

# Response to fragmentation by avian communities is mediated by species traits

Jonathon J. Valente  | Matthew G. Betts 

Department of Forest Ecosystems and Society, Forest Biodiversity Research Network, Oregon State University, Corvallis, Oregon

## Correspondence

Jonathon J. Valente, Migratory Bird Center, Smithsonian Conservation Biology Institute, Washington, DC.  
Email: jonathon.j.valente@gmail.com

## Funding information

Department of Defense Strategic Environmental Research and Development Program, Grant/Award Number: RC-2121; U.S. Army Engineer Research and Development Center Environmental Quality and Installations 6270/896/04 (PE/Project/Task)

Editor: Thomas Albright

## Abstract

**Aim:** The hypothesis that habitat fragmentation negatively influences biodiversity stems from island biogeography and metapopulation theory which predict negative impacts of decreasing patch size on richness and distribution patterns. Empirical support of this idea is weak in terrestrial systems, though tests of fragmentation effects are typically confounded with landscape composition and potentially obscured by imperfect detection. Here, we used multispecies occupancy models and a mensurative experimental design to test competing hypotheses about how forest fragmentation influences distributions of breeding forest bird species and communities.

**Location:** Southern Indiana, USA.

**Methods:** During the breeding seasons of 2011–2013, we recorded over 80,000 bird detections in 202 forest fragments using a sampling design that isolated the effects of patch size per se from the effects of forest amount within a 2 km radius, edge distance, local vegetation and sampling area. We modelled the effects of these covariates on distributions of individual species categorized by ecological trait groups (i.e., forest, forest interior or forest edge), and evaluated how forest loss and fragmentation impact species richness.

**Results:** Though our results indicated little effect of patch size on total species richness, decreasing patch size had a negative effect on interior species, and a positive effect on edge species. The effects of total forest amount were much more variable, and surprisingly had a negative influence on many species, particularly cavity nesters.

**Main conclusions:** Our results do not support theoretical predictions that forest patch size should positively influence bird species richness. However, composition of bird communities shifted towards edge species from interior species with decreasing patch size. Maintaining large forest patches is thus critical for supporting forest interior species, which tend to be of the greatest conservation concern.

## KEYWORDS

breeding bird, community occupancy model, edge effects, forest fragmentation, habitat amount, island biogeography, metapopulation, patch size

## 1 | INTRODUCTION

The notion that environmental patch size should influence community structure and composition has been one of the most persistent and controversial doctrines in landscape ecology and fragmentation research (Fahrig, 2013; Haila, 2002; Laurance, 2008). Rooted in island biogeography (IBT; MacArthur & Wilson, 1967) and metapopulation theory (Levins, 1969), smaller habitat fragments are hypothesized to support smaller populations, leading to higher extinction probabilities (Hanski, 1998; Hanski & Ovaskainen, 2002) and lower colonization rates (Gilpin & Diamond, 1976; Lomolino, 1990) than in larger patches. Yet, empirical studies often report weak or inconsistent patch size effects on distributions of diverse taxonomic groups (Debinski & Holt, 2000; Prugh, Hodges, Sinclair, & Brashares, 2008). This juxtaposition of theory and reality has been the catalyst for an unresolved debate about whether larger habitat patches have greater conservation value for sustaining populations and preserving community richness than small patches (Fahrig, 2013, 2015; Hanski, 2015; Laurance, 2008). This disagreement is not trivial, as science examining landscape composition and configuration effects shapes land use policy (Fahrig, 2017), influencing land acquisition and management strategies (Hadley & Betts, 2016; Villard & Metzger, 2014).

Central to the debate is whether the reduction in patch size per se—stemming from landscape fragmentation—influences species distribution patterns beyond that which can be explained by the habitat lost. Unfortunately, because patch size and habitat amount tend to be highly correlated (Andrén, 1994; Didham, Kapos, & Ewers, 2012; Fahrig, 2003), their independent effects are rarely discernable, despite repeated calls to separate them (Fahrig, 2003; Hadley & Betts, 2016). Yet, evidence is mounting that habitat loss has a much greater influence on biodiversity than fragmentation; while habitat loss tends to have strong negative effects (Andrén, 1994; Trzcinski, Fahrig, & Merriam, 1999; McGarigal & Cushman, 2002; Fahrig, 2003, 2013, 2017; De Camargo, Boucher-Lalonde, & Currie, 2018; Melo, Sponchiado, Cáceres, & Fahrig, 2017), patch size effects tend to be weak (Debinski & Holt, 2000; Melo, et al., 2017; Prugh et al., 2008), and context-dependent (Andrén, 1994; Betts, Forbes, Diamond, & Taylor, 2006; Pardini, Bueno, Gardner, Prado, & Metzger, 2010; Villard & Metzger, 2014).

