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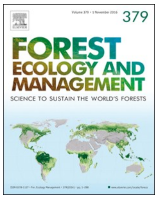

Avian relationships with bark beetle outbreaks and underlying mechanisms in lodgepole pine and spruce-fir forests of Colorado

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ABSTRACT

Bark beetle (*Dendroctonus* spp.) outbreaks have historically shaped the structure and function of western North American conifer forests by contributing to heterogeneous conditions needed to support various wildlife species. Previous studies of beetle impacts have primarily focused on pine-dominated systems within 1–6 years of outbreak, limiting our knowledge for informing wildlife habitat management to a relatively short timeframe and narrow range of forest types. Increases in extent and severity of outbreaks since 1900, caused in part by anthropogenic climate warming and forest management, elevates the value of understanding how bark beetle outbreaks impact wildlife populations. Our objectives were (1) to evaluate species and community relationships with outbreak severity (percent conifer mortality) and years since outbreak, (2) to evaluate potential environmental mechanisms underlying these relationships, and (3) to compare patterns across the two forest types for improved general knowledge. We studied avian species occupancy and richness in relation to outbreak conditions using two 18-year chronosequence datasets collected in 2013 and 2014 representing lodgepole forests (predominantly *Pinus contorta*) and spruce-fir forests (co-dominated by *Picea engelmannii* and *Abies lasiocarpa*) throughout Colorado. We employed hierarchical models to account for imperfect detection and spatial dependencies when analyzing population and community patterns apparent in data representing 73 bird species. We found various relationships and potential underlying mechanisms largely but not entirely consistent with *a priori* hypotheses based on species life histories and previous study. As expected, understory-associated birds related positively with outbreak conditions apparently following understory vegetative release. Consistent with our hypotheses, aerial insectivores and snag-associated species also related positively with outbreak conditions, although our data highlighted understory vegetation more so than canopy structure or snags as potential mechanistic factors. Contrary to our overall hypothesis for canopy-associated species, we did not observe many negative outbreak relationships for this group. Overall, bird species richness increased with years since outbreak, with clear increases in lodgepole forest. In contrast, the data from spruce-fir forest provided statistical support for fewer patterns (i.e., fewer with 90% credible intervals excluding zero), and they supported primarily negative relationships with outbreak severity. Our results suggest potential differences in ecological significance of bark beetle outbreaks in different forest types. At least in lodgepole forest, however, observed patterns were apparently consistent with the purported historical value of bark beetle outbreaks for promoting biodiversity (represented here by birds) despite recent increases in extent and severity.

1. Introduction

Disturbance strongly shapes vegetation structure and ecological function in western North American conifer forests (Saab and Powell, 2005; Bentz et al., 2009; Negrón and Fettig, 2014). Bark beetles (*Dendroctonus* spp.) are key disturbance agents, capable of causing extensive tree mortality spanning thousands of hectares (Taylor et al., 2006; Raffa et al., 2008). At low population densities, bark beetles typically attack old or weakened trees, which opens the canopy, allowing replacement by younger trees. Individual trees can survive bark beetle attacks, but when beetles overwhelm a host tree, their offspring can invade neighboring healthy host trees, precipitating exponential outbreak dynamics (Bentz et al., 2010).

Bark beetle outbreaks affect forest vegetation and related ecological processes at multiple spatial and temporal scales. Within impacted stands, extensive tree mortality leaves numerous standing dead trees (i.e., snags) and reduces canopy cover, allowing sunlight to penetrate and stimulate understory growth. Growth of young trees, shrubs, and herbaceous vegetation, and accumulation of coarse woody debris with the decay and fall of snags further change stand structure by opening the canopy and increasing understory volume and diversity (Raffa et al., 2008; Bentz et al., 2009). Additionally, because bark beetles are host-specific, outbreaks shift vegetation composition toward non-host tree species (e.g., aspen; *Populus tremuloides*). Successional processes reset by outbreaks may last a century or more before forests mature (Raffa et al., 2008). Forest stands impacted by outbreaks proceed through three distinct phases: (1) a green phase corresponding with initial bark beetle attack (post-outbreak years 0–1), (2) a yellow-orange

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or red phase (depending on forest type) when needles die but remain on trees (years 1–3), and a gray phase, which includes needle fall, decline of canopy cover, and vegetative succession (years 3 and onward; Schmid and Frye, 1977; Wulder et al., 2006; Simard et al., 2011). Forest landscapes represent shifting mosaics that include these various conditions maintained by periodic outbreaks (Saab et al., 2014; Johnstone et al., 2016).

Gradients in climate, topography, and soils give rise to geographic variability in forest structure, tree species, and associated bark beetle species (Kärvemo and Schroeder, 2010; Chapman et al., 2012). Recently, mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*D. rufipennis*) outbreaks have significantly impacted forests in the Rocky Mountains of western North America. The two most common and extensive forest types impacted by these species, respectively, are lodgepole forest, predominantly composed of lodgepole pine (*Pinus contorta*), and spruce-fir forests, co-dominated by Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*; Alexander et al., 1990; Alexander and Shepperd, 1990; Lotan and Chritchfield, 1990). Warming temperatures and changes in vegetation structure, due to fire suppression and other human impacts, have increased outbreak extent and severity in these forests (Fettig et al., 2007; Raffa et al., 2008; Bentz et al., 2009, 2010), although whether these changes exceed historical norms is uncertain (Kaufmann et al., 2008). In 1996–2014 specifically, 1.7 million ha of lodgepole and spruce-fir forests were impacted by mountain pine and spruce beetle outbreaks (Fig. 1; Harris, 2018).

Increasing temperatures and other anthropogenic stressors elevate the need to understand how bark beetle outbreaks interact with forest ecological integrity and function, and associated wildlife species. Lodgepole and spruce-fir forests occupy distinct elevational and climatic regions differing in available moisture, light, temperature, and productivity (Benedict, 2008: 499, 542). Warmer and drier conditions, monotypic tree species composition, and homogeneous stand structures make lodgepole forests particularly susceptible to bark beetle outbreaks (Bentz et al., 2009, 2010; Kärvemo and Schroeder, 2010). Additionally, impacted spruce-fir stands typically retain substantial live subalpine fir canopy, at least in the short term (Veblen et al., 1991). Such differences in abiotic drivers and biotic context could modulate post-outbreak vegetative response and thus affect ecological function. In particular, wildlife species may evolve different responses to disturbance in different systems (Bock and Block, 2005; Latif et al., 2016), which in turn can shape species adaptability and ecological integrity (Johnstone et al., 2016).

A central component of forest ecological integrity and function is the maintenance of wildlife populations and their interactions (Wurtzebach and Schultz, 2016). Wildlife studies therefore strongly inform forest conservation, and many ecologists study birds to understand forest ecology (Canterbury et al., 2000; Saab et al., 2005). Birds respond quickly to environmental change, and field surveys provide data on a wide range of species. Studies of birds suggest various population responses to outbreaks modulated by life history, providing insight into mechanisms underlying multiple aspects of ecological function (Matsuoka et al., 2001; Saab et al., 2014; Kelly et al., 2019; Mosher et al., 2019). For example, snags generated by outbreaks provide pulses of both foraging and nesting resources for woodpeckers, resulting in initial population increases followed by declines as snags decay and fall (Edworthy et al., 2011; Saab et al., 2014; Kelly et al., 2019). Bark beetles also provide temporarily abundant food for many insectivores, including woodpeckers and other species that nest in woodpecker-excavated cavities either in beetle-killed snags or adjacent aspen stands (Drever and Martin, 2010; Norris and Martin, 2012). Aerial insectivores forage in canopy openings generated with tree mortality, and growth of shrub and herbaceous vegetation in these openings provide resources for understory-associated species

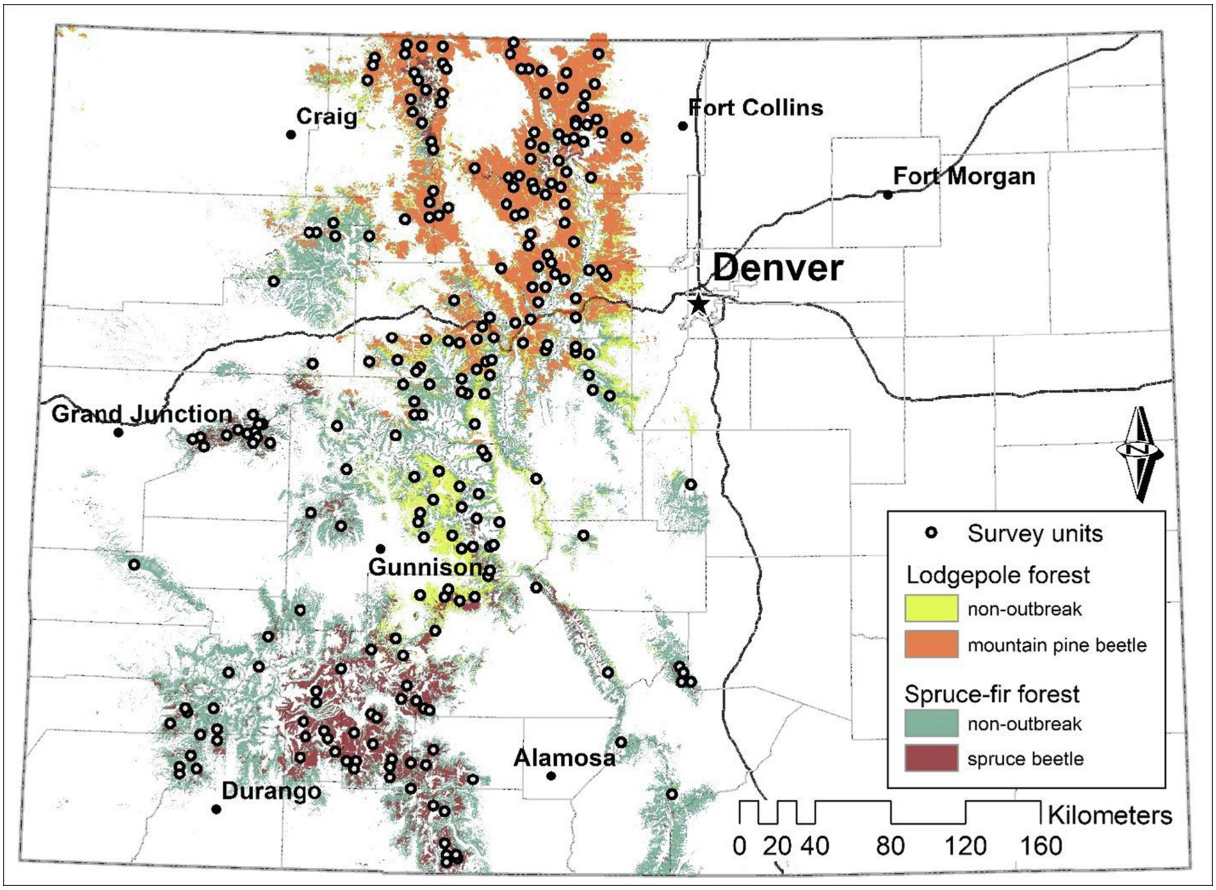

Fig. 1. Distribution of survey units (grid cells), forest types, and bark beetle outbreak conditions for investigating avian outbreak relationships in Colorado.

(Matsuoka et al., 2001; Saab et al., 2014). Conversely, declines in conifer seed production and canopy loss could impact seed-eating and canopy-associated species, although empirical relationships for these species are weaker and less consistent (Matsuoka et al., 2001; Saab et al., 2014). Outbreaks may additionally improve conditions for breeding birds by reducing abundance of nest predators, such as red squirrels (Matsuoka and Handel, 2007; Saab et al., 2014; but see Norris and Martin, 2014). Climatic gradients and associated variability in forest composition and outbreak dynamics can modulate how species interact with outbreaks (reviewed above; e.g., Kelly, 2016).

Bark beetle outbreaks influence how forests function to promote and maintain biodiversity by eliciting individual species responses (described above), giving rise to community patterns (Saab et al., 2014; Janousek et al., 2019; Mosher et al., 2019). Individual bird species responses therefore suggest mechanisms by which outbreaks shape forest biodiversity and ecological function. Many of the conditions under which species have evolved require natural disturbance (Bock and Block, 2005; Johnstone et al., 2016; Latif et al., 2016). Thus, beetle outbreaks contribute to the range of conditions needed to support the full complement of bird species associated with forests (Raffa et al., 2008; Bentz et al., 2009; Saab et al., 2014). Our understanding of how outbreaks affect forest communities remains limited. Empirical studies primarily document changes in species composition rather than species richness or diversity with outbreaks. These studies primarily represent pine forests 1–6 years after outbreak, however, limiting our ability to evaluate general patterns and broader implications for biodiversity (Werner et al., 2006; Saab et al., 2014; Kelly et al., 2019; Mosher et al., 2019).

