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Forest birds exhibit variable changes in occurrence during a mountain pine beetle epidemic

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Citation: Mosher, B. A., V. A. Saab, M. D. Lerch, M. M. Ellis, and J. J. Rotella. 2019. Forest birds exhibit variable changes in occurrence during a mountain pine beetle epidemic. Ecosphere 10(12):e02935. 10.1002/ecs2.2935

Abstract. Recent epidemics of mountain pine beetles (*Dendroctonus ponderosae*) have fundamentally altered forests of the Intermountain West, impacting management decisions related to fire, logging, and wildlife conservation. We evaluated how a recent mountain pine beetle epidemic influenced the site occupancy of 39 avian species in forests dominated by ponderosa pine (*Pinus ponderosa*) on the Helena National Forest, Montana. Point count data were collected during the avian breeding seasons (May–July) of 2003–2006 (pre-epidemic) and 2009–2011 (during-epidemic). We used a community-level Bayesian hierarchical model accounting for imperfect detection to obtain occupancy estimates for all detected forest birds. Our model for site occupancy included the annual presence of mountain pine beetles, the proportion of ponderosa pine at sites, the interaction between the two, and a random effect of year. We observed changes in occurrence over the study period for 23 of 39 species, including shifts toward and away from beetle-killed ponderosa pine. Community turnover increased during the epidemic and then returned quickly to pre-epidemic levels. Our results illustrate the myriad habitat preferences of the small landbird community and suggest that a mosaic of disturbed conifer, intact live conifer, and adjacent aspen forests will be critical for the persistence of populations of native avifauna in the Intermountain West.

Key words: avian community; *Dendroctonus ponderosae;* hierarchical Bayes; multi-species occupancy.

Received 26 June 2019; revised 19 August 2019; accepted 5 September 2019. Corresponding Editor: W. Alice Boyle.

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Introduction

Land management practices and climate change have altered disturbance regimes of many western North American forests (Attiwill 1994, Parker et al. 2006, Raffa et al. 2008, Bentz et al. 2010). With a growing human population and changing climate, increases in the frequency and magnitude of forest disturbances like wildfire, disease, plant invasions, and insect epidemics are expected (Kurz et al. 2008, Bentz et al. 2010, Sambaraju et al. 2012). These disturbances can alter local forest composition, structure, and function (Franklin et al. 2002) and have larger scale impacts on carbon cycling and climate (Kurz et al. 2008, Maness et al. 2013). Species responses to disturbances can be variable and complex (Noss et al. 2006), but understanding these responses is essential for developing appropriate forest management plans that consider conservation goals in addition to other objectives (McCarthy and Burgman 1995, Dorren et al. 2004).

Whether due to insect invasions, wildfire, or drought, conifers are expected to experience especially high rates of mortality under future climate change scenarios (McDowell et al. 2016). In many western forests, lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) are the dominant tree species and provide both timber and wildlife value. Ponderosa pine are widely distributed throughout western North America and are a commercially important lumber species (Willits 1994, Kershner et al. 2008). Ponderosa pine trees are particularly valuable for forest birds, as their foliage and thick bark and sapwood provide both foraging and nesting resources for a variety of species (Bull et al. 1997, Saab et al. 2009). Land management actions that are considered before and after western forest disturbances often focus on pine species, presenting challenges for managers that have legal requirements to maintain biodiversity, including habitat for species reliant on dead and dying trees, while maintaining revenue or reducing fire risk.

Infestations of mountain pine beetle (MPB; *Dendroctonus ponderosae*) are a native part of the disturbance cycle in western North American forests (Sartwell and Stevens 1975). However, fire suppression, climate, and logging have altered the historical interactions between insects and forests resulting in larger outbreaks of epidemic proportions (Carroll et al. 2004, Parker et al. 2006, Bentz et al. 2010). A recent MPB epidemic in British Columbia and the western United States is one of the largest in recent history and affected over 47 million hectares of subalpine and boreal forest since it began in 1999 (Raffa et al. 2008). This large-scale epidemic of MPB has fundamentally altered the Intermountain West and continues to influence decisions related to fire, logging, and wildlife management (Kaufmann et al. 2008). An understanding of wildlife responses to MPB epidemics will aid forest managers in making decisions that balance these values.

Western forest birds are a diverse group, including generalist and specialist species of a variety of nesting and foraging guilds. In part due to their mobility, birds often respond quickly to disturbances and are a valuable indicator of changing forest conditions (Canterbury et al. 2000, O'Connell et al. 2000). Several studies of avian responses to mountain pine beetles have been conducted (reviewed in Saab et al. 2014), but many of these focused on single species or single guilds. Community studies provide information on the range of avian responses to MPB epidemics (Janousek et al. 2019) and will be valuable to land managers. Of high importance are studies that evaluate avian use of timber species like ponderosa pine that are the target of most salvage logging operations.

Beyond individual species responses to a disturbance, another metric of ecological and management relevance is community turnover. Turnover is the change in the composition of a community over space or time (La Sorte and Boecklen 2005) and may reveal impacts of disturbances or management efforts on community stability (Doherty et al. 2003). In the current era of rapid environmental change, land management agencies are tasked with "managing landscapes for resilience" such that key elements of biodiversity are robust to perturbations (Allen et al. 2011). The magnitude and change in temporal turnover resulting from a disturbance and how that turnover compares with pre-disturbance levels may be an indicator of how sensitive the community is to current and future stressors (La Sorte and Boecklen 2005).

We used avian point count data in a hierarchical multi-species occupancy model to explore occupancy probability and turnover proportion for an avian community before and during a mountain pine beetle epidemic in southwestern Montana. Our questions of interest were as follows: (1) How do species occupancy probabilities change over the course of a mountain pine beetle epidemic? (2) Are any of the observed changes in occupancy related to the proportion of trees that were ponderosa pine at each site? and (3) How does temporal community turnover during a mountain pine beetle epidemic differ from that of a pre-epidemic community?