In recent years, the idea that we should be viewing terrestrial habitat patches through the IBT or metapopulation lenses has come under intense scrutiny. Many researchers have criticized the binary patch-matrix habitat model as overly simplistic in general and questioned whether it should be abandoned (Baguette, 2004; Fahrig, 2013; Manning, Lindenmayer, & Nix, 2004; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). Further, even where patch size effects seem to exist, they may not be attributable to metapopulation processes. Rather, they can often be explained by a sample area effect (Cam, Nichols, Sauer, & Hines, 2002; Fahrig, 2013), or local variability stemming from edge effects (Fletcher, Ries, Battin, & Chalfoun, 2007; Ries, Fletcher, Battin, & Sisk, 2004). In fact, Fahrig (2013) provided evidence that patch size itself has no influence on species distribution patterns beyond the amount of habitat it contributes to the

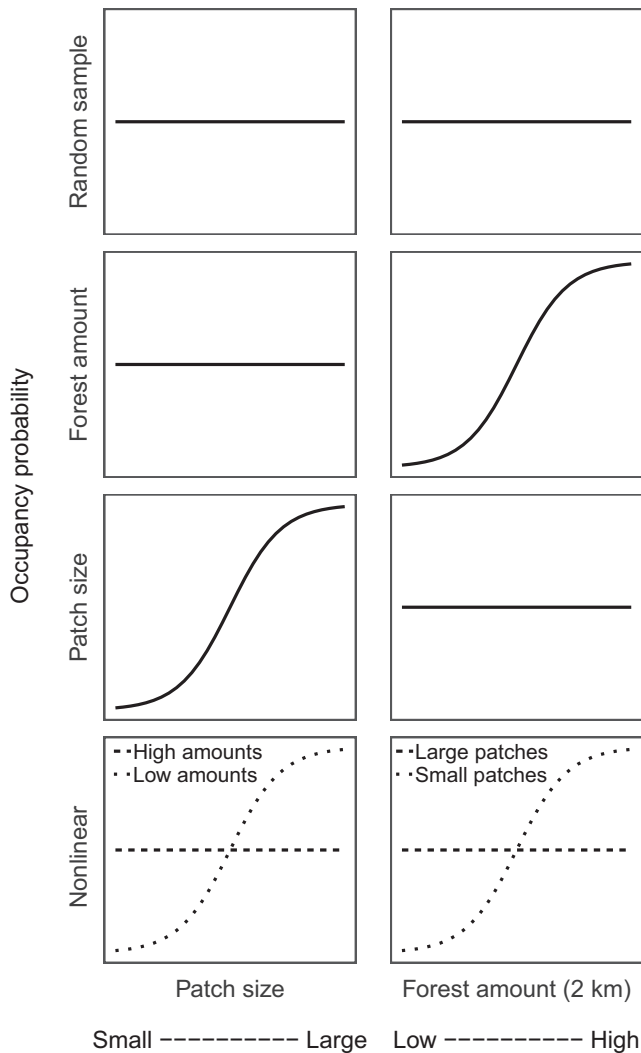
local landscape. These results imply there is no conservation value in large habitat patches beyond the fact that they contain more habitat.

Theoretical predictions about patch size effects relate to species richness (MacArthur & Wilson, 1967), and consequently, most patch size studies examine richness as a response variable (Fahrig, 2013). This approach typically ignores species identities and may poorly capture patch size influences on communities (Iknanayan, Tingley, Furnas, & Beissinger, 2014; Kéry & Royle, 2008; Zipkin, DeWan, & Royle, 2009). Treating all species equivalently can mask important trait groupings, some of which could be highly sensitive to fragmentation (Bender, Contreras, & Fahrig, 1998; Dondina, Orioli, D'Occhio, Luppi, & Bani, 2017; Henle, Davies, Kleyer, Margules, & Settele, 2004). Habitat requirements differ among species, and studies acknowledging this often find habitat specialists are more sensitive to fragmentation effects than generalists (Bender et al., 1998; Cook, Lane, Foster, & Holt, 2002; Betts, Forbes, & Diamond, 2007; Püttker, Bueno, de Barros, Sommer, & Pardini, 2013; Carrara et al., 2015; Dondina et al., 2017; but see Fahrig, 2017).

