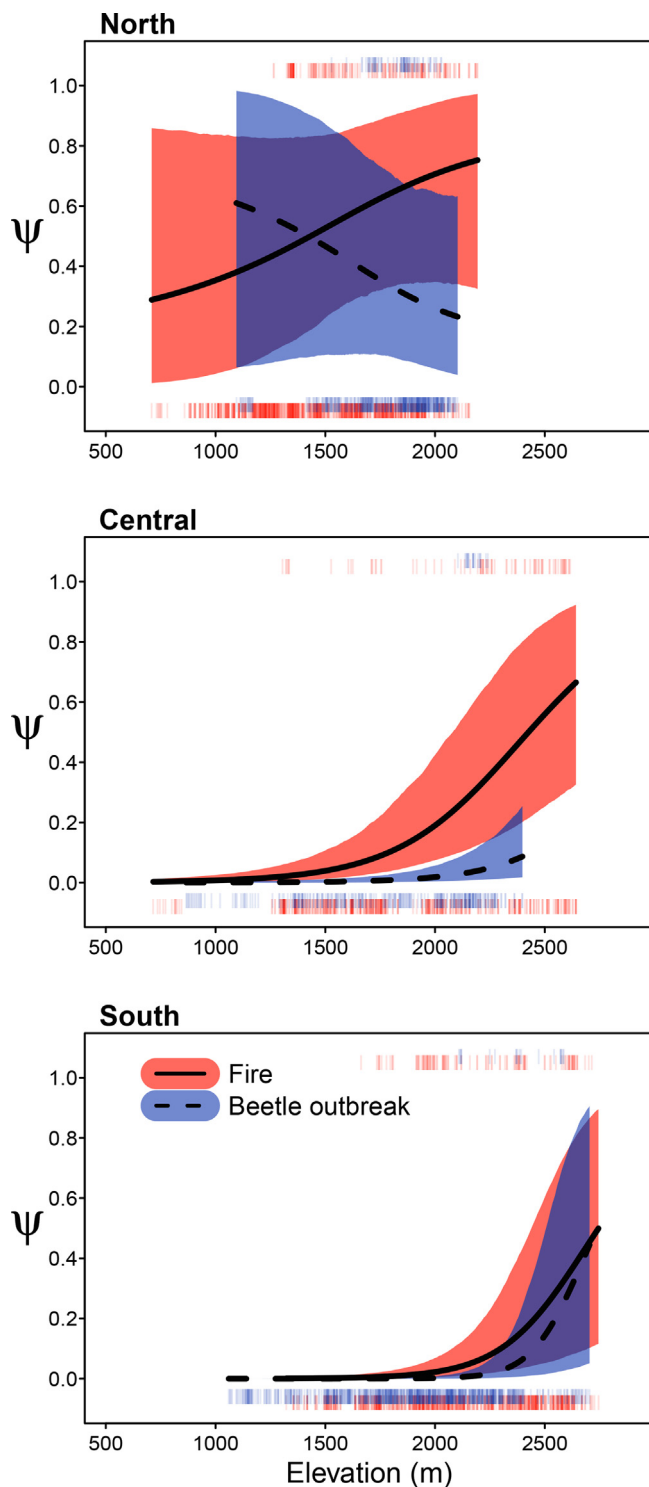| Covariate	Main effects (β) (burned forests)	Interaction effects (δ) (beetle-killed effect)
Detection		
Intercept	−1.67 (−1.91, −1.45)	
Effort	0.12 (−0.23, 0.46)	
Day of year	0.15 (0.00, 0.29)	
Survey type	**1.20 (0.95, 1.45)**	
Occupancy		
Intercept	−2.25 (−3.21, −1.06)	
Disturbance type		**−2.53 (−3.77, −1.36)**
Years since disturbance	**−1.12 (−1.56, −0.68)**	**1.31 (0.51, 2.17)**
Snag density	**0.36 (0.20, 0.53)**	0.38 (−0.36, 1.10)
Elevation	**1.48 (0.93, 2.07)**	0.07 (−0.94, 1.11)
Latitude	**1.62 (1.03, 2.23)**	0.60 (−0.35, 1.57)
Elevation × Latitude	−0.41 (−0.93, 0.15)	−0.92 (−1.89, 0.02)
Random effect: year = 2016	−0.35 (−1.44, 0.39)	
Random effect: year = 2017	0.25 (−0.75, 0.98)	
Random effect: year = 2018	−0.21 (−1.29, 0.54)	
Precision of site-level random effect	0.33 (0.21, 0.49)	

