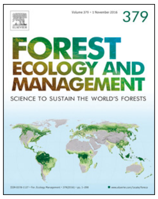
Forest Ecology and Management 444 (2019) 374–381

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



The effects of mountain pine beetle outbreaks on avian communities in lodgepole pine forests across the greater Rocky Mountain region

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ABSTRACT

Disturbance is an integral component of forest ecosystems. Therefore, contemporary changes to the frequency and severity of disturbances in forests may have lasting ecological consequences. In recent decades, widespread mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreaks have contributed more to total tree mortality than other disturbances such as wildfire. Past studies have used a broad range of measurements to evaluate the local effects of beetle outbreaks on birds (e.g., dead trees per acre versus percent mortality) and this has led to some challenges and inconsistencies in generalizing results across larger spatial scales. We sought to address these inconsistencies by using a single data source estimating outbreak-related tree mortality across the western United States to better understand the effect of beetle outbreaks on avian communities in lodgepole pine forests. This study uses five years of avian monitoring data (2008–2012) from the Integrated Monitoring in Bird Conservation Regions program, collected across Colorado, Idaho, Montana, and Wyoming. We developed a hierarchical multispecies occupancy model to quantify changes in the forest bird community following beetle outbreaks while accounting for the imperfect detection of species. Mean species richness (N) did not differ between MPB outbreak sites (N = 19.35, 95%CRI = 17.00, 22.01) and sites with no outbreak (N = 20.23, 95%CRI = 16.83, 24.25). Furthermore, we found weak evidence for a community-level response to increasing outbreak severity and time since outbreak, due in part to the variability among species within each of the four nesting guilds analyzed in this study (canopy, cavity, shrub, and ground nesting birds). However, we did find evidence of turnover in community composition with just over 50% of species (28 of 55) having statistically different occurrence rates following MPB outbreaks. Our study underscores the notion that species richness alone does not fully express changes in the forest bird community. Our results also suggest many species, particularly cavity nesters, utilize beetle-killed forests and persist at higher occurrence rates for up to 10 years post-outbreak. This period includes the timeframe when beetle-killed trees are most readily salvageable and emphasizes the need for continued evaluation of snag-retention policies prior to the implementation of post-outbreak management activities.

1. Introduction

North American forests are expected to change considerably over the next 50 years (Romero-Lankao et al., 2014). Climate change is inducing large-scale hydrological variability which increases the frequency and intensity of natural disturbances and creates challenges for forest management (Dale et al., 2001). Common examples of these disturbances include fire and insect outbreaks which can result in tree die-offs and associated ecological change. Increasing disturbance severity may have serious repercussions for forest ecosystems, by directly affecting wildlife species dependent on forests, and indirectly by influencing management decisions.

Over the past three decades, roughly 13% of trees within coniferous forest in the western United States have been killed by fire or bark beetle outbreaks (Hicke et al., 2016). Bark beetle outbreaks contributed more to total tree mortality, averaging 0.33 Mha of tree mortality per year since the year 2000 (Hicke et al., 2016). Beginning in 2003, widespread outbreaks of mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) reached epidemic levels primarily in lodgepole pine (*Pinus contorta*) where susceptibility to MPB attack was highest (Hicke and Jenkins, 2008). Results of the epidemics are especially pronounced in Colorado and Montana, where MPB outbreaks have accounted for nearly 80% of total tree mortality (Berner et al., 2017). However, little is known about how forest-dependent wildlife species respond to these large-scale tree mortality events which are forecasted to continue based on climate change and favorable forest conditions supporting future beetle outbreaks (Hicke et al., 2006; Bentz et al., 2010).

Resource managers frequently use ecological indicators to gain insight into the functioning of ecosystems. Birds have been identified as useful indicators to predict areas of increased biodiversity and ecological integrity across a range of habitat types (O'Connell et al., 2000; Gregory et al., 2003; Schulze et al., 2004). Bird species vary in foraging strategies and nesting requirements which can be used to categorize

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https://doi.org/10.1016/j.foreco.2019.04.047
Received 4 February 2019; Received in revised form 23 April 2019; Accepted 24 April 2019

species into specific groups, referred to as guilds (Root, 1967). Evaluating variations across bird guilds following a disturbance can elucidate broader ecological change in forested ecosystems (Canterbury et al., 2000; Gaines et al., 2010; Verschuyl et al., 2011; Galitsky and Lawler, 2015).

An MPB outbreak begins with the increase of MPB adults and larvae, directly providing a food resource for many birds, such as American three-toed woodpecker (*Picoides dorsalis*) and other woodpecker species that forage in and around the bark of trees (Edworthy et al., 2011). During the progression of an outbreak, indirect effects, such as changing vegetation structure, become more apparent as MPB outbreaks alter the composition and structure of forest vegetation and thus the resources available to other organisms. For example, MPB-caused tree mortality results in the reduction of the forest canopy and the loss of nesting substrate for canopy nesting species. At the same time, outbreaks can provide an increase in nesting resources for cavity nesting species that predominantly excavate cavities in dead trees (Saab et al., 2014).