Materials and Methods

Study area

Four study units ranging from 130 to 260 hectares were selected based on management priorities within the northern Elkhorn Mountains 16 km southeast of Helena, Montana, USA (46°46′ N, 111°91′ W). The original study was part of a project designed to evaluate the effectiveness of prescribed fire treatments in fuels

reduction and subsequent effects on habitats and populations of the associated avifauna (i.e., Birds and Burns Network; Saab et al. 2006). Pre-fire-treatment data from point count surveys were collected in each study unit during four bird breeding seasons (2003–2006), and pre-fire-treatment vegetation data were collected in 2003. In 2006, litigation prevented the implementation of the prescribed fire treatments, and data collection was suspended. A mountain pine beetle infestation began in the Helena National Forest during 2006, peaked in 2008, and continued through 2009–2011, when beetle-caused tree mortality declined as the epidemic slowed (B. J. Bentz et al., *unpublished data*). Point count surveys were resumed near the end of the epidemic in the summers of 2009–2011. We use the phrases "pre-epidemic" and "during-epidemic" to differentiate the two time periods of interest in the study and to emphasize that the beetle infestation was ongoing in the second time period.

The study units were characteristic of dry mixed coniferous forests, largely dominated by ponderosa pine with lesser amounts of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine. The study units also contained stands of quaking aspen (*Populus tremuloides*), found mainly along snowmelt drainages and creeks.

Point counts

In 2002, we established 76 point count sites throughout the study area. Sites were randomly stationed in ponderosa-dominated habitat, with the constraint that they were located ≥250 m apart and ≥150 m from the study unit boundary. We visited each site three times per season from 22 May to 3 July during the years 2003–2006 (pre-epidemic) and 2009–2011 (during-epidemic). Point counts were standardized to minimize differences in detection probability due to weather or changes in diurnal bird activity. Surveys were conducted just after the dawn chorus in fair weather (i.e., low wind and no precipitation) only. The order that points were visited was randomized, and all surveys were completed within five hours of sunrise. At each site, a single observer recorded all birds detected during a 5-min count period and estimated the distance to each observed individual in distance classes. The data used in our analyses were truncated at 75 m to ensure independence of observations at different sites and because detection probability for some species decreases rapidly after this distance for most observers (Alldredge et al. 2007).

Ponderosa pine measurements

We sampled vegetation at each site using a cross-plot of two intersecting 20 × 100 m rectangles, which were centered on the point count location (Hollenbeck et al. 2013; Fig. 1). We tallied and identified to species all live trees and snags ≥1.4 m in height and >23 cm in diameter at breast height in each vegetation plot. We calculated the proportion of trees that were ponderosa pine at each site and used this value as a covariate (PIPO). A tree was deemed a snag if at least 50% of its needles were dead or missing, and if pitch tubes were present, yielding evidence of an active beetle infestation and imminent mortality. Ponderosa pine measurements were recorded only once during the study, in 2003. Beetle-caused tree mortality in the study area impacted more than 80% of large ponderosa and lodgepole pine trees (B. J. Bentz et al., *unpublished data*), so the proportion ponderosa pine covariate approximates the proportion of the plot comprised of live ponderosa pine trees before, and dead ponderosa pine trees during, the mountain pine beetle epidemic.

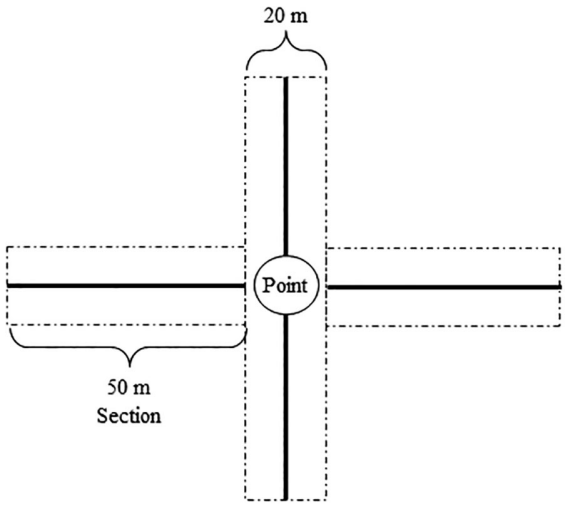

Fig. 1. Schematic of vegetation cross-plots, which were centered on each avian point count station. Trees were tallied and classified to species in each cardinal direction from the center plot along 50 × 20 m transects.

Model overview

Observations were made in seven primary sampling occasions (i.e., years), within which we assumed each site was closed to changes in species occupancy. Within each primary sampling period, we conducted three secondary sampling surveys (i.e., visits). The information collected during visits was used to account for imperfect species-level detection (Pollock 1982, MacKenzie et al. 2017). We used a Bayesian hierarchical multi-species occupancy model (Dorazio and Royle 2005, Russell et al. 2009) to model site occupancy and detection probabilities for all species detected before (2003–2006) and during (2009–2011) the beetle epidemic.

Occupancy model

The state process (occupancy) was treated as a latent Bernoulli random variable (z_{ijt}), such that $z_{ijt} = 1$ if site j was occupied by species i in year t and $z_{ijt} = 0$ if the site was unoccupied. We modeled log-odds occupancy ($\text{logit}(\psi_{ijt})$) with an intercept that varied temporally and could differ between pre- and during-epidemic (β_{0it}). Similarly, the slope, which reflects each species' relationship with ponderosa pine ($PIPO_j$), could vary between the two time periods (β_{1it}). We centered the ponderosa pine covariate.

$$z_{ijt} \sim \text{Bernoulli}(\psi_{ijt})$$

$$\text{logit}(\psi_{ijt}) = \beta_{0it} + \beta_{1it} \times PIPO_j$$

$$\beta_{0it} = \mu_{\beta_0} + \gamma_{1it} + \gamma_{2i} \times \text{ind. Beetle}_t$$

$$\beta_{1it} = \mu_{\beta_1} + \delta_{1i} + \delta_{2i} \times \text{ind. Beetle}_t$$

The intercept term, β_{0it}, was comprised of an average intercept (μ_{β_0}) species- and year-specific intercept (γ_{1it}) and the effect of the annual presence of the beetle epidemic (γ_{2i}) using an indicator variable (ind.Beetle; 0 for years 2003–2006 [pre-epidemic] and 1 for years 2009–2011 [during-epidemic]). The parameter β_{1it} was similarly comprised of an average intercept (μ_{β_1}), a species-specific intercept (δ_{1i}) and the effect of the annual presence of the beetle epidemic (δ_{2i}) using the same indicator variable.