Additionally, richness summaries ignore variability in detection probability among species, sites and surveys (Iknanayan et al., 2014; Kéry & Royle, 2008; Zipkin et al., 2009), which can produce demonstrably biased or misleading results (e.g., Boulinier, Nichols, Sauer, Hines, & Pollock, 1998; Kéry, Royle, & Schmid, 2008). For example, probability of detection is often positively correlated with conspecific (Dorazio, 2007) or heterospecific (e.g., Bailey, Reid, Forsman, & Nichols, 2009) abundance; thus, richness metrics that fail to account for imperfect detection may disproportionately represent common species (Zipkin et al., 2009) at the expense of the rare or cryptic species, often of greater conservation concern (Samu, Csontos, & Szinetar, 2008).

In this study, we examined the effects of patch size on breeding bird distributions in 202 forest patches in Southern Indiana. We used a mensurative experimental design (Hadley & Betts, 2016) that isolated the effects of patch size per se from those of confounding variables such as forest amount, edge distance, local vegetation and sample area. Here, we use those data to compare four hypotheses about the influence of patch size and forest amount on breeding bird distribution patterns (Figure 1). The *random sample hypothesis* posits that only local vegetation characteristics measured at the scale of the animal territory influence distribution patterns (Haila, 1983). The *forest amount hypothesis* states that distributions are positively influenced by the amount of forest at broader spatial scales (Fahrig, 2003, 2013), while the *patch size hypothesis* implies a linear change with decreasing patch size, beyond what can be explained by habitat loss (Villard, Trzcinski, & Merriam, 1999). Finally, the *nonlinear patch size hypothesis* posits that patch size only influences distributions below critical thresholds in landscape habitat amount (Andrén, 1994; Betts et al., 2006).

We analysed the data using community occupancy models (Iknanayan et al., 2014; Kéry & Royle, 2008; Zipkin et al., 2009) that allowed us to test these hypotheses for all species of interest, while accounting for imperfect detection. In addition, we grouped species according to ecological traits defined a priori, and tested whether fragmentation effects differ among interior specialists, edge specialists and forest generalists. This comprehensive approach to



**FIGURE 1** We compared relative support for our four hypotheses by evaluating the effects of forest patch size and forest amount (2 km radius) on breeding forest bird occupancy probabilities. Under the *random sample hypothesis*, neither patch size nor forest amount influences occupancy probability. Under the *forest amount* and *patch size hypotheses*, only forest amount or patch size (respectively) positively influences occupancy. Finally, the *nonlinear patch size hypothesis* would be supported if we find an interaction between these two covariates such that patch size only influences occupancy at low habitat amounts (and vice versa)

disentangling the independent effects of habitat loss and fragmentation will help shine new light on an age-old debate.

## 2 | METHODS

### 2.1 | Sampling design

We sampled forest patches covering 81,832 ha in the central hardwoods region of Southern Indiana (Figure 2). The area is dominated by corn and soybean agriculture and remnant tracts of temperate broadleaf and mixed forests. Mean annual rainfall is approximately