Past studies have used a broad range of measurements to evaluate the effects of beetle outbreaks on birds (e.g., dead trees per acre versus percent mortality, Saab et al., 2014) and this has led to some challenges in generalizing community-level responses to MPB outbreaks across larger spatial scales. For example, some studies have found weak to no relationship between bird species richness and measures of beetle activity in lodgepole pine dominated forest (Drever and Martin, 2007; Chan-McLeod et al., 2008; Drever et al., 2009). Nevertheless, a study in mixed coniferous forests including lodgepole pine found bark beetle activity improved conditions for cavity-nesting species and other bark-foraging insectivores, but when beetle infestations reached epidemic status, resource levels deteriorated for the forest bird community (Martin et al., 2006). This suggests that a prolonged broad-scale bark beetle epidemic, which occurred across the greater Rocky Mountain region in recent decades, may negatively influence forest bird species richness.

Our overall objective was to measure changes in bird species richness by modeling individual species responses to a large-scale mountain pine beetle outbreak across the western United States. We used a single geospatial data source estimating outbreak-related lodgepole pine mortality across the western United States (Meddens et al., 2012; Hicke et al., 2016). We coupled this large-scale MPB outbreak information with avian monitoring data collected across four states: Colorado, Idaho, Montana, and Wyoming. Furthermore, previous studies on beetle outbreaks and forest bird communities have occurred predominantly during the first few years following the onset of a beetle outbreak with studies concluding ≤ six years following peak tree mortality (reviewed by Saab et al., 2014). By using monitoring data collected across a large geographic region we are able to gain insight into a range of forest conditions, including sites with up to 10 years following beetle-related tree mortality.

We hypothesized high levels of beetle infestation results in a large number of dead or dying trees, limiting the forest canopy resources used for nesting and/or foraging by other forest-obligate bird species (Martin et al., 2006). We predicted a negative relationship between forest bird richness and increasing levels of tree mortality due to bark beetle infestations. In addition, the loss in canopy cover following bark beetle outbreaks also promotes the growth of secondary vegetation over time (Pelz et al., 2018). Therefore, we predicted an increase in the number of shrub and ground nesting species over time, such that after a 10-year post-MPB outbreak period, total species richness would be similar to areas where no outbreak occurred.

2. Methods

2.1. Site selection

This study uses five years of avian survey data (2008–2012) collected across Colorado, Idaho, Montana, and Wyoming (Fig. 1). Survey data were obtained from the ongoing Integrated Monitoring in Bird Conservation Regions (IMBCR) program (Pavlacky et al., 2017). IMBCR includes background monitoring across a broad geographic area as well as overlay sampling for focused questions at smaller spatial scales. For the purpose of our study, we included only background monitoring data. We first selected lodgepole pine forest sites using the Landfire Existing Vegetation Type dataset (Landfire, 2008, 2010) to ensure the inclusion of sites with majority forest. We used IMBCR data from 409 unique sites (Fig. 1). Some sites were surveyed in multiple years resulting in a total of 796 complete site-surveys.

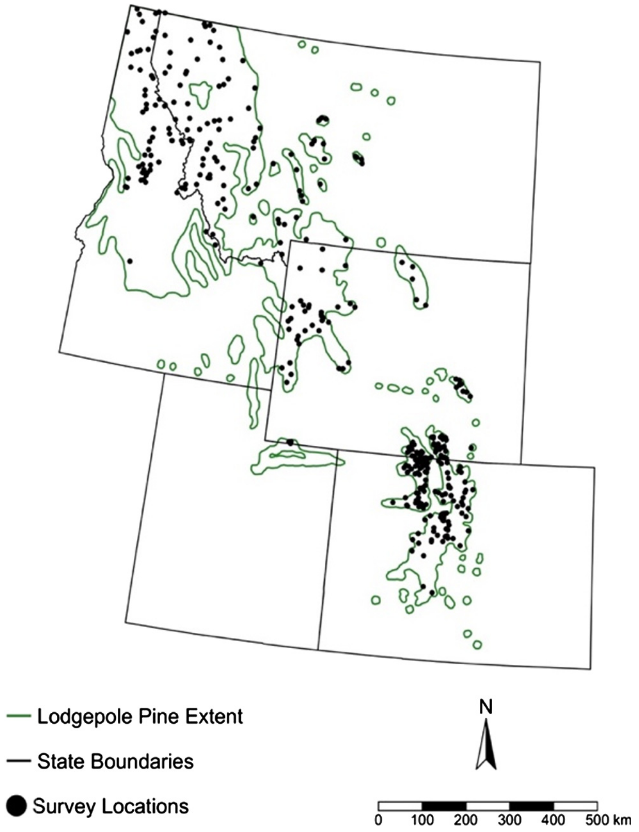

Fig. 1. Map of the multi-state region (black) in the western United States where avian surveys were conducted in lodgepole pine forests (green) from 2008 to 2012. Points represent unique 1-km^2 sampling plots. For illustration purposes, the lodgepole pine extent shown here is based on data from the Atlas of United States Trees (Little, 1971). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Avian survey data

The IMBCR program employs a design-based spatially balanced sampling scheme and a data collection protocol that allows for the estimation of species-specific detection probabilities (Dreitz et al., 2017; Pavlacky et al., 2017). Each survey site consists of a four by four grid of avian survey points spaced evenly 250 m apart across a 1-km^2 area and sampled once between May and July. Surveyors conducted a six-minute count at survey points within each site during which all birds observed (heard or seen) are recorded (Pavlacky et al., 2017). Sites with fewer than six points surveyed were considered insufficiently sampled and excluded from our analyses (Pavlacky et al., 2017). We reduced point-level species counts to presence/absence data to be used for occupancy modeling.