Detection model

The observation process y was treated as a series of binomial trials such that species i was observed on visit k at a site j in year t over the total number of site visits with probability of detection p_i given that the species was truly present ($z_{ijt} = 1$).

$$y_{ijt} \sim \text{Binomial}\,(k, p_{ijkt} \times z_{ijt})$$

$$\text{logit}(p_{ijkt}) = \alpha_i$$

where $\alpha_i \sim N(\mu_\alpha, \sigma_\alpha)$.

We chose commonly used vague prior distributions for all parameters (Data S1).

Hypotheses

We made a priori predictions about species-level occupancy responses based on nesting and foraging guilds (Table 1). To summarize, we predicted that aerial insectivores would respond positively to the MPB epidemic due to increased foraging opportunities resulting from the loss of pine canopy (Janousek et al. 2019). Cavity-nesting bark insectivores were also predicted to respond positively to the MPB epidemic due to increased availability of food resources and nesting substrates (Drever et al. 2009, Russell et al. 2009). We predicted negative responses for cavity-nesting foliage insectivores due to their strong reliance on live pine foliage. We predicted that open-cup foliage insectivores would have mixed responses to the epidemic as many of these species will readily forage and nest in deciduous habitat. We predicted that omnivores and ground and shrub insectivores would largely be unresponsive to the MPB epidemic because minimal understory changes were anticipated during the time frame of our study and because many of these species exhibit generalist foraging tendencies. A caveat was pine seed-consuming omnivores, which were expected to decline in occurrence.

Species-specific metrics

We evaluated beetle-related occupancy responses by investigating four quantities estimated by the model. The quantities are (1) the MPB-related change in log-odds occupancy at a site with average proportion ponderosa pine (γ_{2i}; an intercept term), (2) the change in the

Table 1. Classification of 39 avian forest species to groups based on foraging and nesting life history traits and predicted changes in occupancy based on these traits in relation to a recent, large-scale (<6 yr since peak in beetle-caused tree mortality) mountain pine beetle epidemic

Foraging group	Cavity nesters	Open-cup nesters
Aerial insectivore		
Prediction	Strong positive	Moderate positive
Rationale	Increased foraging opportunities due to reduction in pine canopy‡, and increase in available nesting cavities	The loss of pine canopy, resulting in more open forest conditions, should provide increased opportunities for foraging‡
Species	Mountain bluebird	Dusky flycatcher, Hammond's flycatcher, Townsend's solitaire
Bark insectivore		
Prediction	Strong/moderate positive	None in study
Rationale	Increased availability of nest substrates (i.e., snags) for all species§ and food (i.e., beetle larvae) for bark-drilling species¶	None in study
Species	American three-toed woodpecker, brown creeper, downy woodpecker, hairy woodpecker, red-breasted nuthatch, white-breasted nuthatch	None in study
Canopy foliage insectivore		
Prediction	Moderate negative	Mixed
Rationale	Despite increased nest availability, we expect reductions in food resources from live pine foliage and bark	Most of these species readily use deciduous forest for nesting and foraging, but the ruby-crowned kinglet primarily uses conifer forest
Species	Black-capped chickadee, mountain chickadee	Ruby-crowned kinglet, warbling vireo, western tanager, yellow-rumped warbler
Ground or shrub insectivore		
Prediction	Moderate positive	Neutral
Rationale	Increased nest availability	Minimal changes in understory were expected in the time period of the study
Species	House wren	American robin, Cassin's vireo, hermit thrush, MacGillivray's warbler, orange-crowned warbler, Swainson's thrush
Omnivore		
Prediction	Neutral	Neutral; pine seed consumer moderate negative
Rationale	Generalist foraging strategies for these species will result in minimal distributional changes, despite a potential increase in nesting habitat	Generalist omnivores were not expected to respond to the epidemic while pine seed-consuming specialists were expected to decline with pine seed production
Species	Northern flicker, pileated woodpecker, red-naped sapsucker	Brown-headed cowbird, Cassin's finch, chipping sparrow, Clark's nutcracker*, common raven, dark-eyed junco, evening grosbeak, gray jay, lazuli bunting, Lincoln's sparrow, mourning dove, pine siskin, red crossbill†

Notes: Traits were assigned according to the following: Robinson and Holmes (1982), Raphael and White (1984), Airola and Barrett (1985), Pitocchelli (1995), Jones and Donovan (1996), Hunt and Flaspohler (1998), Mccallum et al. (1999), Gardali and Ballard (2000), Saab and Powell (2005), Foote et al. (2010). Species are listed by common name (see Appendix S1: Table S1 for scientific names).

† Pine seed-consuming (PSC) specialist.

‡ Janousek et al. (2019)

§ Saab et al. (2009), Ghalambor and Martin (1999), Poulin et al. (2013), Foote et al. (2010).

¶ Koplin (1969), Imbeau and Desrochers (2002), Drever et al. (2009).

relationship between occupancy and ponderosa pine (i.e., slope) before versus during the MPB epidemic (δ_{2i}), (3) the total modeled effect of MPB on the log-odds occupancy for a species (i.e., slope + intercept; $\gamma_{2i} + \delta_{2i} \times \overline{\text{PIPO}_j}$), and (4) the change in average occupancy probability from pre- to during-epidemic years (ψ_{diff}, i). For these last two metrics, we used the average value of proportion ponderosa pine at sites where each species was detected over the course of the entire study. This last metric provides the least direct evidence for an effect of MPB on occupancy

because it incorporates annual variability that cannot be directly attributed to MPB, in addition to the direct MPB effects included in the model.