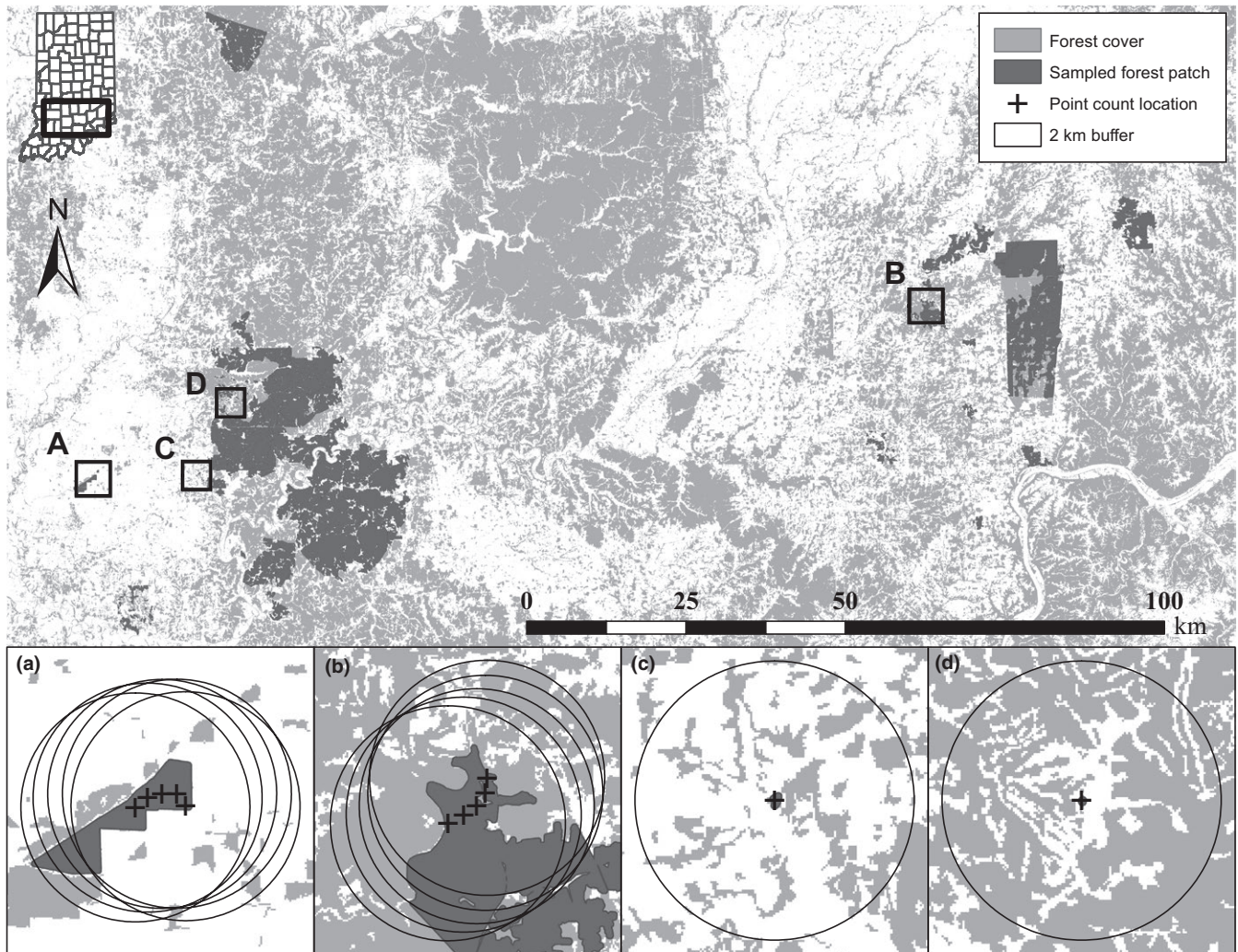
1,190 mm (Indiana State Climate Office, 2002), and mean annual temperatures range from 6°C in winter to 18°C in summer (National Climatic Data Center, 2011). Dominant tree species include oaks (*Quercus* spp.), hickories (*Carya* spp.), tulip poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), American beech (*Fagus grandifolia*), maples (*Acer* spp.) and black walnut (*Juglans nigra*). Dominant understorey shrubs include spicebush (*Lindera benzoin*), multiflora rose (*Rosa multiflora*) and berry bushes (*Rubus* spp.).

We used ARCMAP (v. 9.3.1) to digitize the boundaries of all closed-canopy forest patches on public lands within 50 km of Naval Surface Warfare Center Crane and Big Oaks National Wildlife Refuge. These U.S. Department of Defense installations were chosen because they encompass some of the largest contiguous forest tracts in the region, while much of the remaining landscape is highly fragmented. Patch delineations were based on aerial images collected for the 2010 National Agriculture Imagery Program (data available from the U.S. Geological Survey); we considered patches discrete if separated by canopy gaps >30 m because these would likely represent a movement barrier for many species (Bélisle & Desrochers, 2002). We also separated patches if connected by forest corridors narrower than 100 m, as these would not be sufficiently wide to contain territories for most targeted species (Rodewald, 2015).

We removed patches that were not accessible within 250 m of a road to help standardize edge distances of sampling points in large and small patches. We then classified patches into five size categories: (a) 1–3 ha, (b) 3–10 ha, (c) 10–20 ha, (d) 20–100 ha and (e) >100 ha. We randomly placed up to three potential point count stations in patches ≤20 ha, ensuring that all points were ≥50 m from the nearest edge, and ≥250 m from other points. In larger patches, we randomly selected a single accessible point 50 m from the patch edge as the beginning of a 4 or 5 point transect (with 250 m spacing) stretching towards the patch interior.