Avian community responses to bark beetle outbreaks and stand structure may help inform forest management to meet wildlife conservation and forest health objectives (Samman and Logan, 2000; Bunnell, 2013). Managing bark beetle outbreaks often involves salvage logging for public safety and commercial purposes, planting trees after treatments to accelerate forest restoration, and regeneration harvest or other tree removal methods to promote recovery, regeneration and forest resiliency (Samman and Logan, 2000; USDA, 2011). Bird responses to beetle outbreaks provide insight into how avian species and communities might in turn respond to post-outbreak management of impacted areas (Martin et al., 2006). Understanding potential effects of management on birds would inform management decisions for multiple objectives in post-beetle forest environments (Samman and Logan, 2000; Lyons et al., 2008; USDA, 2011).

Considering the extent of bark beetle impacts in Colorado, we studied avian communities along a chronosequence of bark beetle impacts within lodgepole pine and spruce-fir forests. We aimed to improve general knowledge of how birds respond to beetle outbreaks. We therefore developed hypotheses reflecting current knowledge of avian-outbreak relationships and their underlying mechanisms, and then evaluated our hypotheses in light of observed patterns (Sells et al., 2018). Within this framework, our objectives were (1) to evaluate relationships of bird species occupancy and richness with outbreak conditions, (2) to evaluate potential mechanisms involving species life histories underlying observed relationships, and (3) to compare outbreak-related patterns and underlying mechanisms between lodgepole and spruce-fir forests. We considered linear and non-linear relationships with years since outbreak and interactions with outbreak severity (percent conifer mortality) to represent potentially complex resource dynamics for birds given post-outbreak successional processes (e.g., Saab et al., 2014; Ivan et al., 2018; Kelly et al., 2019). Finally, we considered the implications of our results for forest management.

2. Methods

2.1. Study area

We conducted our study in lodgepole and spruce-fir forests in the state of Colorado (Fig. 1) at elevations ranging 2590–3500 m. Lodgepole forests occur at lower elevations or on relatively dry or south-facing sites at higher elevations in northern Colorado. Conversely, spruce-fir forests in northern Colorado dominated higher elevations while also occurring on relatively cool, north-facing slopes at lower elevations. In southern Colorado, lodgepole forests did not occur, so spruce-fir forests dominated the entire higher elevation forest landscape. Large aspen stands, high elevation meadows, and open valleys commonly interspersed both forests. Douglas-fir (*Pseudotsuga menziesii*), bristlecone pine (*Pinus aristata*), limber pine (*Pinus flexilis*), and blue spruce (*Picea pungens*) also occurred sporadically.

Our study followed a wave of mountain pine beetle outbreaks and coincided with a peak in spruce beetle outbreaks (Harris, 2018), which impacted 1.4 and 0.3 million hectares of lodgepole pine and spruce-fir forests, respectively, in Colorado (Fig. 1). We restricted sampling to public lands managed by federal or state agencies. As such, surveyed areas had little human infrastructure development, but were subject to heavy recreational use and multi-use management. Climate was typical of continental mid-latitude regions at high elevation (Benedict, 2008:149–150), with mean July temperatures of 14.2 °C and mean January temperatures of −6.1 °C. A majority of annual precipitation (37.7 cm) fell as snow in October–April. Snow cover often persisted through early June, especially on north-facing slopes. Mean March snow depth recorded across all SNOTEL weather stations in the study area was 1.3 m. Remaining annual precipitation fell as regular afternoon thunderstorms during mid–late summer (NOAA, 2017). Ivan et al. (2018) provide additional details on our study area.

2.2. Sampling design

We developed our sampling design for assessing avian relationships with bark beetle outbreaks in tandem with a study investigating mammalian relationships (Ivan et al., 2018), wherein we modified the stratification scheme originally developed for the Integrated Monitoring in Bird Conservation Regions (IMBCR) program (Pavlacky et al., 2017). The sampling frame initially consisted of 15,113 1-km^2 grid cells on public land, > 2590 m elevation, and with ≥75% land cover of lodgepole pine or spruce-fir forest stratified by forest type (Ivan et al., 2018). Ivan et al. (2018) selected 150 1-km^2 cells from each stratum (300 total) using spatially balanced sampling (Stevens and Olsen, 2004), with selection weights adjusted to ensure sufficient sampling along a chronosequence of bark beetle impacts in both forest types (Derderian et al., 2016). We located our primary sampling units at a spatially balanced subset (*sensu* Stevens and Olsen, 2004) of Ivan et al.'s (2018) units (Table 1). Additionally, we excluded cells for which > 6 of the 16 equally spaced sampling points (see below) were severely disturbed or non-forest (≤1 unburned tree taller than head height per 150-m radius survey point). We thereby excluded from our sampling frame 16 grid cells severely burned by recent wildfire, and would have similarly excluded non-forested or severely disturbed (e.g., clear cut) forests in principle from the sampling frame had they been encountered. Within the remaining sampling frame, sampling units potentially included areas impacted by relatively low-severity disturbances other than bark beetle outbreak. By applying spatially

Table 1
Number of points and grid cells surveyed by forest type and outbreak history.

Forest	Grid cells		Points	
	outbreak	non-outbreak	outbreak	non-outbreak
Lodgepole	95	25	1071	601
Spruce-fir	88	31	837	751

Outbreak points were those that intersected an outbreak polygon delineated in National Forest Service Aerial Detection Surveys, and outbreak grid cells were those that included at least one outbreak point. 56% of non-outbreak points fell within outbreak grid cells.

balanced unit selection within this sampling frame, however, our units provided a representative sample of the landscape as a whole. Thus, our sampling aimed at measuring outbreak-related patterns of a magnitude detectable over and above other sources of variation characterizing the sampled landscape.

Primary sampling units were 239 1-km^2 grid cells each containing 16 evenly distributed survey points (4 × 4 array with 250 m spacing), where we centered circular point count plots (Table 1). We surveyed grid cells once each either in 2013 or 2014. We surveyed each point in each grid cell for six minutes during the breeding season (dates varied by elevation; Kingery, 1998) between 0.5 h before and five hours after sunrise. Surveyors recorded all individual birds by species detected during the 6-min survey period, along with distances to detected individuals and the survey minute (1,2, …, 6) each detection was recorded (for details, see Hanni et al., 2012). Surveyors also recorded detections of red squirrel (*Tamiasciurus hudsonicus*), an important nest predator for forest birds. Limitations imposed by land access, safety, time constraints, and the sampling frame (i.e., we did not survey points with ≤ 1 unburned tree taller than head height as noted above) sometimes prevented surveying all points within a grid cell. We required a minimum of six points to be surveyed in a grid cell to retain the cell in our sample. Thus, we surveyed 3260 points with a mean of 13.6 points surveyed per grid cell. Of these, 1908 points within 183 grid cells occurred within a beetle outbreak identified during aerial detection surveys conducted from 1995 onwards (hereafter ADS; Table 1; USFS Rocky Mountain Region, 2018).

2.3. Outbreak and vegetation data

We compiled two outbreak metrics and nine metrics of vegetation structure and composition to serve as covariates for modeling avian species occupancy and richness (Table 2). We measured all vegetation metrics and Dead Conifer (DCon) using ocular field estimates for 50 m-radius (0.8 ha) plots centered on survey points (Hanni et al., 2012). We derived years since outbreak (YSO) for each point survey as years elapsed since the point first intersected an ADS outbreak polygon (range 0–18). If none of the points within a grid cell intersected any outbreak polygons, we assigned YSO = −1 for all points in the cell. For points that did not intersect any outbreak polygons but whose neighbors within the same grid cell did, we considered YSO values missing and imputed them using a uniform prior distribution bounded by the YSO range for all other points within the same grid cell that did intersect ADS polygons. This approach assumes sampling units were rarely if ever impacted by more than one distinct outbreak event within the 18-year chronosequence period represented in this study.

We wanted DCon to reflect outbreak severity (i.e., percentage of tree mortality caused by bark beetles) as closely as possible. Upon exploring the distribution of DCon and YSO values, we noted a drop in the range of DCon values in later years, potentially reflecting snags falling with time since outbreak (Fig. 2). To limit the effects of snag fall, we excluded from analysis DCon values from late-outbreak years (YSO > 12 in lodgepole; YSO > 9 in spruce-fire). We accordingly excluded 53 and 91 late-outbreak DCon values in lodgepole pine and spruce-fir forest, respectively. With excluded late-outbreak values and missed field measurements, we had to impute 57 and 105 missing DCon values in lodgepole pine and spruce-fir forests, respectively (missing data imputation described in *Data analysis*).

The two outbreak metrics, DCon and YSO, mostly complemented each other but also overlapped somewhat in information content. DCon primarily quantified outbreak severity whereas YSO primarily quantified time since outbreak. Years since outbreak also contrasted outbreak (YSO ≥ 0) with non-outbreak (YSO = −1) forest stands. Whereas DCon represented relatively fine-scale measurements recorded on the ground, however, YSO provided coarser scale information apparent from aerial surveys. Consequently, we recorded some beetle mortality (DCon > 0) in non-outbreak cells (YSO = −1), presumably representing incipient outbreaks or areas with relatively limited mortality not detected in aerial surveys.

2.4. Hypotheses and mechanisms

To effectively contribute to scientific knowledge (Sells et al., 2018), we developed and evaluated *a priori* hypotheses in light of observed statistical patterns for avian-outbreak relationships and their underlying mechanisms. Because both outbreak metrics contrasted outbreak versus non-outbreak forest stands (see above), hypothesized avian relationships with DCon and YSO largely overlapped. Additionally, we hypothesized non-linear relationships with YSO, reflecting the temporal component of this metric and potential non-linear resource dynamics through various outbreak phases and associated vegetative succession (Schmid and Frye. 1977; Wulder et al., 2006; Simard et al., 2011).

We developed general hypotheses for nesting and foraging life

Table 2

Outbreak and vegetation covariates used to model avian species occupancy and richness in subalpine forests of Colorado.

Covariate (abbrev.)	Description	Role
Dead conifer (DCon)	Percent of conifer canopy (canopy provided by standing conifer trees) that is dead	outbreak
Years since outbreak (YSO)	Years since beetle outbreak initiation detected during aerial detection surveys[D]	outbreak
Canopy cover (CanCov)	Total canopy cover (%)	vegetation
Aspen[A]	Percent of canopy composed of aspen	vegetation[E]
Spruce[A]	Percent of canopy composed of Englemann spruce	vegetation[E]
Pine[A]	Percent of canopy composed of pine	vegetation[E]
Shrub cover (ShrubCov)	Total shrub cover (%)	vegetation
Conifer shrubs (ConShrb)[B]	Percent of shrubs composed of conifer saplings	vegetation
Herbaceous cover (Herb)[C]	Percent of ground covered by live and dead grass and forbs (%)	vegetation
Woody stem cover (Woody)[C]	Percent of ground covered by woody vegetation < 0.25 m and < 15.2 cm diameter (%)	vegetation
Dead and down (DeadDown)[C]	Percent of ground covered by fallen woody debris or standing dead wood > 15.2 cm diameter and (if standing) < 0.25 m high (%)	vegetation
Day of year (DOY)	Number of days elapsed since January 1	detection only
Time of day (Time)	Number of minutes elapsed since 00:00 h	detection only

All spatial covariates (i.e., not YSO, DOY, and Time) were measured in the field for 50 m-radius plots centered on survey points (Scale = 0.8 ha).

[A] The remainder of these three variables (100 minus their sum) was primarily subalpine fir (*Abies lasiocarpa*). In lodgepole pine forest, Pine and Spruce were strongly correlated (r = −0.74), so only Pine was considered.

[B] All shrubs that are not conifer saplings are broad-leafed deciduous species.

[C] The remainder of these three variables (100 minus their sum) is litter.

[D] We acknowledge that bark beetle outbreaks transpire over several years, but we assigned YSO = 0 to the first year outbreak was detected during aerial detection surveys for the sake of analysis.

[E] Canopy composition covariates were included in outbreak models to account for outbreak susceptibility.