For changes in slope related to ponderosa pine (δ_{2i}), species were grouped into different categories (augmented [change in magnitude without a change in direction], reduced [change from positive or negative slope to a slope of 0], new [change from a slope of 0 to a positive or negative slope], reversed [change from positive to negative slope or vice versa], or no change) based on whether the magnitude and/or direction of the relationship with ponderosa pine changed over the course of the beetle epidemic (Table 2: Slope). Species-specific results for all other quantities (beetle-related change in intercept [γ_{2i}], total beetle-related change in occupancy [$\gamma_{2i} + \delta_{2i} \times \overline{\text{PIPO}_i}$], and average change in occupancy [$\widehat{\psi_{\text{diff},i}}$]) were grouped into one of 5 categories (ranging from strongly positive to strongly negative occupancy responses) based on estimated posterior distributions and credible intervals (Table 2: Occupancy).

Table 2. Species responses to a mountain pine beetle epidemic were estimated for 39 species using multiple model parameters

Category	Change in parameter
Slope (w/PIPO)	
Augmented	Evidence of augmented slope (change in magnitude without change in direction)
Reduced	Evidence of removal of slope (change from either direction to slope = 0)
New	Evidence of new slope relationship (change from slope = 0 to either direction)
Reversed	Evidence of reversal of direction of slope (change in direction)
None	No evidence of change in slope
Occupancy	
++	Strong evidence of positive change (90% CRI does not overlap 0)
+	Weak evidence of positive change (80% CRI does not overlap 0)
0	No evidence of change (80% CRI does overlap 0)
−	Weak evidence of negative change (80% CRI does not overlap 0)
−−	Strong evidence of negative change (90% CRI does not overlap 0)

Notes: Responses were classified based on the amount of evidence found. Two categorizations were used. For occupancy metrics including beetle-related change in occupancy at average ponderosa pine (γ_{2i}), total beetle-related change in occupancy (intercept and slope; $\gamma_{2i} + \delta_{2i} \times \text{PIPO}_i$), and average before years vs. during-beetle years change in occupancy ($\psi_{\text{diff},i}$) species responses were classified as strongly positive (++), positive (+), neutral (0), negative (−), and strongly negative (−−). We used a different classification scheme to characterize the evidence for species-specific changes in the relationship with proportion ponderosa pine (i.e., slope; δ_{2i}) for avian species during a mountain pine beetle epidemic. Slope relationships were classified as augmented, reduced, new, reversed, or none.

Community-level metrics

We defined turnover as the proportion of community members whose occupancy status changed between two points in time at a randomly selected site. We calculated turnover between subsequent primary sampling periods and over two-three-year periods (2003–2006 and 2006–2009). We predicted that turnover would be highest in the time period directly after the onset of the mountain pine beetle epidemic, as the largest change in resources likely occurs during this time period. However, we expected that turnover would return to pre-epidemic levels rapidly because avian populations in western North America have evolved in the context of frequent forest disturbance (Saab and Powell 2005, Saab et al. 2014).

Analysis and goodness of fit

The model (Data S1) was fit using JAGS (http://mcmc-jags.sourceforge.net) via the package rjags (Plummer 2011) in the R programming language (R Development Core Team 2012). Convergence was assessed by comparing between- and among-chain variation using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). We used posterior predictive checks (Gelman et al. 2004) of naïve occupancy (the proportion of sites where a species was detected) to assess the fit of the model, and calculated Bayesian *P*-values for every species and year combination to assess the ability of our model to recreate the data.

Results

Thirty-nine avian species were detected at distances of ≤75 m during the study (Appendix S1: Tables S1 and S2). The most commonly detected species were red-breasted nuthatch (*Sitta canadensis*), yellow-rumped warbler (*Setophaga coronata*), dark-eyed junco (*Junco hyemalis*), and mountain chickadee (*Poecile gambeli*) with 917,

798, 733, and 536 total detections, respectively. Cassin's finch (*Haemorhous cassinii*), pileated woodpecker (*Drycopus pileatus*), and mountain bluebird (*Sialia curricoides*) were detected most infrequently, with 3, 3, and 6 total detections each. The posterior predictive check did not indicate a lack of model fit for 98.9% of species by year combinations, indicating that the naïve occupancy generated by our model tended to be similar to the naïve occupancy in the original data set (Appendix S1: Table S3). The posterior predictive check did indicate potential lack of fit for chipping sparrow (*Spizella passerina*) in one year and red-breasted nuthatch in two years (Appendix S1: Table S3), as indicated by Bayesian *P*-values of ≤0.05 (Broms et al. 2016).

Species-specific metrics

We found strong evidence of an increase in occupancy at the average site (γ_{2i}) for five species (chipping sparrow, dark-eyed junco, pine siskin [*Spinus pinus*], red-breasted nuthatch, and yellow-rumped warbler), essentially no evidence of a change in occupancy for most species (28 spp.), weak evidence of a decrease in average occupancy for one species (lazuli bunting [*Passerina amoena*]), and strong evidence of a decrease in average occupancy for five species (black-capped chickadee [*Poecile atricapillus*], Cassin's vireo [*Vireo cassinii*], Clark's nutcracker [*Nucifraga columbiana*], mourning dove [*Zenaida macroura*], and red crossbill [*Loxia curvirostra*]; Table 3: γ_{2i}). Of the 11 species that demonstrated a positive or negative response, four matched our predictions. The live conifer-foraging black-capped chickadee and pine seed-consuming Clark's nutcracker and red crossbill responded negatively as predicted, and the cavity-nesting red-breasted nuthatch responded positively.

Similarly, we found strong evidence of a beetle-related increase in overall occupancy ($\gamma_{2i} + \delta_{2i} \times \text{PIPO}_j$) for five species (chipping sparrow, dark-eyed junco, pine siskin, red-breasted nuthatch, and yellow-rumped warbler), essentially no evidence of beetle-related change in occupancy for most species (28 spp.), weak evidence of beetle-related decrease in occupancy for two species (lazuli bunting and mourning dove), and strong evidence of a beetle-related decrease in occupancy for four species (black-capped chickadee, Cassin's vireo, Clark's nutcracker, and red crossbill) (Table 3: $\gamma_{2i} + \delta_{2i} \times \text{PIPO}_j$). Species responses were related to the proportion ponderosa pine, the timing of the beetle epidemic, or both (Fig. 2; Appendix S1: Table S5).