We then centred a 2 km radius circle on each point and quantified the proportion of the circle dominated by mature forest (forest amount) using the National Land Cover Database (Fry et al., 2011). Though no single landscape scale would be relevant for all species (e.g., Melo et al., 2017; Mitchell, Lancia, & Gerwin, 2001), we had to choose one a priori to design a sampling scheme that minimized the correlation between forest amount and patch size. We chose 2 km because it is likely to include the spatial extent relevant to habitat use (Mitchell et al., 2001), natal dispersal (Bowman, 2003), and extra-territorial movements (Norris & Stutchbury, 2001) for most species we examined.

We classified patches into four forest amount categories based on the mean values among points in the patch: (a) 0%–40%, (b) 40%–60%, (c) 60%–80% and (d) 80%–100%. Although it would have been ideal to split our first category in half (i.e., 0%–20% and 20%–40%), we were not able to do so because very few patches had <20% forest cover within 2 km. Finally, we used stratified random sampling to choose a roughly equal number of patches from each size-by-amount patch group. Note that these groupings were used only in point selection to ensure we sampled the available gradient in patch size and habitat amount; these covariates were treated as continuous variables in our analyses (see below). In all, we selected



**FIGURE 2** A map of the study region in Indiana (upper left) where we conducted breeding bird point counts between 2011 and 2013. Grey areas represent forest cover (National Land Cover Database; Fry et al., 2011), and the darker grey areas highlight the 202 unique forest patches sampled. We designed our study to minimize correlation between patch size and the amount of forest within 2 km at the point level. Thus, we sampled (a) large patches with low forest amount, (b) large patches with high forest amount, (c) small patches with low forest amount and (d) small patches with high forest amount. Larger patches (a and b) contained more point count stations to ensure we sampled the gradient in edge distance

490 point count stations for sampling in 202 forest patches. The distribution of patch size and habitat amounts in our sample are shown in Supporting Information Appendix S1: Figure S1.1.

This design minimized point-level correlation between patch size and forest amount ( $r = 0.22$ ), allowing us to separate their independent effects on occupancy. While others have argued that focal patch studies such as ours do not truly test fragmentation effects (Fahrig, 2003, 2017; McGarigal & Cushman, 2002), these are ideal for distinguishing among the relative effects of within-patch, patch and landscape variables (Thornton, Branch, & Sunquist, 2011). Moreover, theory (Hanski, 1998; Levins, 1969; MacArthur & Wilson, 1967) predicts that the size of the patch itself should influence distribution patterns, rather than landscape-scale patch metrics (e.g., mean patch size). Finally, focal patch size should be a reasonable proxy for fragmentation given that these variables tend to be highly correlated at the landscape scale (Andrén, 1994; Didham et al., 2012; Fahrig, 2003).

## 2.2 | Bird and vegetation sampling

Trained observers conducted three avian point counts per year from 2011 to 2013 at each station between 29 May and 18 July. Repeated visits to a site within a year were separated by approximately 2 weeks, and surveys were conducted between sunrise and 10:30 a.m. in suitable weather conditions (i.e., no rain and minimal wind). Each of the nine counts per site lasted 10 min, and observers recorded all birds seen or heard within 50 m. We excluded birds detected beyond 50 m and those flying overhead.

Our points fell along a gradient in edge distances, and edge effects can substantially alter vegetation (Fletcher et al., 2007; Ries et al., 2004). Thus, we also conducted local vegetation surveys at each point count station. Because the impact of local vegetation on bird communities was not our primary focus, we used a principal component analysis to reduce the dimensionality of these data. Details of how vegetation data were

collected and processed are found in Supporting Information Appendix S2.

### 2.3 | Data analyses

Over 3 years, we recorded 114 bird species (Supporting Information Appendix S1: Table S1.1). Before analysis, we removed all transient migrants, and those species poorly sampled by point counts (e.g., raptors, swifts, hummingbirds). We classified the remaining 74 species into four ecological trait groups: forest interior specialists (8), forest edge specialists (21), forest generalists (23) and habitat generalists (22). We made these classifications a priori based on previous studies (e.g., Lynch & Whigham, 1984; Robbins, Dawson, & Dowell, 1989; Villard, 1998), and by consultation with the Birds of North America accounts (Rodewald, 2015). For habitat generalists (i.e., species regularly occurring outside of forest), forest amount and patch sizes are not biologically relevant metrics of available habitat, and we had no other reason to expect these metrics would influence generalist distribution patterns. Thus, we excluded these species from further analyses.