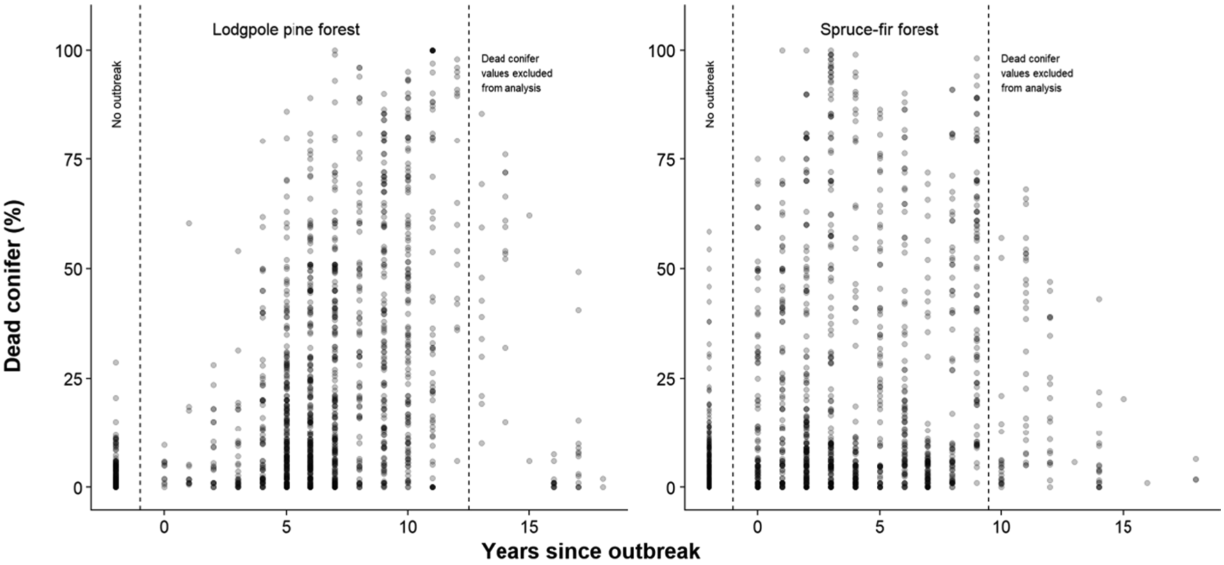

Fig. 2. Scatter plots showing the joint distribution of DCon (Dead conifer [%] recorded on the ground) and YSO (Years since outbreak recorded during aerial surveys) values for survey points. Where possible, points that did not intersect an outbreak were assigned YSO equaling the median of neighboring points in the same grid cell that did intersect an outbreak. We assigned YSO = −1 where none of the points in a grid cell intersected any outbreak polygons delineated during aerial surveys. Vertical lines distinguish points in non-outbreak grid cells and points for which DCon values were excluded from analysis (see text for rationale). These data represent three outbreak phases: green (i.e., initial attack; YSO = 0–1), red or yellow-orange (i.e., needle death; YSO = 1–3), and gray (i.e., needle fall, snag decay and fall, and subsequent vegetative succession; YSO ≥ 3). Additionally, non-outbreak points (YSO = −1) likely represented some incipient (green phase) outbreaks, particularly in spruce-fir forest where early phase spruce beetle outbreaks are more difficult to detect in aerial surveys.

history groups to inform species-level hypotheses (described below). We hypothesized positive outbreak relationships (linear DCon, and linear or non-linear YSO relationships) for primary and secondary cavity nesting species, including snag-foraging woodpeckers, species that nest and forage in the understory, and aerial insectivores, whereas we hypothesized negative outbreak relationships for canopy-associated species and species that feed on conifer seeds (Appendix S1: Table S1).

We informed species-level hypotheses with both life history group-level hypotheses and species-specific patterns reported in the literature (Appendix S1: Table S2; Matsuoka et al., 2001; Saab et al., 2014; Wickersham, 2016; Janousek et al., 2019; Kelly et al., 2019; Rodewald, 2019). Recognizing that species do not fit perfectly within broad life history categories, our hypotheses emphasized species-specific patterns reported in the literature (i.e., habitat associations and empirical outbreak relationships) where they contradicted life-history based expectations. We developed hypotheses for the 73 species detected at least once in either lodgepole or spruce-fir forest. Where expectations were ambiguous due to inconsistent expectations based on nesting versus foraging life histories or varying patterns reported in the literature, we refrained from hypothesizing any relationships (i.e., hypothesized relationship = “unknown”). Under this framework, we hypothesized positive and negative outbreak relationships for 46 and seven species, respectively. Hypotheses for positive relationships included “peaked positive” hypotheses for seven cavity nesting species and “lagged positive” hypotheses for 25 species that nest or forage in the understory. Although we did not explicitly hypothesize interactive outbreak relationships (DCon × YSO), we allowed that species could exhibit hypothesized outbreak relationships (positive or negative) at more severely impacted (higher DCon) sites. We categorized hypotheses for remaining species as either unknown (16 species) or no relationship (four species). Because we hypothesized positive outbreak relationships for most species, we also expected species richness would increase following beetle outbreak at impacted sites. Given the paucity of published studies in spruce-fir (Matsuoka et al., 2001; Werner et al., 2006), we did not attempt to hypothesize similarities or differences between lodgepole and spruce-fir forests in outbreak relationships, although we did inform hypotheses with relevant literature across forest types.

Along with hypothesizing outbreak relationships, we evaluated potential mechanistic pathways for outbreak relationships. We primarily considered mechanistic pathways involving changes in vegetation structure or composition (Appendix S1: Fig. S1). We considered both avian occupancy relationships with vegetation metrics and vegetation relationships with outbreak metrics (DCon, YSO) when evaluating potential mechanisms (Appendix S1: Table S3). We analyzed species-outbreak relationships separately from species-vegetation relationships to minimize confounding outbreak relationships with their underlying mechanisms. Additionally, because birds can adjust their breeding site selection in direct response to the distribution of nest predators (Schmidt et al., 2006; Ibáñez-Álamo et al., 2015), we evaluated potential mechanistic pathways involving nest predators. We summarized outbreak and vegetation relationships for potential nest predators detected during our surveys (Richardson et al., 2009), i.e., potential avian predators (Appendix S1: Table S2) and red squirrel (abundance relationships analyzed separately; Appendix S2).

2.5. Bird community occupancy models

Model structure. – We analyzed breeding bird distributions at two spatial scales using multispecies occupancy models (Zipkin et al., 2010; Mordecai et al., 2011) implemented in a Bayesian state-space framework (Royle and Kéry, 2007). Occupancy models leverage replicate survey data to estimate species detectability (p) (MacKenzie et al., 2002; Tyre et al., 2003; MacKenzie et al., 2018). Here, minute intervals within 6-min surveys served as replicates for estimating detectability following a removal design (Rota et al., 2009; Pavlacky et al., 2012). At a local scale, occupancy of 4.9 ha point count plots represented the probability the species is present and available for detection during a 6-min survey given species occupancy of the 1-km^2 grid cell. Point occupancy likely correlates with local abundance for species with territories $\gtrapprox$4.9 ha, for which we are unlikely to detect $>$ 1 individual at any one point and spacing between points limits detection of the same individual at multiple neighboring points (Linden et al., 2017; Latif et al., 2018). We focused analysis and inference at the local-scale point level, where our data afforded maximum degrees of freedom for estimating non-linear relationships with YSO. Following our sampling design, however, we conditioned point occupancy on larger scale occupancy of grid cells to account for coarse-scale variability and spatial correlation among points within a grid cell (Pavlacky et al., 2012; Pavlacky et al., 2017).

We used a hierarchical multispecies structure to estimate species-specific parameters as random variables governed by community level hyper-parameters. By informing species parameters with community-level parameters that quantify variation among species, we improved the precision of species-specific parameter estimates, particularly for rare species (Dorazio and Royle, 2005; Zipkin et al., 2010). We excluded raptors, owls, grouse, cranes, and water birds because they were not reliably detectable by our survey methods. We only included species known to breed in our study area, but we augmented data to include undetected potential breeders to fully correct species richness estimates for imperfect detection (Dorazio and Royle, 2005; Zipkin et al., 2010). The potential super-community (including potential breeders) was $M = 106$ species representing those detected in lodgepole and spruce-fir forests during 2010–2017 IMBCR surveys within Bird Conservation Region 16 (for forest classification protocol, see Hanni et al., 2012; Table 6).

We considered detection data, $\mathbf{y}$, to represent 3 dimensions; $y_{ijk} = 1$ indicated species i ($i = 1, \ldots, M$; $M = 106$) was detected at point j ($j = 1, \ldots, J$; $J = 16$) within grid cell k ($k = 1, \ldots, K$; for K, see Table 1). A parallel array, $\mathbf{R}$, indicated the minute interval when detections were recorded ($r_{ijk} \in \{1, 2, \ldots, 6\}$ when $y_{ijk} = 1$ or $r_{ijk} = 6$ when $y_{ijk} = 0$). We modeled data generation as

$$y_{ijk} | u_{ijk} \sim \ Binomial(r_{ijk}, p_{ijk} \times u_{ijk}) \tag{1}$$

where p_{ijk} is the detection probability for species i given occupancy of point j in grid k (i.e., given $u_{ijk} = 1$). We modeled point occupancy as

$$u_{ijk} | z_{ik} \sim \ Bernoulli(\theta_{ijk} \times z_{ik}) \tag{2}$$

where θ_{ijk} is the point occupancy probability for species i given occupancy of grid cell k (i.e., given $z_{ik} = 1$). We modeled grid cell occupancy as

$$z_{ik} | w_i \sim \ Bernoulli(\psi_{ik} \times w_i) \tag{3}$$

where ψ_{ik} is the grid cell occupancy probability for species i given that species i belongs in the super community (i.e., given $w_i = 1$). Finally, we modeled whether species i belonged to the super community as $w_i \sim \ Bernoulli(\Omega)$ (Zipkin et al., 2010, Dorazio et al., 2011).

We modeled detection probability and point occupancy as logit-linear functions of covariates (Table 2):

$$logit(p_{ijk}) = \alpha_{0,i} + \boldsymbol{\alpha_i} \times \boldsymbol{X_{jk}} \tag{4}$$

and

$$logit(\theta_{ijk}) = \beta_{0,i} + \boldsymbol{b_i} \times \boldsymbol{X_{jk}} \tag{5}$$

and grid cell occupancy without covariates:

$$logit(\psi_{ik}) = \delta_{0,i} \tag{6}$$

where $\alpha_{0,i}$, $\beta_{0,i}$, and $\delta_{0,i}$ are intercept parameters, $\boldsymbol{X}$ represent arrays of covariate values, and $\boldsymbol{\alpha_i}$ and $\boldsymbol{\beta_i}$ are species-specific vectors containing covariate relationships. We modeled parameters at all three levels as species-specific normal random effects. We used point-level covariates for modeling detection probability (p) and point occupancy (θ; Table 2).

Analogous to single-scale multispecies models (Zipkin et al., 2010; Dorazio et al., 2011), we informed species parameter estimates by incorporating bivariate correlation terms into community level hyper-parameters. These correlation terms related species detectability (p) with point occupancy (θ; $\rho_{\theta p}$), and point occupancy with grid occupancy (ψ; $\rho_{\psi\theta}$). Because rare species tend to be relatively rare across spatial scales and less detectable than common species, we expected models to estimate positive values $\rho_{\theta p}$ and $\rho_{\psi\theta}$. Concomitantly, including these terms ensured occupancy and detectability estimates for rare species would primarily be informed by other rare species more so than common species, improving their accuracy and the accuracy of species richness estimates. We assumed a multivariate logit-scale normal distribution, where $\rho_{\psi p} = 0$, $\rho_{\theta p}$ ranged between $\alpha_{0,i}$ and $\beta_{0,i}$, and $\rho_{\psi\theta}$ ranged between $\beta_{0,i}$ and $\delta_{0,i}$.

Species richness. – We inferred richness patterns represented in our models by plotting richness estimates in relation to covariates. Because we only analyzed point-level occupancy relationships, we primarily reported species richness patterns at this level. We summarized two types of richness estimates. Finite-sample estimates quantified partially observed richness at surveyed points: $\widehat{N}_{\theta,\mathrm{obs},jk} = \sum_{i=1}^{M} u_{ijk}$. We also predicted richness for potential points outside the sample actually surveyed: $\widehat{N}_{\theta,\mathrm{pred},jk} = \sum_{i=1}^{M} \psi_{ik} \times \theta_{ijk}$. By plotting these estimates along covariate gradients, we summarized emergent richness patterns implied by model-estimated species occupancy relationships. Finally, we supplemented inference from point-level patterns with finite-sample grid-level richness estimates ($\widehat{N}_{\psi,k} = \sum_{i=1}^{M} z_{ik}$) for outbreak and non-outbreak grid cells.

Model fitting and statistical inference. – As stated above, we analyzed species occupancy and richness relationships with outbreak separately from vegetation metrics to minimize confounding outbreak relationships with their underlying mechanisms. Accordingly, we first fit a model that quantified bird species occupancy relationships with outbreak covariates (Role = outbreak in Table 2; hereafter "outbreak models"). This model included linear relationships (DCon + YSO), non-linear relationships with YSO (YSO^2 + DCon × YSO) (hereafter "outbreak relationships"), and linear detectability relationships with outbreak covariates (DCon + YSO). Additionally, we included canopy composition covariates in outbreak models to account for bark beetle host prevalence (Aspen + Spruce + Pine; for variable descriptions, see Table 2). Spruce and Pine variables were strongly negatively correlated ($r = -0.74$) in lodgepole forest, so we only considered Pine in lodgepole forest models. Next, we fit a second model that quantified relationships with vegetation covariates (hereafter "habitat relationships") to inform potential mechanistic factors modulating outbreak relationships (hereafter "habitat models"). These models included linear occupancy relationships with all vegetation covariates (Role = "vegetation" in Table 2), and CanCov and ShrubCov as detection covariates. For both outbreak and habitat models, we included quadratic effects of survey date and timing on detection probability ($\text{DOY} + \text{DOY}^2 + \text{Time} + \text{Time}^2$), allowing for potential peaks in singing activity both within a morning and across the breeding season. We scaled all continuous covariates to mean = 0 and SD = 1 for analysis, and considered them statistically supported where their 90% Bayesian credible intervals (hereafter 90% BCIs) excluded zero. Similarly, we inferred statistical support for species richness patterns from posterior median estimates and 90% BCIs for community mean covariate relationships.