To test for changes within the forest bird community in response to MPB outbreaks we first restricted our analysis to species associated with open woodland or interior forest habitat based on the Birds of North

America species accounts (Rodewald, 2015) in combination with a review by Saab et al. (2014). A total of 62 species were considered in the study (see Table A1). Species were categorized into four nesting guilds based on nest location [canopy (n = 28), shrub (n = 11), ground (n = 5), and cavity (n = 18)].

2.3. Mountain pine beetle outbreak data

Annual severity of MPB outbreaks was sampled from a 16-year (1997–2012) 1-km resolution raster dataset from previous studies (Meddens et al., 2012; Hicke et al., 2016). This data set was created using USDA Forest Service Aerial Detection Surveys; the surveyed estimates of the number of trees killed by bark beetles were extracted within 1-km^2 grid cells using tree species-specific mean crown areas and corrected for underestimation using comparisons with remotely sensed data (Meddens et al., 2012; Hicke et al., 2016). At bird survey sites, outbreak severity was calculated using an area weighted average of the $\log_{10}$ number of dead lodgepole pine due to bark beetle infestation based on the intersection of the tree mortality raster (Meddens et al., 2012; Hicke et al., 2016) and a 1-km radius buffer around each bird survey site centroid. Accordingly, 275 of the 409 unique survey sites sustained an MPB outbreak. Repeated annual sampling of bird survey sites resulted in 517 site-surveys that experienced MPB outbreaks.

We included a measure of time since an outbreak to account for the vegetative changes at a site as an outbreak progressed. MPB outbreaks have a one-year time lag from when an outbreak begins to when the evidence of tree mortality is first observed (Meddens et al., 2012; Hicke et al., 2016). To incorporate time into the analyses we calculated the difference in years since an outbreak and when the bird sampling occurred at a survey site. Following these methods, sites received a value of one for the year tree mortality was first observed. The year prior to first observed tree mortality is reflected as year zero.

2.4. Multispecies occupancy model

We used a hierarchical multispecies occupancy model (Dorazio and Royle, 2005; Gelfand et al., 2005) to quantify changes in the forest bird community following beetle outbreaks. Hierarchical occupancy models provide key analytical advantages by providing inference to the entire community as well as individual species, and they allow for the separation of the ecological processes of interest (true presence or absence of a species, z) from the effects of the observation process i.e. species detectability (p). In our study, detectability is a product of species availability throughout a site as well as observer error. We make inference to occupancy at the site-level and therefore our results are not biased by variation in the spatial availability of species across units of replication (i.e., points within sites, see Nichols et al., 2008).

True occurrence for species i at site j in year k, denoted $z_{i,j,k}$, is modeled as a Bernoulli random variable, $z_{i,j,k} \sim \mathrm{Bern}(\Psi_{i,j,k})$ with probability $\Psi_{i,j,k}$ ($z_{i,j,k} = 1$ if species i is present during sampling at site j in year k and zero otherwise). However, $z_{i,j,k}$ is the latent state and only partially observable. Actual observations from point count surveys, $y_{i,j,k,l}$, denote detection or non-detection of species i at site j in year k during point survey l. Species detection was modeled as a Bernoulli random variable, $y_{i,j,k,l} \sim \mathrm{Bern}(p_{i,j,k,l}, z_{i,j,k})$, where $p_{i,j,k,l}$ represents the detection probability for species i at site j in year k during point survey l.

We modeled site-level species occupancy probabilities, $\Psi_{i,j,k}$, incorporating five site-specific covariates using the logit-link function:

$$logit\,(\Psi_{i,j,k}) = \alpha 0_{i,status_{jk}} + \alpha 1_i *Latitude_j + (\alpha 2_i *Severity_{jk} + \alpha 3_i *MortalityYears_{jk} + \alpha 4_i * Severity_{jk} * MortalityYears_{jk}) *w_{jk}.$$

The intercept term ($\alpha 0_i$) is dependent on whether site j in year k has undergone an MPB outbreak ($status_{jk}$ = outbreak or non-outbreak). The parameter $\alpha 1_i$ is the linear effect of latitude, included to account for variation in species ranges across the study area and represents the south to north gradient of decreasing elevation that occurs for this portion of the Rocky Mountains. Parameters $\alpha 2_i$, $\alpha 3_i$, and $\alpha 4_i$ are relevant only to sites with an MPB outbreak and were included in the model via an indicator variable w_{jk} where $w_{jk} = 1$ if site j in year k has an outbreak and zero otherwise. The parameter $\alpha 2_i$ is the linear effect of the mean $\log_{10}$ number of dead trees due to MPB infestation within a 1-km radius buffer of site j ($Severity_j$), $\alpha 3_i$ is the effect of time represented as the number of mortality years that have occurred at site j ($MortalityYears_j$), and $\alpha 4_i$ is the effect of the interaction between beetle-induced tree mortality and time. Outbreak severity, mortality years, and latitude were centered and scaled. This allowed for the intercept ($\alpha 0_i$) to represent the mean occupancy of species i at the average outbreak scenario or the occupancy of species i at the average non-outbreak site.