Table 3. Patterns of change for three occupancy quantities over the course of a mountain pine beetle epidemic

Quantity	Results				
	++	+	0	−	−−
Beetle-related change in intercept (γ_{2i})	Chipping sparrow, dark-eyed junco, pine siskin, red-breasted nuthatch, yellow-rumped warbler	None	All other species	Lazuli bunting	Black-capped chickadee, Cassin's vireo, Clark's nutcracker, mourning dove, red crossbill
Total beetle-related change ($\gamma_{2i} + \delta_{2i} \times \text{PIPO}_j$)	Chipping sparrow, dark-eyed junco, pine siskin, red-breasted nuthatch, yellow-rumped warbler	None	All other species	Lazuli bunting, mourning dove	Black-capped chickadee, Cassin's vireo, Clark's nutcracker, red crossbill
Average change in occupancy ($\widehat{\psi_{\text{diff},i}}$)	American robin, American three-toed woodpecker, brown-headed cowbird, chipping sparrow, downy woodpecker, dusky flycatcher, evening grosbeak, hairy woodpecker, house wren, Lincoln's sparrow, MacGillivray's warbler, pine siskin, ruby-crowned kinglet	Hammond's flycatcher, Northern flicker, Swainson's thrush	All other species	Gray jay, lazuli bunting	Black-capped chickadee, brown creeper, Cassin's vireo, Clark's nutcracker, hermit thrush, mountain chickadee, mourning dove, red crossbill, Townsend's solitaire, white-breasted nuthatch

Notes: Metrics include the following: beetle-related change in occupancy at sites with average ponderosa pine (γ_{2i}), total beetle-related change in occupancy (intercept and slope; $\gamma_{2i} + \delta_{2i} \times \text{PIPO}_j$), and average before years vs. during-beetle years change in occupancy ($\widehat{\psi_{\text{diff},i}}$). Species responses were classified as strongly positive (++), positive (+), neutral (0), negative (−), and strongly negative (described in Table 2). Posterior probabilities of these parameters differing from zero are given in Appendix S1: Table S5.

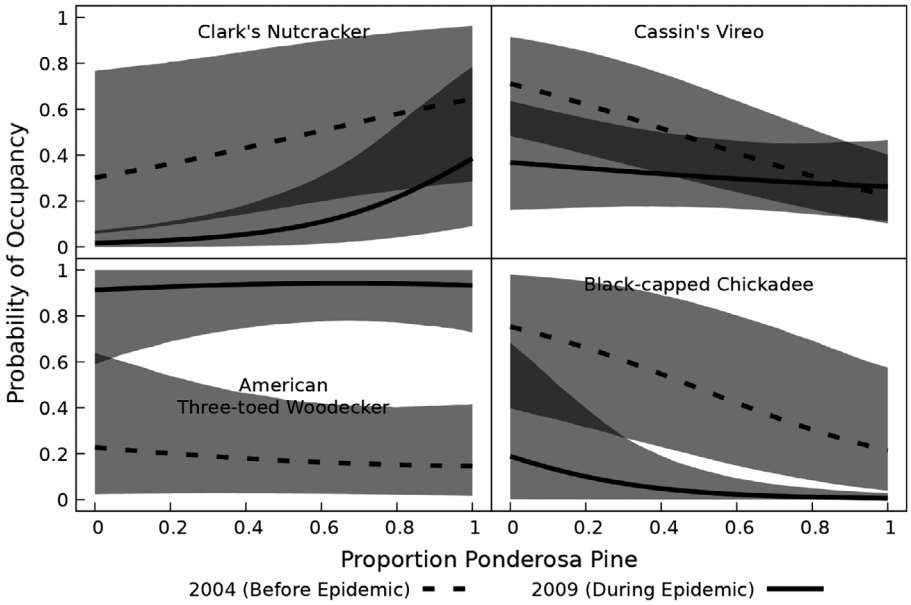

Fig. 2. Posterior mean probability of occupancy and 90% credible bands for selected species before (in 2004; solid line) and during (in 2009; dashed line) a mountain pine beetle epidemic in Montana across the full gradient of percent ponderosa pine.

Based on the estimated difference in average occupancy ($\widehat{\psi_{\text{diff},i}}$), 13 species showed strong evidence of an overall increase in average occupancy probability between the two time periods in the study, three species showed weak evidence of an increase in average occupancy probability (Hammond's flycatcher [*Empidonax hammondii*], Northern flicker [*Colaptes auratus*], and Swainson's thrush [*Catharus ustulatus*]), 11 species showed essentially no evidence of change in occupancy, two species showed weak evidence of a decrease in occupancy (gray jay [*Perisoreus canadensis*] and lazuli bunting), and 10 species showed strong evidence of a decrease in average occupancy probability (Table 3: $\widehat{\psi_{\text{diff},i}}$).

Six of 39 species shifted their relationship with ponderosa pine (Table 4). Of the species showing an augmented relationship with ponderosa pine, brown-headed cowbird (*Molothrus ater*) and evening grosbeak (*Coccothraustes vespertinus*) became increasingly negatively associated with proportion ponderosa pine during the MPB epidemic, while western tanager [*Piranga ludoviciana*] was increasingly positively associated with ponderosa pine during the MPB epidemic (Table 4, Fig. 3). Cassin's vireo was negatively associated with ponderosa pine pre-epidemic and was unassociated with ponderosa pine during the epidemic, while Clark's nutcracker was unassociated with ponderosa pine pre-epidemic but became closely associated with ponderosa pine during the epidemic (Table 4, Fig. 3). American robin (*Turdus migratorious*) was initially unassociated with ponderosa pine but was negatively associated during the epidemic (Table 4, Fig. 3). Estimates of β_{1i} for each time period (pre- and during-epidemic) can be found for all species in Appendix S1: Table S4.