For outbreak models, we defined priors for imputing missing covariate values when fitting models (Gelman and Hill, 2007; Link and Barker, 2010). As described above, we set YSO = −1 for points in non-outbreak grid cells. We imputed missing YSO values in outbreak grid cells using *Uniform* priors bounded by min and max values for neighboring points within the same grid cell. We imputed missing DCon values using *Normal*(μ, SD) priors, where μ and SD are the mean and standard deviation for other points with equivalent outbreak history, YSO = −1 or YSO > −1 (e.g., if a point missing data was not impacted [YSO = −1], we used the mean and standard deviation for all other points that were also not impacted). Computation time was prohibitively long for habitat models with model-based data imputation, so we instead filled missing values with the mean for neighboring points within the same grid prior to model fitting.

We sampled posterior parameter distributions for all models using JAGS v.4 (Plummer, 2003) programmed from R (Kellner, 2017). We used independent non-informative priors for all parameters (for priors, see Appendix S3; for model code, see Appendix S4). We ran three parallel MCMC sampling chains of length = 10,000 each, burn-in 1000, and thinning = 10 to sample posterior distributions. We verified convergence for all parameters in all models using the criterion of $\widehat{R} \leq 1.1$ (Gelman and Hill, 2007).

3. Results

Surveyors detected 73 bird species during the study period (Appendix S1: Table S2). The five most frequently detected species were ruby-crowned kinglet, dark-eyed junco, yellow-rumped warbler, mountain chickadee, and hermit thrush (for taxonomic names, see Appendix S1: Table S2). As expected, community occupancy models estimated and accounted for positive correlations of detectability with point occupancy and point with grid cell occupancy (Appendix S5: Table S1). Posterior median detectability estimates for a 6-min survey ranged 0.27–0.99, and models accounted for statistically supported covariate relationships with detectability for 19 species (Appendix S5: Tables S2–S5). Survey units represented a broad range of outbreak and vegetation conditions (Appendix S6).

3.1. Outbreak relationships

We found statistically supported outbreak relationships for 28 bird species (Appendix S7: Fig. S1). Eleven species exhibited statistically supported non-linear outbreak relationships (i.e., supported $\widehat{\beta}_{\mathrm{YSO}^2}$ or $\widehat{\beta}_{\mathrm{DCon} \times \mathrm{YSO}}$). We found more supported outbreak relationships in lodgepole pine (22 species; Fig. 3) than in spruce-fir (10 species; Fig. 4) forest. Outbreak models accounted for statistically supported relationships with canopy composition for 29 and 24 species in lodgepole and spruce-fir forests, respectively (Metadata S1).

Lodgepole. – We primarily observed positive occupancy relationships with YSO in lodgepole forest; 17 species exhibited such relationships, whereas only three species exhibited negative outbreak relationships (two with YSO and one with DCon), and one species (yellow-rumped warbler) exhibited an interactive relationship (Fig. 3, Appendix S7: Fig. S1). Statistically supported outbreak relationships were consistent with hypotheses for 15 species (14 positive, one negative) and inconsistent with hypotheses for three species (one positive and two negative where the opposite was hypothesized; Table 3). The data supported outbreak relationships for an additional four species lacking clear *a priori* hypotheses (three positive, one negative). Of 21 species for which we hypothesized non-linear (peaked or lagged) positive YSO relationships and had ≥10 detections, only green-tailed towhee and Townsend's solitaire exhibited relationships matching our hypotheses (lagged positive). Hermit Thrush occupancy favored early-to-mid-YSO sites instead of late-YSO sites in contrast with our hypothesis, and western tanager exhibited a lagged positive YSO relationship where no such relationship was hypothesized. An interactive outbreak relationship matched our hypothesis for yellow-rumped warbler in that occupancy declined with increasing YSO at severely impacted sites, but contradicted our hypothesis in that occupancy related positively with DCon at early-YSO sites (Fig. 3).

Positive YSO relationships in lodgepole forest spanned nesting and foraging life history groups (Tables 3, 4). Posterior median estimates for a mean linear (first-order) YSO effect were positive for all groups and statistically supported for all except two (secondary cavity nesting and conifer-seed foraging species; Table 4). In contrast, the data did not support other outbreak effects (mean DCon, YSO^2, or DCon × YSO) for any group (Table 4). Species exhibiting negative or non-linear positive outbreak relationships represented several life history groups with none clearly favored (Table 3).

Spruce-fir. – Species related more so with DCon than YSO (Fig. 4, Appendix S7: Fig. S1), and outbreak relationships were more often negative (five species) than positive in spruce-fir forest (four species; Table 3). Statistically supported outbreak relationships matched our hypotheses for five species (four positive, one negative) but contradicted hypotheses for another five species (all negative where positive relationships hypothesized; Table 3). The data supported outbreak relationships for an additional two species lacking clear *a priori* hypotheses. These two species (common raven, golden-crowned kinglet) along with Clark's nutcracker exhibited interactive relationships whereby their occupancy favored less DCon with increasing YSO (Fig. 4). Of 19 species for which we hypothesized non-linear (peaked or lagged) positive YSO relationships and had ≥ 10 detections, only dark-eyed junco exhibited a relationship matching our hypothesis (lagged positive). Red-breasted nuthatch also exhibited a lagged rather than peaked positive relationship (Table 3, Appendix S7: Fig. S1), although this lagged increase was more apparent at low-DCon sites (Fig. 4). We observed no peaked positive outbreak relationships for species in spruce-fir forest.

Six of eight species exhibiting negative outbreak relationships in spruce-fir forest build open-cup nests in the canopy, and five of eight represent canopy-associated insectivores (bark- or foliage-gleaning) or conifer-seed eating species (Table 3; red-breasted nuthatch are both). The data supported negative average (mean) DCon effects for five life history groups (all except woodpeckers, aerial insectivores, and understory-foraging species; Table 4), and negative DCon × YSO effects for three of these groups. The secondary cavity nesting group exhibited a supported negative DCon × YSO relationship on average even though individual species in this group did exhibit supported DCon × YSO relationships on their own (e.g., red-breasted nuthatch). The four species exhibiting positive outbreak relationships in spruce-fir forest represented distinct nesting and foraging life histories (American three-toed woodpecker, red-breasted nuthatch, pine siskin, and dark-eyed junco).

Species richness. – Bird species richness showed statistically supported outbreak relationships largely reflecting predominant species occupancy relationships (summarized above) in lodgepole and spruce-fir forests (Fig. 5, Appendix S3). Consistent with our general hypothesis of a positive outbreak relationship, point-level species richness in lodgepole increased by approximately four species with increasing YSO over the 18-year post-outbreak chronosequence. Grid-level species richness at outbreak (posterior median [90% BCI] = 24.88 [24.01, 25.99]) exceeded estimates for non-outbreak grid cells (23.76 [22.48, 25.16]) by 1.16 (0.16, 2.13) in lodgepole forest.

In spruce-fir forest, species richness declined by approximately one species with outbreak severity, contradicting our hypothesis for species richness (Fig. 5, Appendix S3). We did estimate somewhat greater species richness at later YSO sites in spruce-fir forest, but this relationship was smaller in magnitude and not as statistically clear as in lodgepole forest (Appendix S3). We estimated similar grid-level species richness at outbreak (posterior median [90% BCI] = 24.25 [23.51, 25.11]) and non-outbreak grid cells (23.97 [23.03, 24.97]; difference = 0.31 [-0.44, 1.05]) in spruce-fir forest.

3.2. Potential mechanisms

Upon considering avian habitat relationships (Appendix S8) and vegetation-outbreak relationships (Appendix S9), we identified potential mechanisms underlying outbreak relationships for 16 species and various species groups in lodgepole forest (Table 5). Potential mechanistic factors for positive YSO relationships (the most widespread outbreak relationship observed) primarily involved relationships with percent canopy composed of pine (hereafter pine canopy; negative), conifer sapling dominance of the shrub layer (hereafter conifer-shrub dominance; negative), and herbaceous and woody ground cover (both positive). We identified some combination of these as the potential mechanistic factors for all species groups defined by life history or hypothesized outbreak relationships exhibiting a positive YSO relationship. Positive relationships with shrub cover provided a potential

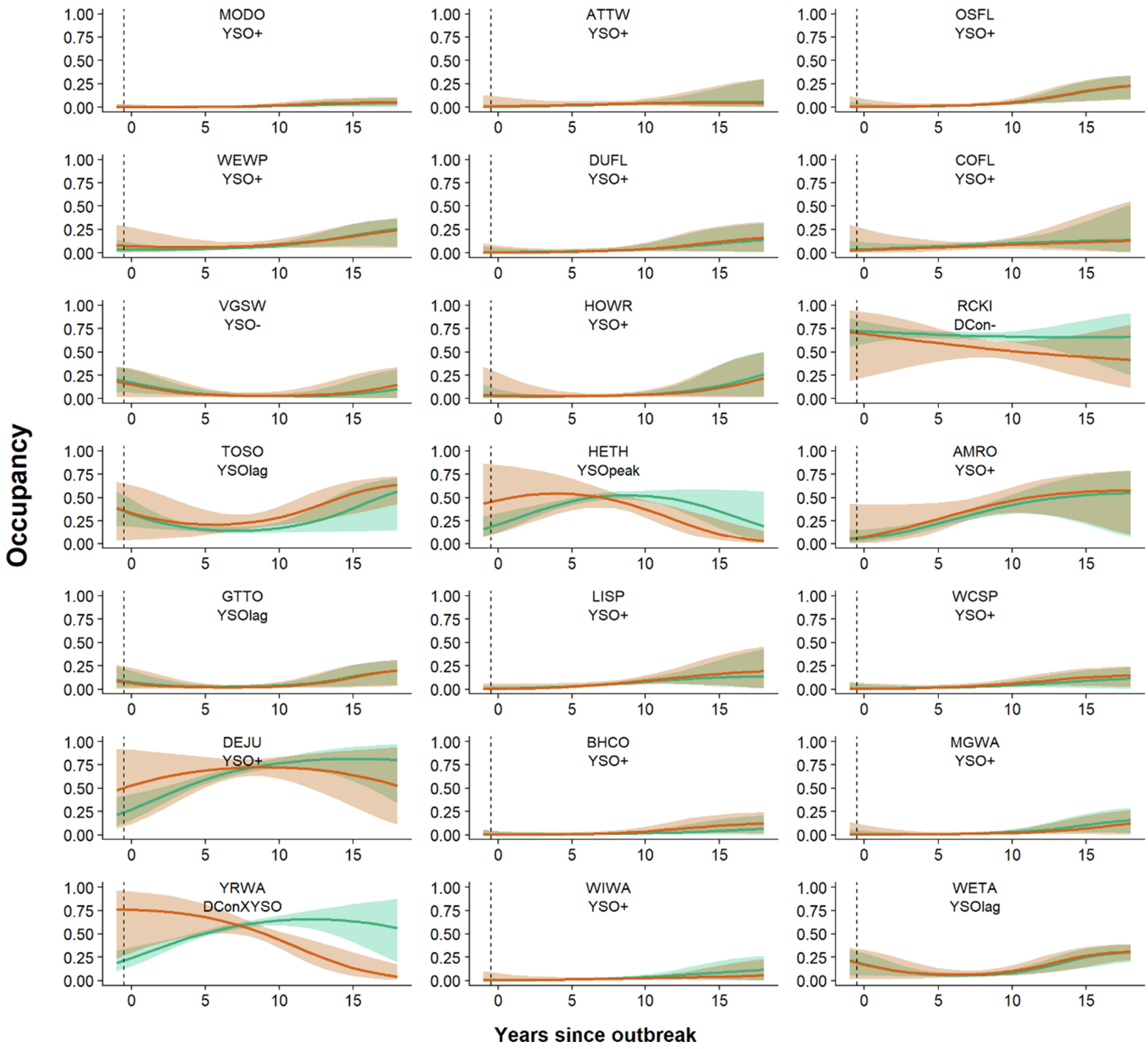

Fig. 3. Predicted occupancy probabilities (with 90% Bayesian credible intervals) for 21 species with statistically supported outbreak relationships in lodgepole forest. Species are mourning dove (MODO), American three-toed woodpecker (ATTW), olive-sided flycatcher (OSFL), western wood-pewee (WEWP), dusky flycatcher (DUFL), cordilleran flycatcher (COFL), violet-green swallow (VGSW), house wren (HOWR), ruby-crowned kinglet (RCKI), Townsend's solitaire (TOSO), hermit thrush (HETH), American robin (AMRO), green-tailed towhee (GTTO), Lincoln's sparrow (LISP), white-crowned sparrow (WCSP), dark-eyed junco (DEJU), brown-headed cowbird (BHCO), MacGillivray's warbler (MGWA), yellow-rumped warbler (YRWA), Wilson's warbler (WISA), and western tanager (WETA). Plots show relationships with YSO (Years since outbreak) in areas with low (green; percent dead conifer = 0) versus high (red; percent dead conifer = 100) beetle impact. The dashed line separates beetle-outbreak (YSO ≥ 0) from non-outbreak (YSO = −1) forest. Secondary labels indicate outbreak relationships that were statistically supported for each species: positive or negative YSO (YSO+, YSO-), lagged positive YSO (YSOlag), peaked positive YSO (YSOpeak), negative DCon (DCon-), and DCon × YSO interaction (DCon × YSO).

mechanism for open-cup understory species relating positively with YSO. A negative relationship with percent canopy composed of aspen (hereafter aspen canopy) provided a potential mechanism for a secondary decline in occupancy at later-YSO sites (negative YSO^2 relationship) for hermit thrush, an understory-associated species. Relationships with conifer-shrub dominance (negative), pine canopy (negative), herbaceous cover (positive), and woody ground cover (positive) provided potential mechanisms for non-linear YSO relationships for yellow-rumped warbler and western tanager, both canopy-associated species.