We modeled survey-level species detection probabilities, $p_{i,j,k}$, as:

$$logit\,(p_{i,j,k}) = b0_i + b1_i Date_{jk} + b2_i Date_{jk}^2.$$

The parameters $b1_i$ and $b2_i$ are the linear ($Date_{jk}$) and quadratic ($Date_{jk}^2$) effects of the date, measured in Julian day, on which survey k at site j was conducted to account for temporal variation in the probability of encountering species with differing breeding phenology and seasonal vocalization patterns. The linear and quadratic forms of date were also mean centered on zero allowing the intercept, $b0_i$, to represent the mean detection probability for species i.

Multispecies models link single-species occupancy and detection at the community level by treating slope and intercept parameters as species-specific random effects (Royle and Dorazio, 2008). Following previous examples of studies using avian survey data of similar structure and scale we modeled species random effects using vague normal prior for community means and gamma distributed variances (e.g. Zipkin et al., 2010; Dreitz et al., 2017).

The model was formulated in R (R Core Team, 2016, v. 3.3.2) and generated using the *jagsUI* package (Kellner, 2016). We ran four Markov Chain Monte Carlo (MCMC) chains of 45,000 iterations each and retained 7000 values per chain, after discarding 10,000 for adaptation and burn-in and thinning by five. Statistical support for species responses determined by examining whether the 95% Credible Interval (CRI) of the response coefficient overlaps zero (following Latif et al., 2016). Site-level species richness was calculated as the sum of latent species occurrences at each site,

$$N_{jk} = \sum_{i=1}^{I} z_{i,j,k}.$$

We conducted a posterior predictive check to assess the fit of the model by calculating deviance-based Bayesian p-values for each species. Following the methodology of Broms et al. (2016) and Dreitz et al. (2017), for each species, we calculated the deviance of the observed data for each iteration (n) of the MCMC samples,

$$D_i^{(n)} = -2\sum_{j=1}^{J} \log(y_{i,j}|\psi_{i,j}^{(n)}, p_{i,j}^{(n)})$$

and then compared the observed deviance to the deviance of data predicted from the model ($\tilde{y}$),

$$\tilde{D}_i^{(n)} = -2\sum_{j=1}^{J} \log(\tilde{y}_{i,j}|\psi_{i,j}^{(n)}, p_{i,j}^{(n)}).$$

Bayesian p-values were calculated as the proportion of MCMC samples in which the deviance of the observed data, $D_i^{(n)}$, was greater than the deviance using predicted data, $\tilde{D}_i^{(n)}$. Generally, models with poor fit to data have a p-value ≤ 0.05 or ≥ 0.95 (Broms et al., 2015).

3. Results

In total, 9123 six-minute avian point counts were conducted resulting in 51,291 point-level observations of species. Survey sites ranged in forest cover from 0.5 to 1-km^2, and averaged 0.89-km^2 (sd = 0.12) of forest cover. Sites ranged in elevation from 815 to 3786 m, (mean = 2292.50, sd = 613.11) and across a latitudinal gradient from 38 to 49 degrees latitude (mean = 43.70, sd = 2.96). Average MPB outbreak severity at survey sites was 1870.33 dead trees per km^2 (sd = 2496.09) with a maximum severity of 17,300 dead trees. The site-level severity we observed was comparable to average levels of severity found throughout the range of lodgepole pine in greater Rocky Mountain region (mean = 1163.06 dead trees per km^2, sd = 2436.34). Bird surveys were conducted at sites affected by MPB outbreaks across a temporal gradient from the start of an outbreak (year zero) and up to 10 years after an outbreak began (mean = 4.71 years, sd = 2.83).

A summary of individual species responses to the explanatory variables used in the analyses can be found in the accompanying Appendices. Of the 62 species we modeled, only 7 had a Bayesian *p*-value ($0.05 < p < 0.95$) that indicated a lack of model fit (Table A1). Species varied by mean detection rate from 0.08 (95%CRI = 0.06, 0.11) for White-breasted nuthatch (*Sitta carolinensis*) to 0.56 (95%CRI = 0.54, 0.57) for Yellow-rumped warbler (*Setophaga coronata*). Detection rates changed significantly with survey date for 41 species. Further, we found a quadratic relationship between detection and survey date for 18 of those 41 species (Table B1).

3.1. Species richness

Modeled mean species richness (N) did not differ between MPB outbreak sites (N = 19.35, 95%CRI = 17.00, 22.01) and sites with no outbreak (N = 20.23, 95%CRI = 16.83, 24.25). We found support for a negative relationship between increasing MPB outbreak severity and community mean occurrence ($\mu_{\alpha2} = -0.12$, 95%CRI = -0.20, -0.04) but this translated into small changes in species richness across the tree mortality gradient; a net loss of 1.53 (95%CRI = 0.80, 2.14) species at maximum outbreak severity (Fig. 2a). The community-level response to time, years since outbreak start, was positive and larger in magnitude than the community-level response to increasing tree mortality ($\mu_{\alpha3} = 0.17$, 95%CRI = 0.10, 0.24). However, 10 years after the start of an outbreak, species richness was not different from sites where outbreaks did not occur (Fig. 2b). We also found support for a negative interaction between outbreak severity and number of mortality years, the smallest effect of all model parameters ($\mu_{\alpha4} = -0.06$, 95%CRI = -0.12, -0.04). Finally, we found a positive community-level response to latitude ($\mu_{\alpha1} = 0.22$, 95%CRI = -0.03, 0.46), though with more variability than other explanatory covariates. Individual species occupancy probabilities changed at different rates in relation to latitude, resulting in stable to decreasing species richness at lower latitudes and increasing species richness at higher latitudes (Fig. 2c).