Avian community turnover between neighboring primary sampling periods ranged from 37% to 40% (over 1-yr time intervals) before the MPB epidemic and was higher (47%) during the peak of the beetle epidemic (over a three-year time interval; Fig. 4). This pattern matched our predictions. Turnover was also calculated for three-year intervals, yielding turnover estimates of 41% (90% CRI 0.37–0.44) in the pre-epidemic period and 47% (90% CRI 0.43–0.50) in the during-epidemic period.

Discussion

We found evidence of changes in occupancy that were associated with the MPB epidemic for

Table 4. Change in species' slope relationship with ponderosa pine (δ_i) was classified as augmented, reduced, new, or none (described in Table 2)

	Change in slope (δ_i)			
Species	Augmented	Reduced	New	None
Western tanager**	(+ to ++)			
Brown-headed cowbird**	(− to −−)			
Evening grosbeak**	(− to −−)			
Cassin's vireo**		(− to 0)		
Clark's nutcracker*			(0 to +)	
American robin*			(0 to −)	
All other				None

Notes: No species exhibited a reversed relationship with ponderosa pine. Symbols in parentheses describe whether the slope was positive (+), very positive (++), negative (−), very negative (−−), or neutral (0) during each time period (before and during the epidemic).

* 80% CRI for δ_{2i} does not overlap 0.

** 90% CRI for δ_{2i} does not overlap 0.

several species and some of these changes matched our predictions (e.g., positive responses by cavity nesters and negative responses by pine seed specialists). However, many species responses did not match our predictions illustrating the complexity of interactions that shape species distributions. Few species exhibited altered associations with ponderosa pine as the trees transitioned from live to dead. Western tanager and Clark's nutcracker, however, were more closely associated with dead stands of ponderosa pine during the epidemic than live stands before the epidemic while the reverse was true for evening grosbeak. Finally, the baseline site-level turnover probability of this community was high, and turnover increased during the epidemic as predicted. High turnover may be characteristic of communities that are adapted to disturbance (Ledger et al. 2012) and may prove to be adaptive in the face of other novel disturbances (Elmqvist et al. 2003, Mulder et al. 2012).

Though we found direct evidence of MPB-related occupancy changes for few species, we found indirect evidence of a change in average occupancy between the two time periods studied for many species. Our findings were partially consistent with our predictions and concurred with previous literature regarding avian occupancy in relation to a mountain pine beetle outbreak (Drever and Martin 2010, cf. Saab et al. 2014, Janousek et al. 2019). Bark-drilling woodpeckers and some species dependent on open-air maneuvers for foraging regularly had higher occupancy rates during the epidemic, while pine seed consumers were less common. Results for foliage-gleaning, canopy insectivores and omnivores were less consistent.

Beetle-foraging woodpeckers (i.e., American three-toed woodpecker [*Picoides dorsalis*], downy woodpecker [*Dryobates pubescens*], and hairy woodpecker [*Dryobates villosus*]) in our study likely experienced short-term benefits from the beetle outbreak, corresponding with predicted increases in nesting substrate and foraging opportunities for these species. Forest insect outbreaks influence habitat preferences of cavity-nesting birds, particularly bark-drilling specialists (*Picoides* and *Dryobates* spp.) that rely on beetle larvae as a primary food source (Steeger and Hitchcock 1998, Norris and Martin 2010). Increased occurrence may not be related to increased densities or more importantly, fitness of these species. Information on other factors, including nest density, nest success, fecundity, and survival, is necessary to determine whether species experienced greater fitness during the mountain pine beetle epidemic (Saab et al. 2019).

Conversely, cavity-nesting species that primarily glean insects from needles and bark of live trees (e.g., white-breasted nuthatch [*Sitta carolinensis*], brown creeper [*Certhia americana*], black-capped chickadee, and mountain chickadee) declined during the study which only partially matched our predictions. While increases in weakened trees that are more easily excavated may have increased the availability of nest resources, food limitations may have complicated responses for these species (Norris and Martin 2010). In addition, some of these species compete for cavities and subsequently can negatively affect each other's populations (Martin 1993, Martin et al. 2004, Aitken and Martin 2008). Interactions among members of the cavity-nesting community can strongly affect the availability of both cavities and food, which subsequently can result in distributional and abundance changes for secondary cavity nesters (Blanc and Walters 2008, Drever et al. 2009).

We observed increased occupancy for many open-cup, canopy insectivores (ruby-crowned kinglet [*Regulus calendula*] and yellow-rumped warbler) and omnivores (brown-headed