In spruce-fir forests, we most frequently identified negative relationships with conifer-shrub dominance as a potential mechanistic factor underlying negative DCon relationships (Table 5). Negative relationships with conifer-shrub dominance provided potential mechanisms for open-cup nesters in the canopy and understory, foliage or bark insectivores, species for which we hypothesized positive outbreak relationships, and warbling vireo, an open-cup canopy nesting foliage insectivore. Positive relationships with canopy cover provided a potential mechanism for negative DCon relationships for foliage and bark insectivores and Steller's jay, an open-cup canopy nesting species. A positive relationship with woody ground cover potentially explained a negative DCon relationship for pine siskin, a canopy nesting and conifer-seed eating species. A positive relationship with herbaceous cover provided a potential mechanism for a lagged increase in occupancy with increasing YSO relationships for dark-eyed junco, an understory-associated species.

Upon considering habitat relationships (Appendix S8) and vegetation-outbreak relationships (Appendix S9), we identified potential mechanisms underlying species richness relationships with outbreak covariates in both forest types (Table 5). In lodgepole forest, negative relationships with pine canopy and conifer-shrub dominance, and positive relationships with herbaceous and woody ground cover provided

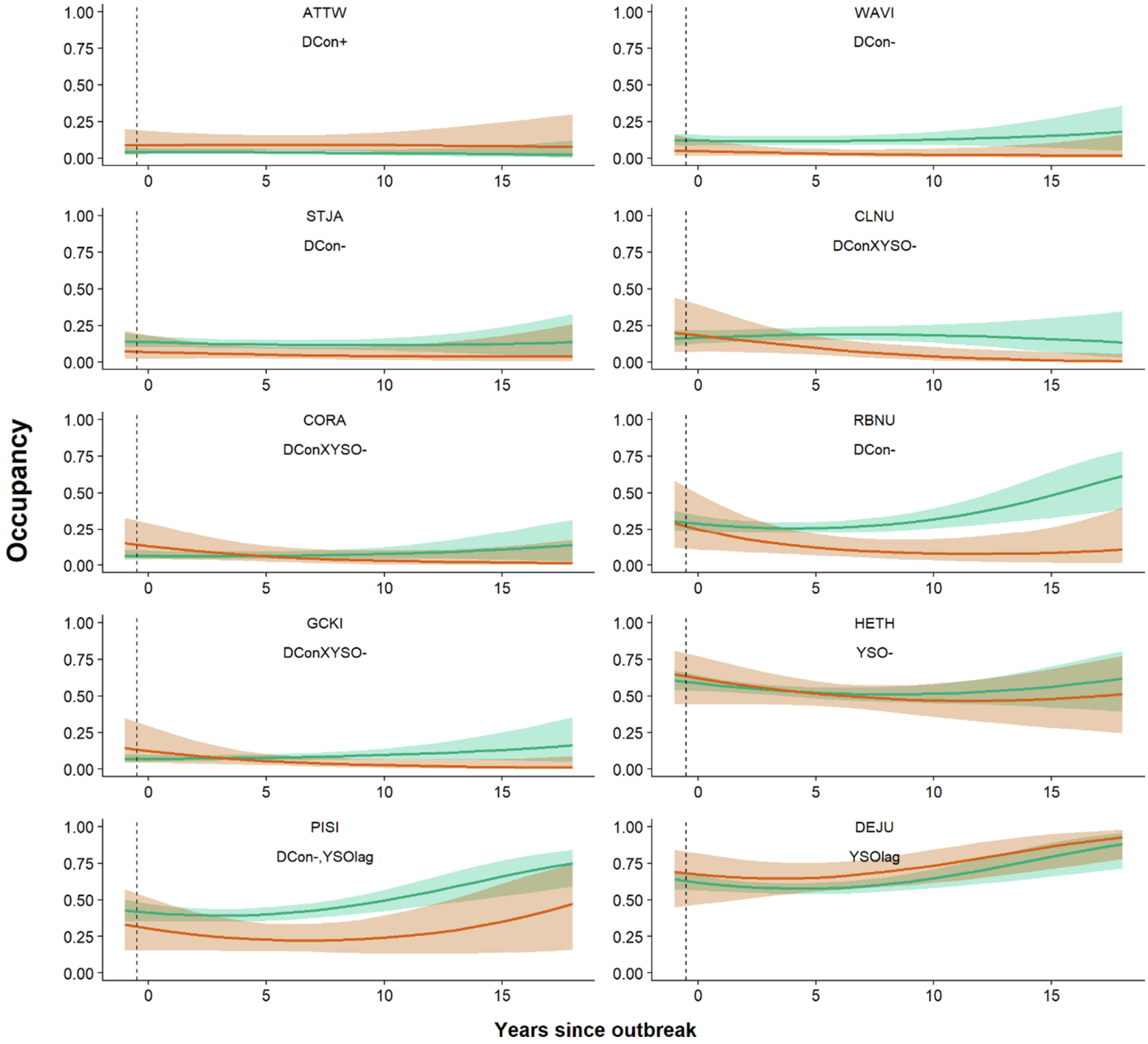

Fig. 4. Predicted occupancy probabilities (with 90% Bayesian credible intervals) for 10 species with statistically supported outbreak relationships in spruce-fir forest. Species are American three-toed woodpecker (ATTW), warbling vireo (WAVI), Steller's jay (STJA), Clark's nutcracker (CLNU), common raven (CORA), red-breasted nuthatch (RBNU), golden-crowned kinglet (GCKI), hermit thrush (HETH), pine siskin (PISI), and dark-eyed junco (DEJU). Plots show relationships with YSO (Years since outbreak) in areas with low (green; percent dead conifer = 0) versus high (red; percent dead conifer = 100) beetle impact. The dashed lines separate outbreak (YSO ≥ 0) from non-outbreak (YSO = −1) forest. Secondary labels indicate outbreak relationships that were statistically supported for each species: negative DCon (DCon-), negative YSO (YSO-), lagged positive YSO (YSOlag), and negative DCon × YSO interaction (DCon × YSO-).

potential mechanisms for species richness increasing with increasing YSO. In spruce-fir forest, conifer-shrub dominance was the only potential mechanistic factor identified for the negative species richness relationship with DCon. These potential mechanisms largely followed the primary mechanisms identified for species groups and individual species in each forest type (see above).

We found statistically supported outbreak relationships for some nest predator species in both forest types (Appendix S2). In lodgepole forest, we found positive YSO relationships for two avian predators (house wren and brown-headed cowbird), but avian predators as a group did not exhibit any statistically supported outbreak relationships. We also found a negative DCon relationship for red squirrel density in lodgepole forest. This relationship, however, does not provide a potential mechanism for any of the outbreak relationships observed in lodgepole forest (no positive DCon relationships observed). In spruce-fir forest, we found negative DCon relationships for Steller's jay and red squirrel, and negative DCon × YSO relationships for Clark's nutcracker and common raven. Additionally, we found a statistically supported negative DCon relationship for avian predators as a group. Relationships for one nest predator, red squirrel, in spruce-fir forest provided a potential mechanism for positive DCon relationships only observed for American three-toed woodpecker.

4. Discussion

4.1. Avian relationships with bark beetle outbreak

We observed outbreak-related patterns somewhat but not entirely consistent with our hypotheses. Positive species and community relationships with YSO in lodgepole forest generally matched our hypothesis that most species would exhibit positive outbreak relationships. Most species for which we hypothesized positive outbreak relationships did in fact increase in occupancy with increasing YSO in lodgepole forest. Nevertheless, non-linear YSO and negative outbreak relationships did not consistently match our hypotheses. In spruce-fir forest, we observed predominantly negative DCon relationships, contradicting our overarching hypothesis of generally positive outbreak relationships. Moreover, species outbreak relationships observed in

Table 3
Statistically supported outbreak relationships by species group.

Forest	Species group	$n_{\geq 10}$	Supported species relationships			
			Positive			Negative[D]
			any	lagged YSO	peaked YSO	
Lodgepole	Hypothesized relationship:					
	Positive (any)	35	14	2	1	2
	Positive (lagged YSO)	14	8	2	1	1
	Positive (peaked YSO)	7	1	0	0	0
	Negative	3	1	0	0	1
	Unknown	10	3	1	0	1
	Nesting life history:					
	Primary cavity[A]	5	1	0	0	0
	Secondary cavity	9	2	0	0	1
	Open-cup canopy	20	5	1	0	2
	Open-cup understory	15	9	2	1	1
	Foraging life history:					
	Aerial insectivore	9	5	1	0	1
	Understory	13	7	1	1	1
	Foliage / bark insectivore	10[C]	3	1	0	2
	Snag[B]	3	1	0	0	0
	Conifer seed	4[C]	0	0	0	0
Spruce-fir	Hypothesized relationship:					
	Positive (any)	32	4	3	0	5
	Positive (lagged YSO)	13	1	1	0	1
	Positive (peaked YSO)	6	2	1	0	1
	Negative	4	0	0	0	1
	Unknown	11	0	0	0	2
	Nesting life history:					
	Primary cavity[A]	4	1	0	0	0
	Secondary cavity	9	1	1	0	1
	Open-cup canopy	21	1	1	0	6
	Open-cup understory	14	1	1	0	1
	Foraging life history:					
	Aerial insectivore	8	0	0	0	0
	Understory	12	1	1	0	1
	Foliage / bark insectivore	12[C]	1	1	0	3
	Snag[B]	3	1	0	0	0
	Conifer seed	4[C]	2	2	0	3

Groups are defined by *a priori* hypothesized outbreak relationships or life history. For each group, the number of species that we detected at ≥10 point surveys is listed (n_{10}). For tallies of supported species relationships, any species with a statistically supported positive or negative outbreak effect (DCon, YSO, or YSO^2) is counted under "any positive" or "any negative", respectively. After considering predicted occupancy (Figs. 3, 4), the interactive relationship for yellow-rumped warbler (DCon × YSO) in lodgepole forest was included in both "any positive" and "any negative", and interactive relationships for three species in spruce-fir forest were included in "any negative." Lagged positive YSO (years since outbreak) tallies consist of species with a supported positive YSO^2 effect. Peaked positive YSO tallies consist of species with a supported negative YSO^2 effect and a positive posterior median YSO effect.

[A] All species in this group are woodpeckers.

[B] This group represents a subset of primary cavity nesting species, i.e., woodpeckers

[C] Red-breasted Nuthatch is classified as both a bark insectivore and a conifer-seed forager.

[D] Includes negative DCon × YSO interactive relationships. In lodgepole forest, yellow-rumped warbler switched from occupying severely impacted forests during early outbreak years to minimally impacted forests in later outbreak years. In spruce-fir forest, several species exhibited declines with increasing YSO primarily at severely impacted sites.

spruce-fir forest contradicted more often than matched our hypotheses. Our more frequent observations of positive outbreak relationships in lodgepole forest compared to spruce-fir forest suggests a substantial role of ecological context in modulating outbreak effects. Nevertheless, we never observed statistically supported but contradictory relationships between forest types for any species, highlighting the strong role of species ecology in determining outbreak response.

Having informed our hypotheses with available literature on life history, habitat associations, and empirical patterns, our failure to find support for hypothesized species outbreak relationships indicates limitations to general knowledge. These limitations reflect both limited data representing broad post-outbreak timeframes and limitations in our understanding of species habitat and resource requirements. Nevertheless, inter-specific variability in outbreak relationships here reinforces similar observations in other studies, providing mounting evidence for the value of mosaic forest landscapes for supporting an array of species (Fontaine and Kennedy, 2012; Saab et al., 2014). Additionally, by building on our hypotheses and results, future research could serially update current knowledge as new data arise to drive knowledge generation (e.g., Nichols et al., 2019).