3.2. Individual species responses

Fig. 2. Site-level estimates of richness (dots) for sites with outbreaks (2a and 2b) and for all sites (2c). Solid lines represent mean richness (N) across outbreak sites. Dashed lines represent mean richness at sites where no outbreak occurred, which are fixed in Fig. 2a and b. 2a. Species richness at MPB outbreak sites as a function of increasing outbreak severity. Outbreak severity is measured as the $\log_{10}$ of the number of dead trees per 1 km^2 (survey unit area). 2b. Species richness as a function of increasing time since the start of an MPB outbreak in years. Mortality year zero of the outbreak represents when MPB began attacking trees and mortality year one is the first year tree mortality was observed. 2c. Species richness as a function of latitude for outbreak and non-outbreak sites.

Nearly 18% of the species (10 out of 55 species) showed a significant response to increasing severity of MPB outbreaks (Table A1). The direction of species' responses to outbreak severity, defined as the number of dead trees at a site, was predominantly negative (nine of ten species). The only species with a positive response to increasing outbreak severity was Townsend's solitaire (*Myadestes townsendi*), an aerial insectivore that nests on the ground. Townsend's solitaire increased in occurrence from 0.46 (95%CRI = 0.43, 0.50) to 0.64 (95%CRI = 0.50, 0.77) across the range of outbreak severity. The strongest negative change in occupancy to increasing outbreak severity was in Pine grosbeak (*Pinicola enucleator*), a canopy-nesting pine seed specialist, which declined in occurrence from 0.43 (95%CRI = 0.36, 0.50) to 0.23 (95%CRI = 0.18, 0.28), however, this species was still more common after an outbreak occurred than before (Table A1). In addition, four of the nine species [Pacific wren (*Troglodytes pacificus*), Pileated woodpecker (*Hylatomus pileatus*), Townsend's warbler (*Myadestes townsendi*), and Varied thrush (*Ixoreus naevius*)] exhibiting negative responses to increasing outbreak severity were rare throughout the study region (mean occurrence ≤ 0.15) and declines in occurrence with increasing outbreak severity for these rare species likely had little influence on site-level species richness (Table A1).

We found a much larger number of significant responses among individual species to the time covariate (years since the start of an outbreak). Just over 40% of all species (23 out of 55 species) exhibited a temporal change in mean occurrence during an outbreak, of those all but one species responded positively (Table A1). Swainson's thrush (*Catharus ustulatus*), a foliage-gleaning insectivore that nests in the shrub layer, exhibited the largest increase in occurrence over time, increasing from an occurrence of 0.25 (95%CRI = 0.21, 0.29) at the start of an outbreak to an occurrence of 0.53 (95%CRI = 0.48, 0.59) at 10 years after an outbreak began. Swainson's thrush was also the only species to have a significant interaction between MPB outbreak severity and time (Table A1). The only species to decline in occurrence over time after an outbreak was Clark's nutcracker (*Nucifraga columbiana*), a canopy-nesting pine seed specialist, which decreased in occurrence from 0.59 (95%CRI = 0.57, 0.61) to 0.22 (95%CRI = 0.10, 0.41).

The effect of latitude on species occupancy was split, with 69% of species responding to changing latitude (38 out of 55 species). Of 38 species with significant responses to changing latitude, 17 were more common at lower latitudes while 21 were more common at higher latitudes (Table A1). Broad-tailed hummingbird had the largest decrease in occurrence with increasing latitude, declining from 0.96 (95%CRI = 0.91, 0.99) at 38 degrees latitude to < 0.01 at 49 degrees latitude. Townsend's warbler (*Setophaga townsendi*) had the largest increase in occurrence across the latitudinal gradient of the study, increasing from functionally zero to 0.88 (95%CRI = 0.81, 0.93).

3.3. *Community change following beetle outbreaks*

Although we found weak support for general responses of nesting guilds to outbreak severity and time since outbreak, we did find turnover in community composition with just over 50% of species (28 of 55) having statistically different occurrence rates following MPB outbreaks. The majority of community turnover is attributable to 22 species with different occupancy rates where MPB outbreaks occurred, irrespective of the outbreak's severity or time since the outbreak began (species in Fig. 3). Within this collection of 22 species, we found more consistent responses among nesting guilds. Nearly all cavity nesting species (6 of 7) increased in occurrence while a similar amount of shrub nesting species (6 of 7) had significantly lower occurrence rates following MPB outbreaks (Fig. 3). Canopy nesting species had mixed responses with 4 of 8 species increasing in occurrence following outbreaks (Fig. 3). The largest difference in mean occurrence (of these 22 species) was observed for American three-toed woodpecker, a species known to forage on bark beetle adults and larvae, and whose occupancy probability increased 100% from 0.20 (95%CRI = 0.14, 0.27) in non-outbreak sites to 0.40 (95%CRI = 0.33, 0.47) in outbreak sites.