4.2. Elevation and latitude

Black-backed woodpeckers were much less likely to occur in burned or beetle-killed areas at lower elevations. Our results additionally show a latitudinal cline in the lower-elevation boundary of occupied black-backed woodpecker habitat, roughly conforming to the expected negative relationship between elevation and latitude for life zones in the region (Brock and Inman, 2006; Merriam, 1894; Siegel et al., 2011). As such, black-backed woodpeckers are found at lower elevations at higher latitudes where conifer forests also extend to lower elevations. Independent of elevation, the woodpeckers were also less likely to occur at lower latitudes, with standardized slopes showing latitude and elevation having equal effect sizes within the respective covariate range of sampling.

We know some of the factors that contribute to this broad relationship with elevation and latitude. Previous studies showed that

black-backed woodpeckers eschew burned low-elevation forests and woodlands in the Sierra Nevada that are dominated by foothill pine (*Pinus sabiniana*) and oak (*Quercus sp.*) or other hardwood species in favor of mid- and higher-elevation forests dominated by montane conifers (Saracco et al., 2011). These preferred forests dominated by pines (*Pinus* sp.) and firs (*Abies* sp.) are present across all elevations in the northern portion or our study region, but they are absent from lower elevations in the southern portion. Our findings extend this generalization of woodpecker associations with high latitude and elevation to beetle-killed forests in the region. Importantly, much of the severe tree mortality in the Sierra Nevada and Southern Cascades that developed during the past decade has been concentrated at lower latitudes (Asner et al., 2016) and elevations (Fettig et al., 2019) – including relative to fire-killed forest (Table 2) – and is therefore less likely to serve as habitat for black-backed woodpeckers. We emphasize, however, that even where beetle-killed forests did occur at high

Fig. 2. Modeled relationships between occupancy and years since disturbance (left) and snag density (right), showing contrasting effects on black-backed woodpeckers depending on disturbance agent (fire versus bark beetle outbreak). Data rugs show naïve occurrence in both burned and beetle-killed surveys as a function of covariates (jittered to enhance visibility).

Fig. 3. Black-backed woodpecker occupancy as a function of elevation and latitude (shown here as three descending panels at 42°, 38.5°, and 35.5° N, respectively) for forests affected by two different disturbance agents, fire and bark beetle outbreaks. Data rugs show naïve occurrence in both burned and beetle-killed surveys as a function of elevation in each latitudinal band.

Table 2
Average (± standard deviation) environmental conditions of black-backed woodpecker surveys and survey points, characterizing variation in available potential habitat.

Environmental variable	Burned	Beetle-killed	p-value*
Snag density (hectare^{-1})	35.8 ± 39.4	15.2 ± 15.9	< 0.001
Year since disturbance	6.1 ± 3.2	2.5 ± 1.6	< 0.001
Latitude (°)	38.7 ± 1.9	38.5 ± 1.8	< 0.001
Elevation (m)	1794 ± 441	1853 ± 338	< 0.001

 * Differences in environmental variables between burned and beetle-killed survey points determined by a Wilcoxon rank sum test.

variable in burned forests, we did not test it in this study.