We fit a temporally-dependent, Bayesian community occupancy model to the point count data for the 52 forest-associated species. Community occupancy models estimate species-specific occupancy and detection parameters within a hierarchical framework where estimates are related through community-level hyperparameters (Kéry & Royle, 2008; Zipkin et al., 2009). The full advantages of such a modelling approach are detailed elsewhere (Iknayan et al., 2014; Kéry & Royle, 2008; Royle & Dorazio, 2008; Zipkin et al., 2009), but we chose this approach for three primary reasons. First, it allows explicit modelling of detection probabilities. Second, by sharing information across species, the approach allowed us to increase the accuracy and precision of parameter estimates via Bayesian shrinkage (i.e., “borrowing strength”), and thus retain rare species for richness summaries (Iknayan et al., 2014; Royle & Dorazio, 2008; Zipkin et al., 2009). Lastly, we were interested in the community hyperparameter estimates themselves to summarize differences among trait groups.

In our model,  $y_{hijklm}$  represents observed detections, taking a value of 1 if species  $i$  in trait group  $h$  was detected in patch  $j$  at site  $k$  during survey  $m$  of year  $l$ , and 0 otherwise. We assumed  $y_{hijklm} \sim \text{Bernoulli}(Z_{hijkl} * p_{hijklm})$  where  $Z_{hijkl}$  represents the true species-specific occurrence state, and  $p_{hijklm}$  represents the species-specific probability of detection at the site during the sampled time. This model assumes that sites are closed to occupancy changes within a breeding season (about 7 weeks), which is likely reasonable for most of our species (Valente, Hutchinson, & Betts, 2017). We assumed that  $Z_{hijkl} \sim \text{Bernoulli}(\psi_{hijkl})$ , and incorporated covariate effects on occupancy ( $\psi_{hijkl}$ ) and detection ( $p_{hijklm}$ ) probabilities into the model on the logit scale.

We expected detection probability for most species would decline with increasing Julian date (JULIAN), and increasing tree basal area (TREE). Thus, we modelled detection probabilities as

$$\text{logit}(p_{hijklm}) = \alpha 0_{hi} + \alpha 1_{hi} \text{JULIAN}_{jklm} + \alpha 2_{hi} \text{TREE}_{jkl}$$

We modelled occupancy probability as a function of the first three local vegetation principal components (PC1, PC2 and PC3; Supporting Information Appendix S2), edge distance (EDGE), log-transformed patch size (SIZE), amount of forest within 2 km (AMNT), and an interaction between SIZE and AMNT. While many points had overlapping 2 km landscapes (Figure 2), this is not, itself, a statistical concern (Zuckerberg et al., 2012). To account for autocorrelation among points within the same patch, we included a unique random patch effect (PATCH) for each trait group in each year. For the first year, we specified the occupancy model as

$$\text{logit}(\psi_{hijk1}) = \beta 0_{hi} + \text{PATCH}_{hij1} + \beta 1_{hi} \text{PC1}_{jk1} + \beta 2_{hi} \text{PC2}_{jk1} + \beta 3_{hi} \text{PC3}_{jk1} + \beta 4_{hi} \text{EDGE}_{jk} + \beta 5_{hi} \text{SIZE}_{jk} + \beta 6_{hi} \text{AMNT}_{jk} + \beta 7_{hi} \text{SIZE}_{jk} \text{AMNT}_{jk}$$

In subsequent years, we assumed the covariate effects remained constant, but occupancy probability was dependent on occupancy in the previous year. Thus, for  $l > 1$ ,

$$\text{logit}(\psi_{hijkl}) = \gamma 1_{hi} Z_{hijk(l-1)} + \text{PATCH}_{hijl} + \beta 1_{hi} \text{PC1}_{jkl} + \beta 2_{hi} \text{PC2}_{jkl} + \beta 3_{hi} \text{PC3}_{jkl} + \beta 4_{hi} \text{EDGE}_{jk} + \beta 5_{hi} \text{SIZE}_{jk} + \beta 6_{hi} \text{AMNT}_{jk} + \beta 7_{hi} \text{SIZE}_{jk} \text{AMNT}_{jk}$$

where  $\gamma 1_{hi}$  is a species-specific autologistic parameter (Royle & Dorazio, 2008), representing the change in the occupancy intercept if the site was previously occupied. We chose this model specification over a dynamic model (e.g., MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003) because we were not explicitly interested in rates of distributional change, but rather community structure in each year. We standardized all covariates to assist with model convergence. Although SIZE and EDGE were moderately correlated ( $r = 0.62$ ), the correlation between all other variable pairs was weak ( $|r| < 0.25$ ; Supporting Information Appendix S1: Table S1.2).