The remaining community turnover was due to six species increased in occurrence with time since the start of an MPB outbreak, four of which [Golden-crowned kinglet (*Regulus satrapa*), Gray jay (*Perisoreus canadensis*), Swainson's thrush (*Catharus ustulatus*), and Western tanager (*Piranga ludoviciana*)] increased in occurrence after the start of an outbreak and were more common after 10 years at sites where MPB outbreaks occurred (Fig. 4). In contrast, two species, Dark-eyed junco (*Junco hyemalis*) and Yellow-rumped warbler (*Setophaga coronata*), increased in occurrence following the start of an outbreak but were also consistently more common at sites with outbreaks irrespective of time (Fig. 4). Four of the six species that increased in occurrence over time following the start of an outbreak were canopy nesting species (Fig. 4).

4. Discussion

In contrast to our initial predictions, our results suggest bird species richness changes minimally following MPB outbreaks in lodgepole pine forests. Forests with extremely high tree mortality show potential for reduced richness if mortality approaches > 10,000 dead trees per km^2 (Fig. 2a). Importantly, species richness alone does not fully express changes in the forest bird community as we also observed considerable turnover in the species composition. Half of all species (28 of 55) had significantly different occurrence rates at sites after outbreaks took place (Table A1). All nesting guilds were represented among the 28 species that exhibited differences following MPB outbreaks and the majority of these differences are attributable to cavity and shrub nesting species (Figs. 3 and 4). In partial agreement of our initial predictions, we found a predominantly positive response by cavity-nesting species to MPB outbreaks. However, the positive response by cavity nesting species was only due to the presence of a beetle outbreak and did not change with increasing outbreak severity as predicted. In particular, those species that forage on beetle larvae (e.g., American three-toed woodpecker, Fig. 3) had the largest increase in occurrence, which agrees with other studies (Edworthy et al., 2011; Saab et al., 2014). Additionally, several non-excavating cavity nesting species, such as the Mountain chickadee (*Poecile gambeli*), that are not known to exclusively forage on bark beetles also increased in occurrence following an outbreak. This is likely due to the increase in availability of cavities created by excavating species such as woodpeckers (Norris et al., 2013).

Our model suggests an increase in mean species richness through time following an outbreak, about three species over 10 years, but the variability in site-level richness estimates provides little support that the net increase in mean species richness was meaningful (Fig. 2b). This result matched our initial prediction of a no supported change in species richness over ten years after an outbreak, but this was not due to a decrease in canopy nesters and an increase in shrub nesters as we initially predicted. Rather, our results indicate that only six species became significantly more common after outbreaks (Fig. 4). Thus, gains of these six species were offset by species that were less common in outbreaks in general, resulting in the lack of evidence for a change in richness we observed over time following an outbreak.

Our findings of mixed species responses and limited changes to species richness echo previous research on the effects of MPB outbreaks on forest birds (Drever and Martin, 2007; Chan-McLeod et al., 2008; Drever et al., 2009; Saab et al., 2014). The mixed responses to MPB outbreaks among canopy nesting species found in this study and elsewhere may indicate the importance of interspecific competition in driving community composition. The loss in canopy resources may increase the competition between species that nest or forage in the canopy. Whereas the pulse in resources beetle outbreaks provide to cavity nesting species and bark-foraging insectivores may reduce competition among those type of species (Drever et al., 2009). Although competition in beetle outbreak-bird relationships remains understudied.

We also note an increase in species richness as a function of increasing latitude, which is contrary to latitudinal-richness gradient theory that suggests species richness decreases from the equator to the poles (MacArthur and Wilson, 1963). The inverse latitudinal-richness gradient we found is reported in other studies on birds at this scale (e.g., Cook, 1969; Dreitz et al., 2017). One potential explanation is that gross primary production increases with latitude in western portions of the contiguous United States (Mekonnen et al., 2016), and generally bird richness increases with increasing productivity (Hurlbert and Haskell, 2003). In addition, the range of most forest bird species expands with increasing latitude, creating the potential for increased overlap in species occurrences at higher latitudes. Collectively, these results highlight the importance of accounting for the geographic location of data when working with multiple species over broad spatial scales (e.g., > 1,000,000 km^2 in this study).

4.1. *Informing management and conservation*

The moisture content of sapwood in beetle-killed trees can decline ~100% within the first three years following mortality (Chow and Obermajer, 2007). This moisture reduction accelerates wood