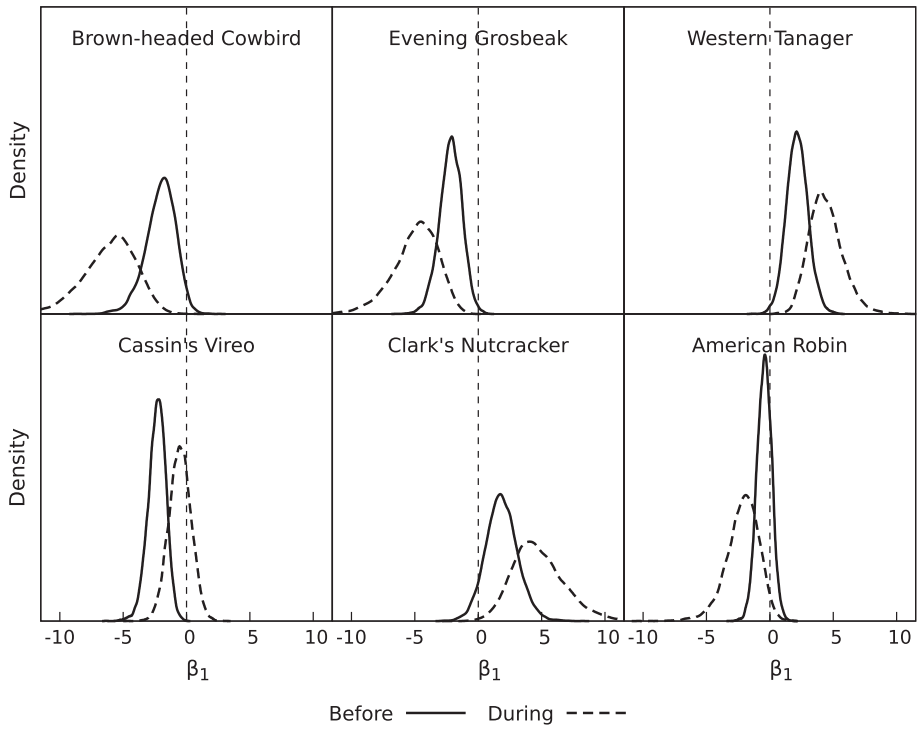

Fig. 3. Posterior distribution of β_{1i} (slope, or relationship with proportion ponderosa pine) before (solid line) and during (dashed line) mountain pine beetle epidemic for select avian species in a Montana study that took place before (2003–2006) and during (2009–2011) a mountain pine beetle epidemic. The top panel shows species with various augmented ponderosa pine relationships (change in magnitude without a change in direction) while the bottom panel shows one reduced ponderosa pine relationship (change from negative relationship to neutral; Cassin's vireo), and two new ponderosa pine relationships (change from a neutral to a positive or negative relationship; Clark's nutcracker and American robin).

cowbird, chipping sparrow, dark-eyed junco, evening grosbeak, Lincoln's sparrow [*Melospiza lincolnii*], and pine siskin) while we initially predicted mixed responses. Our study was conducted at a location where other live conifer (*Pseudotsuga menziesii*) and deciduous (*Populus tremuloides*) trees were available as foraging substrate for canopy-gleaning insectivores. Increased occupancy for insectivores and omnivores is consistent with findings in British Columbia, where retention of Douglas fir and especially aspen trees was likely essential to maintaining avian habitat in post-outbreak forests (Drever and Martin 2010, Edworthy et al. 2011). Unlike post-disturbance conditions created by wildfire, tree species unaffected by bark beetles (non-host species) continue to provide valuable avian habitat (Drever and Martin 2010, Edworthy et al. 2011, Kroll et al. 2012, Saab et al. 2014).

Increasing occupancy for omnivores potentially indicates that ground and shrub vegetation changes may have occurred earlier in the epidemic than we had predicted. Many of the species that thrived during the epidemic are widely distributed across North America, breed in relatively open coniferous forests, and have generalist foraging habits (e.g., brown-headed cowbird, chipping sparrow, dark-eyed junco, Northern flicker, and pine siskin; Dawson 1997, Middleton 1998, Nolan et al. 2002). Openings in the canopy created by the outbreak (Boucher and Mead 2006, Carlson et al. 2017) likely increased light availability and productivity of herbaceous- and shrub-derived seeds consumed by omnivores.

Several species experienced altered relationships with ponderosa pine during the outbreak. Western tanager was more positively associated with ponderosa pine during the

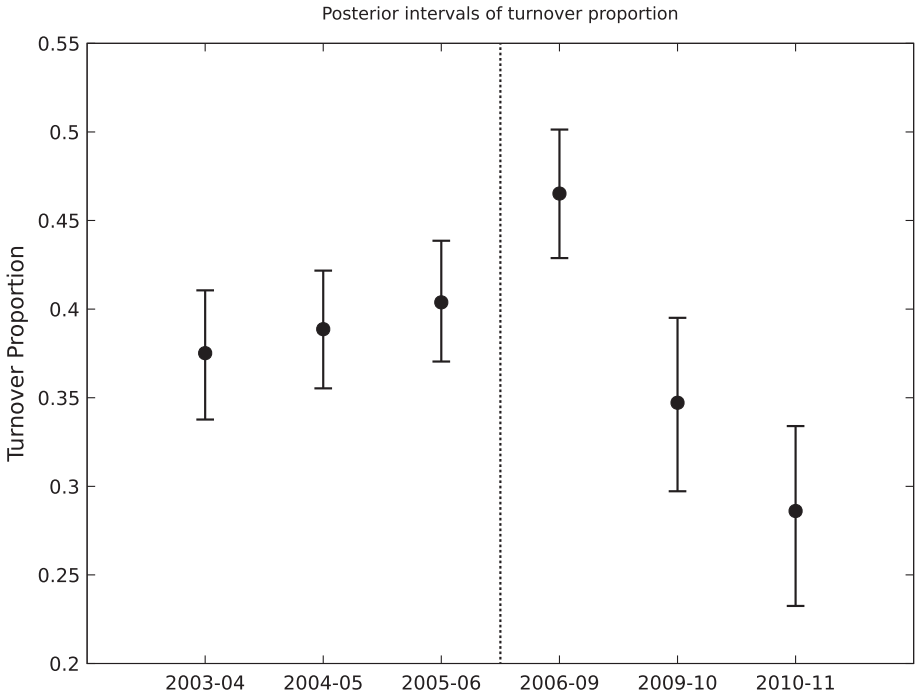

Fig. 4. Posterior means and 90% credible intervals for forest bird community turnover calculated using subsequent study years in a Montana study of bird populations. We define turnover as the average proportion of avian community members whose occupancy status changed between two points in time. The dashed line indicates the start of the mountain pine beetle epidemic. We did not collect data from 2007 to 2008, so one estimate of turnover was calculated over a 3-yr interval (2006–2009), while all others were calculated over a 1-yr interval.

epidemic than before the epidemic. This species favors open woodlands for breeding habitat (Hudon 1999), which might explain their shift into outbreak forest conditions. In contrast, brown-headed cowbird and evening grosbeak revealed stronger negative relationships with ponderosa pine during the epidemic. Nest parasitism opportunities for brown-headed cowbird likely declined in ponderosa pine forests because beetle-caused tree mortality reduced nesting habitat for cowbird host species in this region such as McGillivray's warbler (*Geothlypis tolmiei*), yellow-rumped warbler, dark-eyed junco, and hermit thrush (*Catharus guttatus*). Concomitant with the MPB epidemic in our study area was a western spruce budworm (*Choristoneura occidentalis*) outbreak (Aerial Detection Survey 2009; https://www.fs.fed.us/foresthealth/aviation/aerialsurvey.shtml) which affects Douglas fir. Spruce budworm is highly favored as a food source by evening grosbeaks (Gillihan and Byers 2001), which might have influenced their movement away from ponderosa pine and into Douglas fir stands. These relational differences with ponderosa pine suggest shifts in habitat use as new nesting and foraging resources became available.