4.3. Time since disturbance

Woodpecker occupancy demonstrated a negative response to time since disturbance in burned areas, but not in beetle-killed areas. While we attempted to assign a biologically relevant "time of disturbance" to all beetle-killed plots, our method relied on spatial polygon boundaries drawn in a potentially quasi-arbitrary fashion around visual evidence of beetle mortality during aerial ADS surveys. Assigning a single year of disturbance to beetle-killed plots simplifies the incremental and chronic progression of beetle-caused tree mortality – particularly compared to the acute decline of snags following fire (Grayson et al., 2019) – but we believe that our method adequately approximates the timing of the beetle disturbance event in a manner conducive to comparisons with fire mortality events. Nevertheless, given the entirely different temporal nature of these two disturbance types, it is perhaps not surprising that post-fire occupancy dynamics are distinguished by strong temporal effects, whereas beetle-killed dynamics show no such effect.

4.4. Overall importance of disturbance agent

Recent bark beetle outbreaks have caused substantial pulses of dead trees in California's forests, but our results suggest that these disturbances do not support black-backed woodpecker populations at similar densities to burned forests. During the spring of 2017, about 4800 km^2 of our 50,450 km^2 study area had burned within the last 10 years, but over twice as much land area (> 10,000 km^2) consisted of disturbed forests where bark beetles were the primary disturbance agent. Despite the vast difference in land area between these two disturbance types, the finding that woodpecker occupancy is 12 times higher in burned forests suggests that the combined land area of beetle-killed areas likely does not even come close to matching the overall contribution of burned forest to black-backed woodpecker populations. Disturbance agent matters for this species, and all other things being equal, habitat created by wildfire appears to support populations at much higher densities than beetle-killed forests.

It is unclear how critical the strong difference in temporal progression of these two forest disturbance mechanisms is for long-term population dynamics of black-backed woodpeckers and other snag-associated wildlife. Black-backed woodpeckers are already known to benefit strongly from ephemeral resource pulses associated with forest fire, with woodpecker occupancy peaking then strongly declining between 5 and 7 years post-fire (Tingley et al., 2018). Our results indicate that even if occupancy in beetle-killed forest is much lower than in burned forests, long-term (> 10 years) occupancy of woodpeckers in beetle-killed forests could be greater than in burned forest – although this may be no different from background rates in undisturbed forests (Fogg et al., 2014). Longer-term study of occurrence in forests affected by both disturbance agents and in undisturbed forest could provide a better understanding of population dynamics of this snag specialist (Taillie et al., 2018), possibly resolving how they are able to persist across the broader landscape while utilizing patchy and ephemeral

elevations and latitudes in our sample, occupancy in these patches was significantly lower than in comparable patches of burned forest (Fig. 2, Table 1). In addition to latitude and elevation, aspect has also been identified, though somewhat equivocally, as a predictor of black-backed woodpecker occurrence in undisturbed forest (Fogg et al., 2014), but lacking any *a priori* indication of aspect as a predictive

habitat conditions.

4.5. Management conclusions

Global change is creating larger and more frequent disturbances in forest biomes. Managers are challenged with balancing multiple objectives in managing disturbed forests, including resource extraction, forest restoration, reducing risks of future disturbance, and retaining habitat for species that thrive in disturbed forests. Although black-backed woodpeckers are described as 'snag specialists,' and are often assumed to appear wherever adequate resources are generated, it is clear that at least across our study area their habitat needs are not that simple; the species does not occur in equal abundance given equal densities of standing dead trees. As increasingly large tracts of California forest are killed by drought and bark beetles, our study indicates that these newly available snag patches may be a poor substitute for burned-forest habitat for black-blacked woodpeckers. Ultimately, the contribution of beetle-killed forest stands to black-backed woodpecker conservation may depend more on the extent to which beetle disturbance pre-disposes forests to burn – and the relative value of that burned forest as habitat – rather than the direct contribution of the beetle-killed habitat itself.

Data accessibility

Input data and model code in JAGS language are available as Research data for this article via Mendeley.

Author contributions

MT, BW, RS, and SS conceived the ideas and designed methodology; BW and RS oversaw data collection; MT and AS analyzed the data; MT and RS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117694.

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