Our study along with others highlights the potential for bark beetle outbreaks to shape avian diversity. Most studies to date primarily report changes in species composition (implied by variability in response across species) and comparatively limited changes in species richness or diversity with mountain pine beetle outbreaks during early outbreak years (Saab et al., 2014). With similar data and sampling methods to ours, Janousek et al. (2019) report a statistically supported increase in species richness of limited magnitude 0–10 years post-outbreak in lodgepole forests across the Rocky Mountains of the central to northern United States. Over a narrower spatial extent (Colorado) but broader timeframe (0–18 years post outbreak), we found a more pronounced increase in species richness. Differences between our results may in part reflect differences in scale of measurement (i.e., fine- versus coarse-scale species richness estimation) or differences in outbreak metrics

Table 4

Posterior median (and 90% Bayesian credible intervals [BCI]) for average (mean) parameter estimates quantifying outbreak effects for species groups.

Forest	Species group	*n*	Posterior median β (90% BCI)			
			DCon	YSO	YSO^2	DCon × YSO
Lodgepole	Hypothesized relationship:					
	Positive (any)	49	0.01(−0.03,0.05)	0.24(0.16,0.33)*	0(−0.05,0.05)	−0.01(−0.08,0.07)
	Positive (lagged YSO)	7	−0.01(−0.09,0.06)	0.11(−0.09,0.29)	−0.03(−0.12,0.06)	−0.05(−0.14,0.05)
	Positive (peaked YSO)	13	−0.03(−0.09,0.03)	0.12(−0.01,0.24)	0(−0.07,0.07)	−0.04(−0.12,0.04)
	Negative	25	0.01(−0.04,0.06)	0.28(0.17,0.4)*	0(−0.06,0.07)	0(−0.08,0.09)
	Unknown	7	0(−0.07,0.07)	0.18(0.06,0.3)*	−0.04(−0.12,0.03)	−0.07(−0.16,0.02)
	Nesting life history:					
	Primary cavity[A]	6	0(−0.08,0.08)	0.23(0.07,0.39)*	−0.04(−0.15,0.05)	−0.05(−0.16,0.05)
	Secondary cavity	11	−0.01(−0.07,0.05)	0.08(−0.05,0.2)	0.02(−0.05,0.09)	−0.04(−0.12,0.05)
	Open-cup canopy	28	0(−0.05,0.04)	0.15(0.05,0.24)*	−0.01(−0.07,0.04)	−0.03(−0.09,0.05)
	Open-cup understory	26	0(−0.05,0.05)	0.29(0.18,0.42)*	0.01(−0.06,0.07)	−0.01(−0.08,0.09)
	Foraging life history:					
	Aerial insectivore	10	0.02(−0.04,0.09)	0.25(0.12,0.39)*	0.05(−0.03,0.13)	0(−0.08,0.11)
	Understory	23	0(−0.05,0.05)	0.28(0.17,0.41)*	−0.01(−0.07,0.06)	−0.01(−0.09,0.08)
	Foliage / bark insectivore	16[C]	−0.02(−0.07,0.04)	0.11(0,0.23)*	0.01(−0.05,0.08)	−0.06(−0.13,0.02)
	Snag[B]	3	0.02(−0.08,0.12)	0.27(0.07,0.47)*	−0.08(−0.21,0.03)	−0.04(−0.17,0.09)
	Conifer seed	5[C]	−0.02(−0.1,0.06)	0.09(−0.08,0.25)	−0.03(−0.12,0.05)	−0.03(−0.12,0.07)
Spruce-fir	Hypothesized relationship:					
	Positive (any)	49	−0.07(−0.12,-0.03)*	−0.03(−0.08,0.03)	0.03(−0.01,0.06)	−0.04(−0.1,0.01)
	Positive (lagged YSO)	7	−0.1(−0.21,0)*	−0.03(−0.11,0.05)	0.03(−0.02,0.09)	−0.06(−0.15,0.02)
	Positive (peaked YSO)	13	−0.1(−0.18,-0.03)*	−0.03(−0.09,0.04)	0.02(−0.03,0.07)	−0.07(−0.15,0)*
	Negative	25	−0.06(−0.13,0)*	−0.03(−0.09,0.03)	0.03(−0.02,0.07)	−0.03(−0.1,0.04)
	Unknown	7	−0.03(−0.11,0.06)	−0.03(−0.09,0.04)	0.02(−0.03,0.07)	−0.06(−0.14,0.01)
	Nesting life history:					
	Primary cavity[A]	6	−0.02(−0.12,0.09)	−0.02(−0.1,0.06)	0.01(−0.06,0.07)	−0.04(−0.13,0.04)
	Secondary cavity	11	−0.08(−0.16,0)*	−0.02(−0.08,0.05)	0.01(−0.04,0.06)	−0.07(−0.16,0)*
	Open-cup canopy	28	−0.1(−0.16,-0.05)*	−0.02(−0.08,0.03)	0.03(0,0.07)	−0.05(−0.12,0)
	Open-cup understory	26	−0.08(−0.15,-0.02)*	−0.03(−0.09,0.03)	0.03(−0.02,0.07)	−0.04(−0.1,0.03)
	Foraging life history:					
	Aerial insectivore	10	−0.05(−0.14,0.03)	−0.03(−0.1,0.05)	0.01(−0.04,0.06)	−0.04(−0.11,0.05)
	Understory	23	−0.06(−0.13,0)	−0.03(−0.08,0.03)	0.03(−0.02,0.07)	−0.04(−0.1,0.03)
	Foliage / bark insectivore	16[C]	−0.12(−0.19,-0.06)*	−0.03(−0.09,0.03)	0.03(−0.02,0.07)	−0.07(−0.14,0)*
	Snag[B]	3	0.09(−0.03,0.21)	−0.02(−0.11,0.09)	0(−0.09,0.08)	−0.02(−0.11,0.1)
	Conifer seed	5[C]	−0.16(−0.27,-0.06)*	−0.02(−0.1,0.05)	0.06(0.01,0.11)*	−0.09(−0.21,-0.01)*

Groups are defined by *a priori* hypothesized outbreak relationships or life history. Only species detected at least once at a point survey are included in these estimates, and *n* is the number of species included in each group-level estimate. Statistically supported group effects (90% BCI excludes zero) are indicated with an asterisk (*).

[A] All species in this group are woodpeckers.

[B] This group represents a subset of primary cavity nesting species, i.e., woodpeckers.

[C] Red-breasted Nuthatch is classified as both a bark insectivore and a conifer-seed forager.

(field-measured outbreak severity in our analysis versus remotely-sensed in theirs). Nevertheless, comparison of studies representing early outbreak years (Saab et al., 2014) to longer timeframes (ours and Janousek et al., 2019) suggests broad community-level patterns at least in pine-dominated (especially lodgepole pine) forests. Although outbreaks may primarily affect species composition during early outbreak years, species richness can apparently increase over longer time frames following mountain pine beetle outbreaks. More studies would be needed to investigate such patterns in spruce-fir forests (discussed further below).

4.2. Mechanisms underlying outbreak relationships

Outbreak relationships and their potential mechanisms matched most of our hypotheses for understory birds. We expected species that nest and forage in the understory to benefit from growth and development of shrub and ground cover stimulated by bark beetle outbreaks. In lodgepole forest several lines of evidence supported this hypothesis: point-level occupancy was positively related with YSO, shrub cover, and herbaceous and woody-stem ground cover for this species group in general and for many members within the group (house wren, American robin, Lincoln's sparrow, white-crowned sparrow, and dark-eyed junco). We did not hypothesize potential mechanisms involving reduced understory dominance of conifer saplings, but these results echo patterns in inland northwest conifer forests (see also Hagar, 2007; Betts et al., 2010). Our data suggest a potential role of broad-leaf shrubs (complement of conifer saplings) in modulating outbreak effects in lodgepole forests.

Although positive responses by understory species were supported, the data did not generally support our more specific hypothesis of lagged positive YSO relationships for this group in particular any more than species representing other life histories. Contrary to our expectations, we found only limited evidence of late-YSO acceleration of understory development (except see ConShrb relationships in lodgepole forest; Appendix S9), potentially explaining the apparent lack of lagged outbreak responses expected for understory birds.

The lack of positive YSO relationships for understory species in spruce-fir forest may in part reflect a relative lack of understory development within 18 years following spruce beetle outbreak. Concomitantly, conifer sapling dominance related positively with outbreak severity more so in spruce-fir compared to lodgepole forest, potentially explaining less occupancy of severely impacted (high-DCon) points by open-cup nesting understory birds.

Understory development may also contribute to habitat for species less obviously associated with understory microhabitats. Positive YSO relationships for aerial insectivores in lodgepole forest matched our hypotheses, but potential mechanisms pointed to understory vegetation more so than canopy openings *per se* as mechanistic factors. Flying insect prey associated with productive understories within canopy openings (Hagar, 2007; Betts et al., 2010) might explain positive

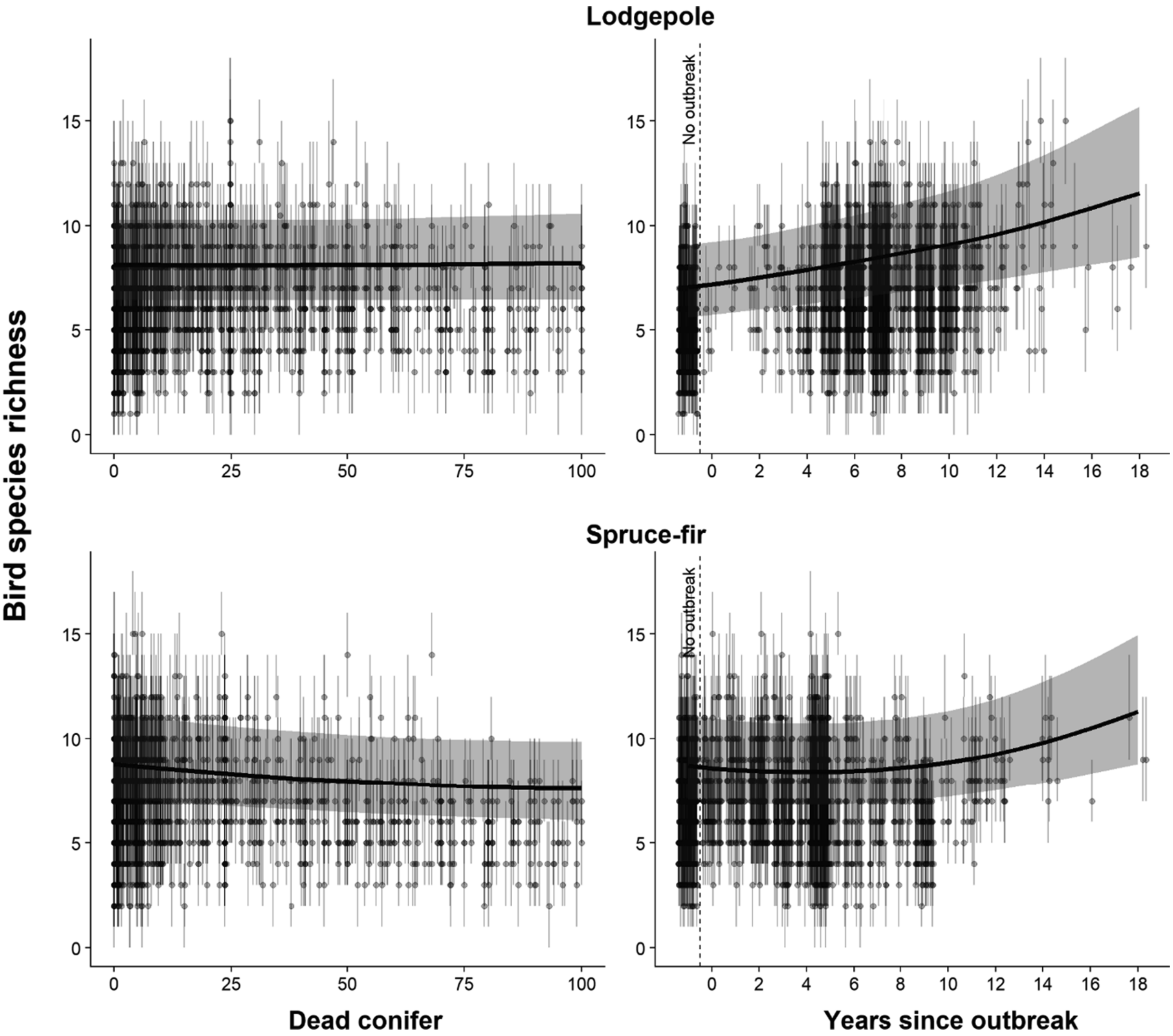

Fig. 5. Bird species richness estimates (median, 90% BCIs) in relation to outbreak metrics. Points and error bars are finite-sample estimates ($\widehat{N}_{\theta,\text{obs}}$), whereas lines and error bars are predicted richness ($\widehat{N}_{\theta,\text{pred}}$; see text for equations and definitions).

outbreak relationships for these species. Members of other foraging life histories that secondarily engage in aerial insectivory or understory foraging may also benefit from understory development (e.g., western tanager, warbling vireo, and pine siskin; Hudon, 1999; Gardali and Ballard, 2000; Dawson, 2014).