Understanding transient occurrence dynamics during a perturbation offers insight into community resilience to environmental changes. Turnover in our system was high and consistent prior to the mountain pine beetle epidemic (Peterson et al. 2002, Tingley and Beissinger 2013, Jarzyna et al. 2015), and increased further during the mountain pine beetle epidemic. The fine-scale annual distributional shifts observed in our study may reflect an ability to capitalize on a patchy resource distribution, potentially indicating high resilience to novel stressors (La Sorte and Boecklen 2005). The high baseline turnover in our system may have reflected either dynamic ongoing disturbances (i.e., spruce budworm

defoliation), annual population fluctuations, or sampling variation (Maron et al. 2005).

High turnover estimates for western landbirds were also noted by Russell et al. (2009) in a prescribed fire study. The MPB epidemic was likely a more severe disturbance resulting in greater habitat change and subsequent species turnover than the prescribed burn, which may explain the brief increase in turnover we observed. However, we measured only occurrence in our study. Other studies that measure abundance, survival, or reproductive success will be necessary to provide a more nuanced view of resilience and stability.

Limitations and future directions

We found evidence of an average change in occurrence between the pre-epidemic and during-epidemic time periods for most (>70%, or 23 of 39) species. While these changes in occurrence cannot be directly linked to the mountain pine beetle epidemic, they might be suggestive of epidemic-related changes that we failed to detect due to small sample sizes, or due to environmental covariates that we failed to measure and incorporate in this analysis. A model incorporating multiple metrics, including an index of mountain pine beetle severity, snag densities, shrub and canopy cover, and time since disturbance, may provide better inference across the entire community of small landbirds. However, our results were largely similar to a recent study by Janousek et al. (2019) which used many of these metrics, indicating that a simple binary variable adequately captures variation in occupancy due to this beetle epidemic for many species.

While our study yields short-term information on avian responses, long-term responses must also be considered. Saab et al. (2019) found that an eventual decline in the pulse of mountain pine beetles may result in decreases of nest densities for woodpeckers several years after the peak of a beetle outbreak. In addition, dramatic changes in understory growth, downed wood, and canopy cover in the years following the epidemic (Stone and Wolfe 1996, Page and Jenkins 2007, Jenkins et al. 2008) might result in occupancy increases for ground- and shrub-nesting and foraging species on a longer time horizon than what we studied (Janousek et al. 2019).

Conclusions and management implications

Mountain pine beetle outbreaks increase woody fuels and litter depth of an area during the post-epidemic years (Jenkins et al. 2008, 2012, Hicke et al. 2012) which potentially lead to an increased risk of wildfire depending on site-specific conditions (Jenkins et al. 2014). Concern for wildfires following beetle outbreaks on public lands has provided reason for many agencies to consider logging as part of their post-beetle management plans. In addition, salvage logging of beetle-killed trees within two years of the peak in the beetle epidemic has been suggested as a means to maximize timber profits because timber quality deteriorates quickly (Chow and Obermajer 2007, Lewis and Thompson 2011). Suppression and salvage logging, however, remove trees and snags that provide nesting and foraging habitat for cavity-nesting birds and other wildlife species (Lindenmayer and Noss 2006, Saab et al. 2009). Thus, land managers face important challenges implementing post-beetle management policies, while concurrently maintaining wildlife habitat for species associated with dead trees.

In accordance with other studies, we found increases in occurrence for cavity-nesting species immediately after the MPB epidemic (Drever and Martin 2010, Edworthy et al. 2011, Janousek et al. 2019), suggesting that these species use beetle-killed pine during the timeframe that logging operations are likely to occur. Thus, maintaining stands of beetle-killed trees is likely to provide valuable resources for these species. However, we also detected declines in occurrence for Clark's nutcracker, a species of conservation concern in Montana (Montana Fish, Wildlife and Parks Department 2019) and a pine seed-consuming specialist (Giuntoli and Mewaldt 1978).

This study provides fundamental information for developing post-beetle management guidelines that will improve conditions for the persistence of avian populations within dry coniferous forests. The community-wide nature of this analysis elucidates the variety and degree of changes exhibited and gives managers more information upon which to base their decisions regarding post-beetle management activities. Decisions will be dependent on management objectives (Gregory et al. 2012). For instance, post-outbreak salvage or suppression logging operations that retain both bark beetle host and non-host tree

species likely will be the key to maximizing avian species richness in forests recently affected by mountain pine beetles (Drever et al. 2009, Edworthy et al. 2010, Kroll et al. 2012). For species of concern negatively impacted by a MPB epidemic, managers may consider targeted pre-epidemic logging to slow the invasion and use of pheromone treatments to maintain some patches of live pines (Seybold et al. 2018).

Finally, our species turnover results suggest that western landbird communities may be resilient to novel disturbances, provided patches of varying habitat types are available. The turnover results, combined with the large variation in species responses we observed even within guilds, suggest that this community possesses response diversity, which is hypothesized to lead to maintenance of ecosystem function even in the midst of disturbances (including experimental management interventions). Maintaining biodiversity is critical for harnessing this resilience and may be achieved by providing a mosaic of disturbed conifer, intact live conifer, and adjacent aspen forests that support a variety of western landbirds.

Acknowledgments

This work was supported by the US Forest Service, the US Forest Service Rocky Mountain Research Station, the Helena National Forest, Montana Fish, Wildlife & Parks, and the Montana Audubon Society. D. Pengeroth of the Helena National Forest was instrumental in coordinating fieldwork. C. deCaussin, S. Haywood, S. Hyland, L. Forrest, and others collected field data. We thank J. Hollenbeck for his help in developing an earlier version of this model and M. Higgs for her valuable contributions to this manuscript. Two anonymous reviewers and Dr. Alice Boyle provided valuable feedback on this manuscript.

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