We expected that species sharing a trait group would respond to occupancy covariates similarly. However, we did not expect random patch effects or detection covariates to vary systematically between these groups. Thus, we specified parameter-specific hyperdistributions for the covariate effects in the following way:

$$\theta_{hi} \sim \text{Normal}(\mu_{\theta,h}, \sigma_{\theta,h}^2), \quad \text{for } \theta = \beta 0 - \beta 7, \gamma 0, \text{ and } \gamma 1$$

$$\theta_{hi} \sim \text{Normal}(\mu_{\theta}, \sigma_{\theta}^2), \quad \text{for } \theta = \alpha 0 - \alpha 2$$

$$\text{PATCH}_{hijl} \sim \text{Normal}(0, \sigma_{\text{patch}}^2)$$

Because our initial model indicated only weak support for a significant SIZE\*AMNT interaction for most species, we fit a second model that excluded this term. We fit both models in JAGS (Plummer, 2003) using the “JAGSUI” package (v. 1.4.2; Kellner, 2016) in R (v. 3.1.2; R Core Team, 2014). We specified vague priors for all community hyperparameters, and for each model, we ran three Markov chain

Monte Carlo (MCMC) chains for 400,000 iterations with a burn-in of 200,000 and thinned by 100. We assessed model convergence by visually inspecting traceplots and ensuring the Gelman–Rubin statistic for monitored parameters was  $<1.1$  (Gelman, Carlin, Stern, & Rubin, 2004). For the full model specification, including our model fit assessment, see Supporting Information Appendix S3.

We evaluated support for our hypotheses for each species and trait group mean based on 95% posterior credible intervals for the variables SIZE and AMNT (Figure 1). We deemed effects significant if the intervals did not overlap zero. Because SIZE and AMNT were only weakly correlated, we interpreted a significant positive SIZE effect as support for the *patch size hypothesis*, and a significant positive AMNT effect as support for the *forest amount hypothesis*. A significant negative SIZE\*AMNT term supported the *nonlinear patch size hypothesis*, and the *random sample hypothesis* was supported if credible intervals overlapped zero for all landscape terms.

Because all species are detected imperfectly, point-level species richness could not be directly observed. Thus, our model does not explicitly examine the relationship between richness and covariates. Following Zipkin et al. (2009), we instead inferred these relationships by examining predicted species richness as an emergent value from the model. For each of the posterior draws, we first calculated predicted probability of occupancy for each species by varying the values of SIZE or AMNT and holding all other covariates constant at their means. We then calculated predicted richness for the entire community and for each trait group separately by summing these values at each iteration, resulting in a posterior distribution of predicted richness for each SIZE or AMNT value.

### 3 | RESULTS

We found little support for the *nonlinear patch size hypothesis*. The SIZE\*AMNT interaction term was non-significant for 88% of species, and only significantly negative for Hooded Warbler (*Setophaga citrina*, Supporting Information Appendix S1: Figure S1.2). We found no evidence for lack of fit in the model that included ( $p = 0.571$ ) or excluded ( $p = 0.568$ ) the interaction term. Indeed, the posterior distributions for all parameters shared between the two models were nearly identical (Supporting Information Appendix S1: Figure S1.2). Therefore, we present the results from the more parsimonious model below (and see Supporting Information Appendix S1: Tables S1.3, S1.4).

We found evidence for the *random sample hypothesis* for one interior species (13%), 11 edge species (52%) and eight forest generalists (35%). Note, however, that we had very few detections for most of these 20 species, resulting in large posterior credible intervals for the effects of SIZE and AMNT (Figure 3). One or more local covariates (edge distance, PC1, PC2 or PC3) influenced the probability of occupancy for 26 (50%) species (Supporting Information Appendix S1: Table S1.3). In fact, estimates of the effects of edge distance confirmed our trait group classifications. On average, probability of occupancy was greater at points further from the edge for interior specialists, and greater at points close to the edge for edge

specialists; for all forest generalists, the credible intervals for the edge distance effect overlapped zero (Figure 3).