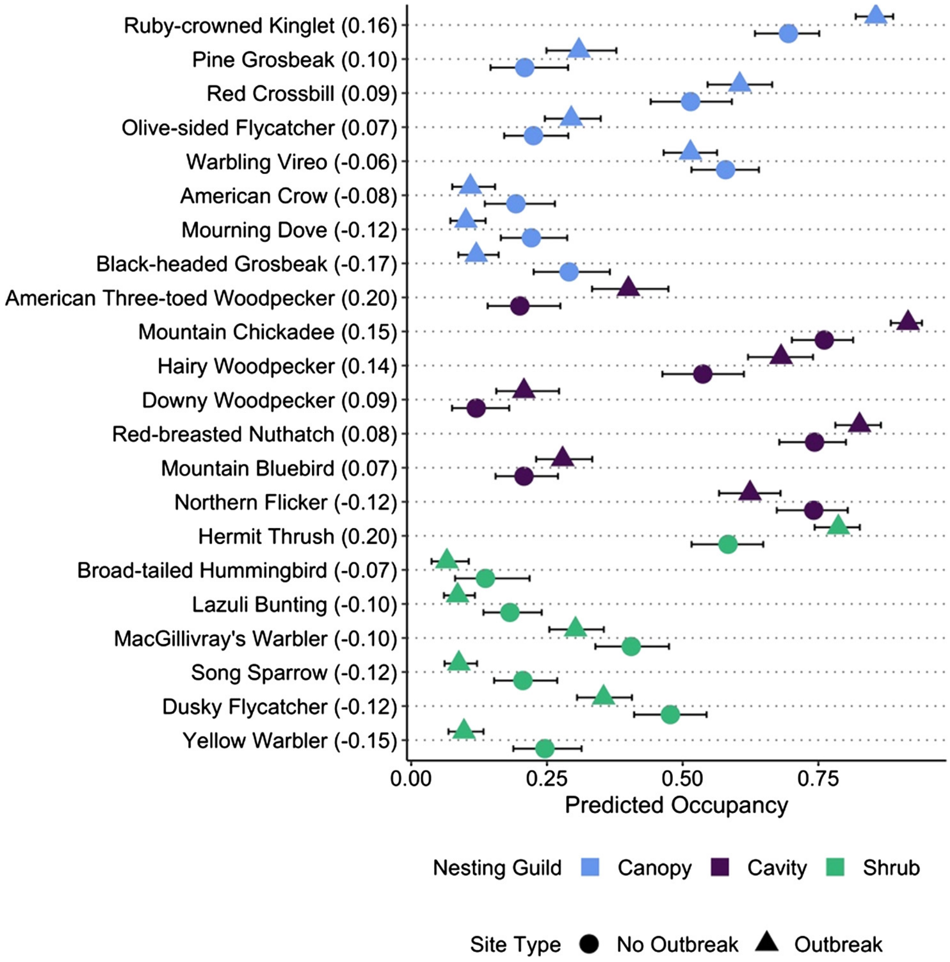

Fig. 3. Predicted occupancy, based on slope and intercept parameters, for species exhibiting a difference in occurrence between sites with and without an MPB outbreak (error bars represent 95% CRI). Difference in occupancy assumed when CRI's did not overlap the mean of corresponding site types. The net difference in predicted mean occurrence from no outbreak to outbreak is listed in parentheses. Points are colored to highlight guild associations for shrub (green), cavity (purple), and canopy nesting species (blue). Species are sorted by magnitude of difference in occupancy (positive to negative) within each guild. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

degradation decreasing the potential value of unharvested timber. Early and large-volume harvesting of MPB-killed trees has been suggested to mitigate the lower profitability of beetle-killed lumber (Zhu et al., 2007). The findings from our study suggest many species, particularly cavity nesters, utilize beetle-killed forests and persist at higher occurrence rates up to 10 years post-outbreak, which includes the timeframe when beetle-killed trees are most readily salvageable. This provides motivation for continued evaluation of snag retention policies during the planning of post-outbreak harvest. Additionally, shrub nesting species, which showed a consistent reduction in occurrence rates following outbreaks (Fig. 2) may also be negatively impacted by salvage logging depending upon the management of woody debris (slash) generated during logging operations. Experimental manipulations have found retaining slash on-site following salvage logging can promote the preservation of the shrub layer (Fornwalt et al., 2018), thereby potentially limiting additive impacts of salvage logging on shrub nesting species. Incorporating fire history and timber harvest information will be helpful in future analyses to provide insight about potential interactive effects of tree density, forest stand age, and bark beetle exposure in governing forest bird diversity. This information may be especially helpful when making decisions about the manner and extent of salvage logging that may occur in affected landscapes (Chan-McLeod, 2006).

Furthermore, the diversity metric we used in this study, species richness, is just one aspect of diversity as it does not incorporate species-level abundance estimates like other metrics such as the Simpson or Shannon-Weiner indices (Iknayan et al., 2014). Future research on the relationship between forest bird diversity and disturbance should examine the differences between a variety of diversity metrics to make the most informed conclusions. Bark beetles can also create a lasting ecological footprint in affected areas (e.g., a substantial change in tree species composition within affected stands, Collins et al., 2011), thus, considering the wildlife-habitat relationships remaining after outbreaks have ended (15–30 years) will provide additional valuable information.

4.2. Conclusions

Mountain pine beetle outbreaks influence the community of forest birds living in affected lodgepole pine forests. We observed changes to species composition within the forest bird community, and the presence of MPB outbreaks did increase the occurrence of species that otherwise would have been less common had outbreaks not occurred. While we did not find a significant difference in bird richness at the scale of inference in this study, the occurrence of MPB outbreaks may create heterogeneity in the resources used by birds and support greater bird richness at larger spatial scales, for example across the continent.

Over the last decade, a renewed emphasis on the conservation of biodiversity has surfaced, in part, due to the threat climate change poses to communities of organisms and collective ecosystems (Thomas et al., 2004; Romero-Lankao et al., 2014). There is mounting evidence that birds are good indicators of changes in biodiversity and the health and functioning of many ecosystems across the globe (O'Connell et al., 2000; Gregory et al., 2003; Schulze et al., 2004), though more research in disturbance-prone systems such as those across the greater Rocky Mountain region is needed. Future studies that formally establishes the connection between changes in bird diversity and total biodiversity will be an important step in promoting the utility of monitoring bird populations as a management tool for forest ecosystems. Towards this greater objective, our research provides an example that can be