Bark beetle outbreaks may affect avian communities by altering canopy composition (Collins et al., 2011), with which we found numerous avian relationships for species, species groups, and species richness overall (Appendix S8). Outbreaks primarily impact areas where host species dominate, and where climate, drought, and disturbance history maximize susceptibility (Bentz et al., 2010; Biedermann et al., 2019). Host prevalence subsequently declines over time (at least within the first several decades after outbreak), reflecting tree mortality and snag fall. We primarily observed negative relationships with host dominance (i.e., pine in lodgepole and spruce in spruce-fir forests), suggesting a general potential for outbreaks to increase species richness by affecting canopy composition. We controlled for canopy composition and thus host prevalence when analyzing outbreak relationships, but pre-outbreak associations with canopy composition could nevertheless confound relationships with outbreak severity (DCon) with our data. Regardless, we identified mechanisms involving host (pine) dominance for positive YSO relationships in lodgepole forest for various species and life history groups, likely reflecting various factors related to canopy composition (e.g., climate, soils, and disturbance history). Negative relationships with pine dominance in both forest types may reflect avoidance of pure lodgepole pine stands, where structural homogeneity and low productivity limit biodiversity (Benedict, 2008: 499). Mountain pine beetle outbreaks likely especially benefit biodiversity by boosting vegetative structure and diversity in these stands. Studies document strong benefits of aspen for avian diversity (Griffis-Kyle and Beier, 2003; Earnst et al., 2012), and our data met our expectations that bark beetle outbreaks would allow aspen growth (Appendix S9). Studies considering how species alter their relationship with tree species following outbreaks could provide further insights into the interplay between outbreaks and canopy composition as determinants of bird distributions (e.g., Mosher et al., 2019).

American three-toed woodpecker specialize on beetle-impacted forests where they prey directly on bark beetles and excavate nest cavities in beetle-killed snags (Edworthy et al., 2011; Tremblay et al., 2018; Kelly et al., 2019). Patterns observed here in spruce-fir forest were consistent with those reported elsewhere, although our data failed to capture their particular affinity for early-outbreak conditions when bark beetle prey are active (Kelly et al., 2019). The positive relationship with YSO found in lodgepole forest was not entirely consistent with the species' specialization on bark beetle prey during outbreaks. Secondary bark beetle species (described by Safranyik, 1989) may extend foraging resource benefits provided by mountain pine beetle outbreaks, although we would expect such benefits to arise primarily in severely impacted

Table 5
Potential mechanisms for outbreak relationships for species groups and individual species.

Group	Lodgepole		Spruce-fir	
	Relation	Potential mechanisms	Relation	Potential mechanism
All (species richness)	YSO(+)	Decreased pine dominance of the canopy and conifer sapling dominance of the shrub layer, and increased herbaceous and woody ground cover with increasing years since outbreak.	DCon(−)	More conifer sapling dominance of the shrub layer at severely impacted sites.
Hypothesized relationship:				
Positive	YSO(+)	Decreased pine dominance of the canopy and conifer sapling dominance of the shrub layer, and increased herbaceous and woody ground cover with increasing years since outbreak.	DCon(−)	More conifer sapling dominance of the shrub layer at severely impacted sites.
Unknown	YSO(+)	Decreased pine dominance of the canopy, and increased herbaceous and woody ground cover with increasing years since outbreak.	DCon(−)	
Nesting life history:				
Primary cavity	YSO(+)	Decreased pine dominance of the canopy, and increased herbaceous ground cover with increasing years since outbreak.	–	
Secondary cavity			DCon(−)	
Opencup canopy	YSO(+)	Decreased pine dominance of the canopy, and increased herbaceous and woody ground cover with increasing years since outbreak.	DCon(−)	More conifer sapling dominance of the shrub layer at severely impacted sites.
Opencup understory	YSO(+)	Decreased conifer sapling dominance of the shrub layer, increased shrub cover, and increased herbaceous and woody ground cover with increasing years since outbreak.	DCon(−)	More conifer sapling dominance of the shrub layer at severely impacted sites.
Foraging life history:				
Aerial insectivore	YSO(+)	Decreased conifer sapling dominance of the shrub layer, and increased herbaceous cover with years since outbreak.	–	
Understory	YSO(+)	Decreased pine dominance of the canopy and conifer sapling dominance of the shrub layer, and increased herbaceous and woody ground cover with increasing years since outbreak.	–	
Foliage or bark insectivore	YSO(+)	Decreased pine dominance of the canopy, and increased herbaceous and woody ground cover with increasing years since outbreak.	DCon(−)	Less canopy cover at severely impacted sites.
Snag	YSO(+)	Increased herbaceous ground cover with increasing years since outbreak.	–	
Individual Species:				
American three-toed woodpecker	YSO(+)	Decreased pine dominance of the canopy, and increased herbaceous ground cover with increasing years since outbreak.	DCon(+)	
olive-sided flycatcher	YSO(+)	Decreased conifer sapling dominance of the shrub layer.	–	
western wood-pewee	YSO(+)	Decreasing conifer sapling dominance of the shrub layer, and increasing herbaceous ground cover with increasing years since outbreak	–	
dusky flycatcher	YSO(+)	Decreased conifer sapling dominance of the shrub layer, and increased herbaceous ground cover with increasing years since outbreak.	–	
cordilleran flycatcher	YSO(+)	Decreased pine dominance of the canopy and conifer sapling dominance of the shrub layer with increasing years since outbreak.	–	
warbling vireo	–		DCon(−)	More conifer sapling dominance of the shrub layer at severely impacted sites.
Steller's jay	–		DCon(−)	Less canopy cover at severely impacted sites.
red-breasted nuthatch	–		DCon(−)	Less canopy cover at severely impacted sites.
house wren	YSO(+)	Increasing herbaceous ground cover with increasing years since outbreak	–	
hermit thrush	YSO^{2}(−)	Lagged increase in aspen canopy component with increasing years since outbreak	YSO(−)	
American robin	YSO(+)	Increasing herbaceous ground cover with increasing years since outbreak	–	
pine siskin	–		DCon(−)	Less woody ground cover at severely impacted sites.
Lincoln's sparrow	YSO(+)	Decreased pine dominance of the canopy and conifer sapling dominance of the shrub layer, and increased herbaceous ground cover with increasing years since outbreak.	–	
white-crowned sparrow	YSO(+)	Decreasing conifer sapling dominance of the shrub layer, and increasing herbaceous ground cover with increasing years since outbreak	–	
dark-eyed junco	YSO(+)	Decreased pine dominance of the canopy, and increased herbaceous and woody ground cover with increasing years since outbreak.	YSO^{2}(+)	Lagged increase in herbaceous ground cover at sites representing later post-outbreak years.
brown-headed cowbird	YSO(+)	Decreasing conifer sapling dominance of the shrub layer with increasing years since outbreak	–	
MacGillivray's warbler	YSO(+)	Decreasing conifer sapling dominance of the shrub layer with increasing years since outbreak	–	
yellow-rumped warbler	YSO(+)	Decreased pine dominance of the canopy, and increased woody ground cover with increasing years since outbreak.	–	
	DCon × YSO(−)	Decreased conifer sapling dominance of the shrub layer during later years since outbreak at severely impacted sites.		

(*continued on next page*)

Table 5 (*continued*)

Group	Lodgepole		Spruce-fir	
	Relation	Potential mechanisms	Relation	Potential mechanism
Wilson's warbler	YSO(+)	Decreased conifer sapling dominance of the shrub layer, increased shrub cover, and increased herbaceous ground cover with increasing years since outbreak.	–	
western tanager	YSO^2(+)	Accelerated decline in pine canopy dominance, and accelerated increases in herbaceous and woody ground cover during later post-outbreak years[A]	–	

Groups are defined by *a priori* hypothesized outbreak relationships or life history. Outbreak covariates (defined in Table 2) and the direction of relationships (+ or −) are listed here if relationships were statistically supported (90% credible interval excludes zero) and associated with a potential mechanism in at least one forest type. Potential mechanisms are statistically supported relationships with vegetation covariates of a direction capable of explaining the corresponding outbreak relationship (see text and Appendix S1 for further rationale). Outbreak effects were confounded with host prevalence with respect to DCon, so mechanisms involving canopy composition variables (Aspen, Pine, and Spruce) are not considered for DCon relationships. We found no potential mechanisms for species groups hypothesized to have lagged or peaked positive YSO relationships, so those groups are not represented here.

[A] Decreased pine dominance and increased herbaceous and woody stem cover could explain lagged increase but not the initial decrease in Western Tanager occupancy.

areas. The limited range of post-outbreak years represented in the literature (Saab et al., 2014; Janousek et al., 2019; Mosher et al., 2019) restricts our ability to evaluate the generality of the YSO relationship for American three-toed woodpecker observed in lodgepole forest. Available evidence does, however, suggest variability in outbreak associations across the species range (Kelly, 2016).

Other than American three-toed woodpecker, our results provide relatively limited information on cavity-nesting and snag-associated birds, but others clearly document the value of beetle outbreaks for this group (Drever and Martin, 2010; Saab et al., 2014, 2019). Nest searching or call broadcast surveys may be needed to fully inform relationships for this group (e.g., Edworthy et al., 2011; Saab et al., 2019). Secondary cavity nesting species benefit from increased availability of cavities initially excavated by woodpeckers following disturbance (Norris et al., 2013; Norris and Martin, 2014; Saab et al., 2014). In addition to snags, aspen provide valuable substrate for cavity excavation. Although our results did not suggest many mechanisms involving aspen, associations with aspen could contribute to outbreak relationships for some species (e.g., house wren, warbling vireo). Although red-breasted nuthatch can excavate nest cavities, excavation incurs greater energetic costs than cavity reuse. Mountain pine beetle outbreaks initially represent resource pulses for this species potentially due to both increased cavity availability and increased opportunity for foraging on bark beetle prey (Norris and Martin, 2014). During years after active bark beetle infestation, however, foraging needs may outweigh cavity availability for determining outbreak relationships.

In principle, we expected reduced canopy cover to negatively impact species that build open-cup nests, insectivores that forage in the canopy (bark or foliage), and conifer-seed eating species. In practice, however, we hypothesized positive outbreak relationships or refrained from making any hypotheses more frequently than hypothesizing negative relationships for members of these life history groups (Appendix S1). Our hypotheses reflected frequent observations of mixed or positive outbreak relationships reported in the literature and general associations with open habitats for many of these species (Matsuoka et al., 2001; Saab et al., 2014; Wickersham, 2016; Janousek et al., 2019). Our results add to growing evidence that membership in these life history groups provides limited information for explaining outbreak responses. Conifer-seed eating species tend to be nomadic and follow mast crop availability, making their distributions heterogeneous and potentially difficult to predict regardless of disturbance history. Even ruby-crowned kinglet, a species that nests and forages in the canopy and associates with mature dense forest, does not necessarily exhibit consistent relationships with outbreak severity across studies (compare results here with Matsuoka et al., 2001; Saab et al., 2014). We found more statistically supported positive relationships with canopy cover in spruce-fir compared to lodgepole forest (Appendix S8). Canopy cover may play a greater role in modulating outbreak relationships in spruce-fir forests, which at maturity are historically characterized by relatively closed and denser canopies (Benedict, 2008).

Nest predation limits many bird populations, and several studies describe birds adjusting breeding site selection patterns to avoid nest predators (reviewed by Ibáñez-Álamo et al., 2015). Various authors describe the red squirrel as an important nest predator for forest birds (Matsuoka and Handel, 2007; Norris and Martin, 2014; Saab et al., 2014). Some suggest disturbance avoidance by red squirrels and other nest predators as one possible factor underlying avian associations with disturbed habitats (Saab et al., 2011, 2014). The outbreak relationship for American three-toed woodpecker was consistent with predator avoidance in spruce-fir forest, although foraging resources may primarily drive this species distribution (discussed above). Cavity-nesting birds can suffer reduced nest survival during low-resource years for red squirrels, although such effects may involve changes in red squirrel foraging behavior more so than their abundance (Mahon and Martin, 2006). We did not observe any other outbreak relationships consistent with predator avoidance, suggesting nest predators may only modulate outbreak effects on parameters measured with nesting data (e.g., nest site selection and nest survival; Matsuoka and Handel, 2007; Norris and Martin, 2014; Saab et al., 2019).

4.3. Species richness and ecological function across forests

Outbreak relationships and their potential mechanisms for species richness reflected dominant patterns across species, which differed substantially between lodgepole and spruce-fir forests. In lodgepole forest, avian species richness increased substantially with time since outbreak, with changes in both canopy and understory vegetation potentially contributing to this pattern. In contrast, species richness related more negatively with outbreak severity in spruce-fir forest, similar to relationships reported in lodgepole forest over a shorter post-outbreak timeframe (Janousek et al., 2019). Although not statistically different, mean posterior species richness estimates were somewhat greater at late-YSO spruce-fir sites (Fig. 5). Additional data representing a longer post-outbreak period might reveal patterns in spruce-fir comparable to those observed here in lodgepole forest.