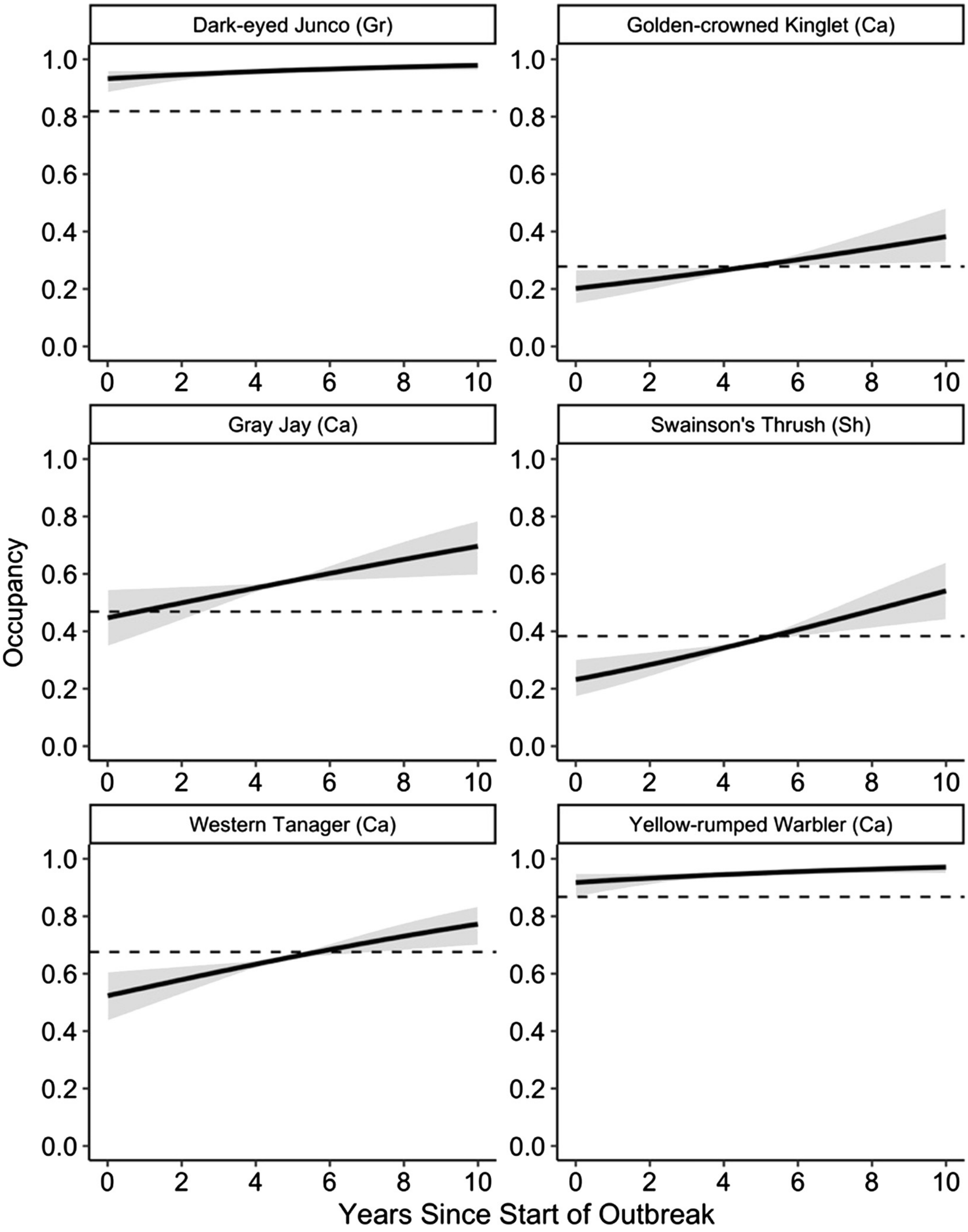

Fig. 4. Six species responded positively to increasing time since the start of an MPB outbreak and became more common after 10 years where outbreaks occurred. Solid lines are the predicted mean occurrence for species following an outbreak of mean severity (no interaction term). Shaded areas represent the 95% credible intervals. For comparison, dashed lines are the predicted mean occurrences for species at sites where outbreaks did not occur. Species nesting guilds associations listed in parentheses (Ca = canopy, Sh = shrub, Gr = ground).

compared to other studies assessing the response of birds to additional forms of disturbance, such as timber harvest and forest fire.

Acknowledgments

We would like to thank the efforts of the Bird Conservancy of the Rockies and the many volunteers and funding agencies that support the Integrated Monitoring in Bird Conservation Regions program. A special thanks to Drs. W. Lowe, P. Lukacs, B. Hahn, and M. Mitchell for constructive feedback. We also thank our reviewers for their feedback improving this manuscript. W.M.J acknowledges funding from the U.S. Forest Service, the Wildlife Biology Program at the University of Montana, and the Richard F. Johnson Legacy in Forestry & Conservation Scholarship, Danny On Memorial Scholarship, Thomas H. Leik, Sr. Wildlife Biology Scholarship, and Bertha Morton Scholarship funds. A.J.H.M. acknowledges funding from the USDA Forest Service Western Wildland Environmental Threat Assessment Center [Agreement Number 18-CR-11221633-109] and the USDA Forest Service Special Technology Development Program [Agreement Number 18-JV-11221633-195].

Appendices A and B. Supplementary material

Supplementary data to this article can be found online at https://

doi.org/10.1016/j.foreco.2019.04.047.

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