Relative dominance of conifer saplings versus broad-leafed species could be an important factor determining species richness patterns and outbreak impacts in higher elevation forests of Colorado. Although not hypothesized, patterns found here parallel those reported in Pacific Northwest conifer forests (Hagar, 2007; Betts et al., 2010; Swanson et al., 2014). We saw increases in shrub cover with YSO in both forest types, but dominance of broad-leafed (non-conifer) shrub species only increased with YSO in lodgepole forest. Additionally, we found predominantly negative relationships with conifer sapling dominance in both forest types (Appendix S8). Thus, similar patterns could arise in spruce-fir forests depending on growth and recruitment of broad-leaf shrubs there over a longer post-outbreak timeframe. Post-outbreak increases in herbaceous cover may also contribute to avian species richness, but herbaceous relationships with outbreak metrics were more similar between lodgepole and spruce-fir forests (Appendix S9).

The ecological significance of bark beetle outbreaks for promoting and maintaining biodiversity depends on outbreak contributions to forested landscapes at broad spatial scales, which depend in part on how outbreaks influence both local species richness and composition (determined by the magnitude and variability of species relationships). Bird species richness and composition showed stronger outbreak relationships in lodgepole forest, perhaps reflecting the homogeneous vegetation structure and composition of this forest type, along with limited understory development and dependence on disturbance for system maintenance (Fahey and Knight, 1986; Kaufmann et al., 2008). Conversely, spruce-fir forests are commonly characterized as stable climax communities in more mesic habitats with greater vegetative diversity (Jenkins et al., 1998). Accordingly, we found a larger difference in grid-level richness between outbreak and non-outbreak grid cells in lodgepole compared to spruce-fir forest, although even this difference was modest (see also Janousek et al., 2019).

A slower or more muted avian response to bark beetle outbreak in spruce-fir compared to lodgepole forest could reflect various factors. Mountain pine beetle outbreaks were far more extensive in lodgepole forest than spruce beetle outbreaks in spruce-fir forest at the time of this study, potentially influencing varying responses to each. Vegetation data also suggests differences in the speed or character of vegetative regrowth between forest types, with potential implications for birds (discussed by Saab et al., 2014). A longer growing season and warmer climate in lower elevation lodgepole forest could increase productivity, further modulating differences in how wildlife respond to disturbance (McWethy et al., 2010). Conversely, we estimated slightly higher bird species richness in spruce-fir compared to lodgepole forests at non-outbreak sites, perhaps reflecting moister conditions and greater vegetative diversity. Being less diverse to begin with (Benedict, 2008: 499), lodgepole forests may have more to gain with heterogeneity introduced by bark beetle outbreaks. Conversely, live subalpine fir canopy retained following outbreaks may mute spruce beetle impacts in spruce-fir forest. The relative role of disturbance in species evolutionary histories could also modulate ecological responses to disturbance (Bock and Block, 2005; Latif et al., 2016).

Our approach to quantifying outbreak conditions could contribute somewhat to differences in outbreak-related patterns between forest types. Slower spread may make spruce beetle outbreaks less detectable by aerial surveyors during initial outbreak years. Given lagged detection of outbreaks, avian responses to spruce beetle outbreak may lag behind responses to mountain pine beetle outbreak even more than is suggested by our data. Conversely, non-outbreak grid cells may have represented more incipient or green-phase outbreaks in spruce-fir forest, potentially making it harder to separate relationships with outbreak severity versus age. Having included both aerial and ground metrics, our overall conclusion of stronger avian responses to outbreak in lodgepole compared to spruce-fir forest within an 18-year post-outbreak timeframe is likely robust to measurement approach. Nevertheless, studies using alternate outbreak metrics would inform the generality of these patterns.

Whether recent outbreaks exceed historical norms is unclear and subject to ongoing debate (Kaufmann et al., 2008). Regardless, our study suggests beetle-killed forests remain valuable for promoting landscape heterogeneity and biodiversity despite recent increases in the extent of outbreaks. Avian relationships with stand structure and composition (Appendix S8) suggest important keystone features underlying the ecological value of outbreaks in lodgepole pine and spruce-fir forests (Tews et al., 2004; Martin et al., 2006). These features include release of broad-leaf shrub species, and herbaceous ground cover release following bark beetle outbreaks. Reductions in host tree species dominance, especially lodgepole pine, and greater canopy diversity may also represent important factors.

The extent to which birds represent general biodiversity patterns in relation to bark beetle outbreaks remains unclear. Ivan et al. (2018) largely pooled their data representing mammal distributions across lodgepole and spruce-fir forests because they found limited differences between forest types, but their sample sizes were an order of magnitude smaller than ours (i.e., one camera trap per grid cell). Larger datasets from avian monitoring may reveal broad patterns in vertebrate diversity not as readily observable in taxa that are harder to survey (e.g., Rosenberg et al., 2019).

We focus here on understanding species relationships modulated by life history as the foundation for community patterns. Analyses that disentangle species from their traits (Dray et al., 2013; Brown et al., 2014) could complement our study for understanding the implications of disturbance for forest ecological integrity and functional diversity.

4.4. Study strengths and limitations

Our study leverages a chronosequence approach to fill a notable knowledge gap. Saab et al. (2014) reported that most published studies they reviewed only represented the early post-outbreak period (years 1–5), limiting our understanding of long-term impacts and system recovery. Extending our knowledge base informs biodiversity management across mosaic landscapes representing various forest conditions. Using a chronosequence approach (advocated by Hutto and Belote, 2013), we were able to inform longer term changes in wildlife populations and communities following bark beetle outbreak within a relatively short sampling period (see also Ivan et al., 2018). In employing a chronosequence approach, we assume that our sampling units are following comparable post-disturbance ecological trajectories, an assumption that has been criticized without strong tests (Johnson and Miyanishi, 2008; Damgaard, 2019). Chronosequences could fail to capture landscape-wide (e.g., across Colorado) population responses or inter-annual variation, which could influence habitat responses, particularly for irruptive species. By coupling a chronosequence approach with spatially balanced sampling (Stevens and Olsen, 2004; Pavlacky et al., 2017), however, we provide statistical rigor needed to infer broad patterns.

In the context of understanding ecological integrity of forests to disturbance (Wurtzebach and Schultz, 2016; Stevens-Rumann et al., 2018), most published studies primarily inform resistance by focusing on initial response of wildlife communities within six years (reviewed by Saab et al., 2014). Along with Ivan et al. (2018), our study begins to inform resilience by studying longer term post-outbreak trends. We found substantive differences in bird species occupancy and richness patterns over 18-year chronosequences in both lodgepole and spruce-fir forests. Considering projected times required for vegetation to return to a climax state (Collins et al., 2011), however, chronosequences of ≥ 100 years may be needed to fully understand ecological resilience to beetle outbreaks. In the meantime, resurveys of our sampling units every 10–20 years could further inform post-outbreak trends or document transition to alternative ecological states with climate change. Additionally, longitudinal data could inform modeling of community dynamics and trajectories (Kéry et al., 2013; De Cáceres et al., 2019; Mosher et al., 2019) while addressing limitations of chronosequences (Damgaard, 2019).

Unmeasured spatial heterogeneity may confound inference of outbreak relationships from chronosequence data, although temporal heterogeneity would not confound our results as is possible with time series studies. We relied primarily on a spatially balanced sampling design to both represent the sampling frame and minimize the potential for unmeasured heterogeneity to confound our inferences. For example, secondary insect outbreaks can confound inference of avian response to bark beetle outbreak (e.g., spruce budworm; Mosher et al., 2019), but such secondary disturbance would need to systematically accompany bark beetle outbreaks across Colorado to confound inferences drawn here. Nevertheless, focused studies with before-after, control-impact sampling could complement ours by documenting temporal shifts in populations with the onset of disturbance and post-disturbance response (Popescu et al., 2012). Such studies may be necessarily opportunistic and limited in sampling extent, however (e.g., Russell et al., 2015). Alternatively, long-term and broad-scale monitoring may eventually yield data that broadly represent conditions before and after disturbance along spatial gradients of disturbance severity or proximity.

To inform ecological function, we considered mechanisms underlying species outbreak relationships, but our analysis did not allow formal evaluation of evidence for particular mechanisms. We therefore only identify potential mechanistic pathways with which our data were consistent and offer these as hypotheses for future study. Path analyses (Clough, 2012) could help evaluate support for potential mechanisms identified here, which may be only feasibly implemented one species at a time. Where supported by sufficient data, analyzing abundance rather than occupancy may maximally inform species-level investigation of mechanisms with path analyses.

Population distribution (represented here by occupancy) may not reflect all impacts of beetle outbreaks on breeding birds. For example, Matsuoka et al. (2001) found no outbreak relationship with dark-eyed junco abundance but found greater nest survival in impacted areas (Matsuoka and Handel, 2007). Studies examining outbreak impacts on avian fitness components and other population parameters complement species distributions to fully inform ecological function of bark beetle outbreaks (Matsuoka and Handel, 2007; Norris et al., 2013; Norris and Martin, 2014; Saab et al., 2019).

Evaluating goodness-of-fit and predictive performance are important steps towards model application, but meaningfully evaluating community occupancy models requires non-trivial levels of analysis that are beyond the scope of this study (e.g., Zipkin et al., 2012; Broms et al., 2016). For now, we lean on the large body of literature establishing the utility of these models (Iknayan et al., 2014; Warton et al., 2015; Ovaskainen et al., 2017) and leave model evaluation for future work.

4.5. Conservation, management, and ecological monitoring

The current U.S. Forest Service planning rule mandates forest management to promote and maintain ecological integrity (36C.F.R. § 219 2012). Two major components of ecological integrity include resistance, the ability of forests to withstand disturbance, and resilience, ability to recover initial conditions following disturbance (Wurtzebach and Schultz, 2016; Stevens-Rumann et al., 2018). Managers often implement restoration to reestablish ecological integrity of forest ecosystems, which includes the degree to which ecological relationships are present, functioning, and capable of self-renewal (Samman and Logan, 2000). Managers can design treatments to encourage stand and landscape structures approximating natural forests, including long-term harvest rotations, stand structural retention, and stand structural restoration. Structural retention involves maintaining significant structural elements (e.g., large, old, decadent trees and snags) as a basis for succeeding forest components, whereas restoration involves measures to speed up the development of structural complexity in a young stand. Following a large-scale outbreak, forest managers may implement preventative measures aimed at reducing future susceptibility to bark beetle outbreaks (Samman and Logan, 2000; but see Dobor et al., In Press). Following substantive evaluation (e.g., Zipkin et al., 2012; Broms et al., 2016), models here provide a potential means to predict avian species and community responses to post-outbreak salvage logging, harvest rotations, stand structural retention, and stand structural restoration, which could help inform management plans that include both socioeconomic and conservation objectives.

In lodgepole forest, various species whose occupancy declined with increasing canopy cover (Appendix S8) may benefit from thinning also aimed at reducing forest susceptibility to future bark beetle outbreaks. Other species associated with denser canopies but also associated with aspen could benefit from thinning of lodgepole pine. Regeneration harvest and coppice cuts targeting regeneration of seral species and stand complexity may benefit species exhibiting positive relationships with aspen (Appendix S8). In spruce-fir forest, thinning to reduce the susceptibility of future bark beetle outbreaks may be detrimental to several groups of bird species exhibiting positive relationships with canopy cover (Appendix S8), along with snag-associated species. Considering primarily negative relationships with both pine and spruce dominance, retention of subalpine fir may be important for maintaining avian diversity following spruce beetle outbreaks (see also Pavlacky and Sparks, 2016; but see American three-toed woodpecker relationships here). In both forest types, regeneration harvest and coppice cuts to simulate aspen regeneration (USDA, 2015) is expected to benefit several aspen associated species (Pavlacky and Sparks, 2016), but may be detrimental to several closed canopy species (Appendix S8). Similar to the pattern in lodgepole pine, stand structural restoration resulting in understory release may have a large positive effect on avian biodiversity. Management that stimulates or avoids hindering regeneration of deciduous shrubs and saplings may promote or maintain understory species and aerial insectivores.

We caution that salvage logging on balance likely impacts biodiversity negatively, with particularly strong negative impacts for woodpeckers, especially American three-toed woodpecker, secondary cavity nesting birds, and other saproxylic organisms (Hutto and Gallo, 2006; Lindenmayer et al., 2008; Thorn et al., 2018). Understory species may also suffer temporary negative impacts. Thus, post-outbreak timber harvest is unlikely to enhance ecological function for promoting or maintaining biodiversity. Nevertheless, our results could inform post-outbreak forest management to at least minimize negative biodiversity impacts while pursuing multiple objectives. To complement the broad patterns documented here, we recommend incorporating effectiveness monitoring into structured decision making frameworks to develop and evaluate biodiversity and other objectives for post-disturbance management (Schwartz et al., 2018).

CRediT authorship contribution statement

Quresh S. Latif: Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Jacob S. Ivan:** Conceptualization, Methodology, Investigation, Data curation, Writing - review & editing. **Amy E. Seglund:** Conceptualization, Methodology, Investigation, Writing - review & editing. **David L. Pavlacky:** Conceptualization, Methodology, Supervision, Writing - review & editing. **Richard L. Truex:** Conceptualization, Methodology, Investigation.

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.

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Appendix A. Supplementary material

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