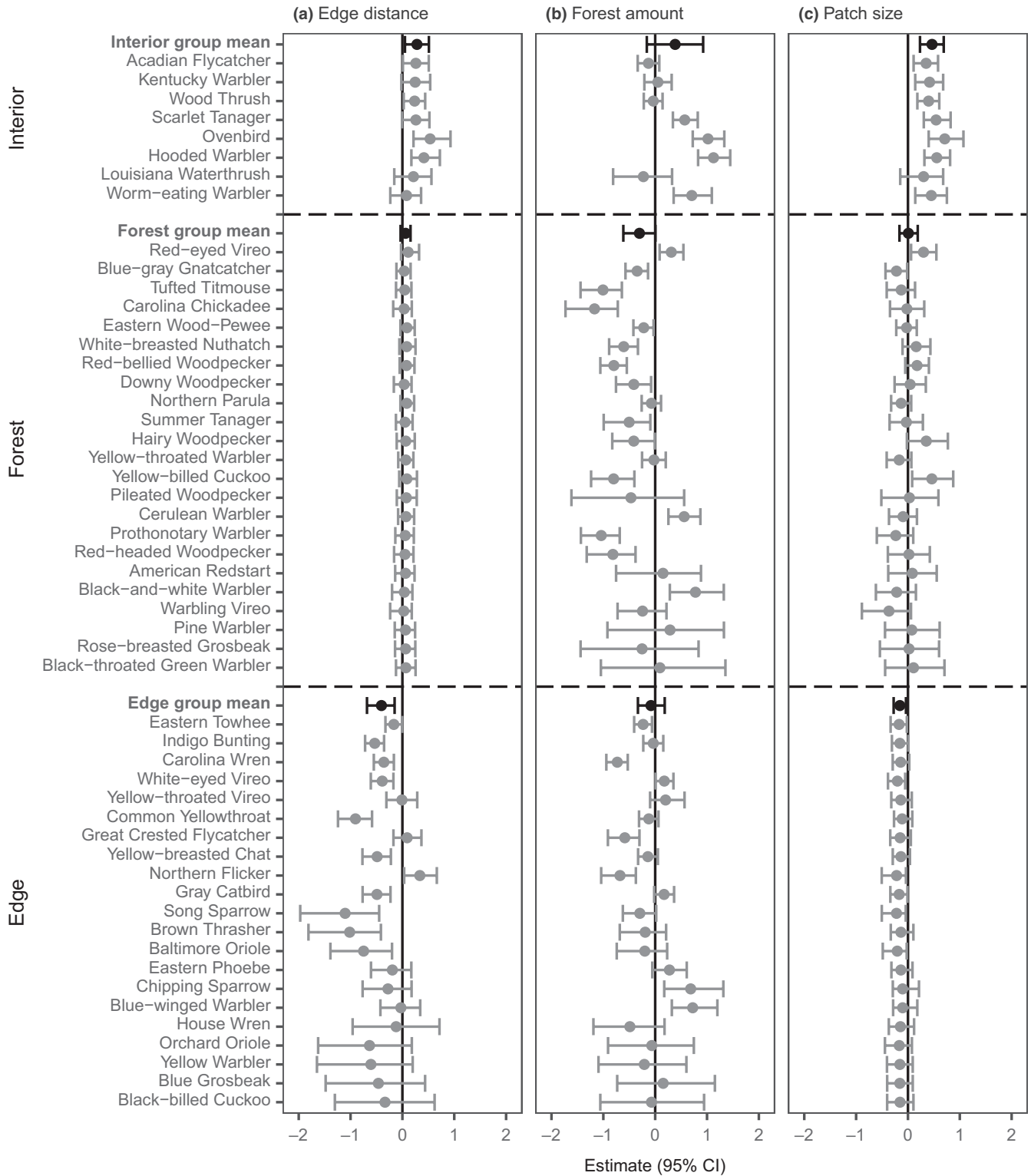
Our test of the *patch size hypothesis* revealed substantial differences in responses by ecological trait groups. The mean patch size effect was significantly positive for interior specialists, significantly negative for edge specialists and approximately zero for forest generalists (Figure 3). Indeed, 78% of species that were significantly positively associated with patch size were interior specialists, and 86% that were significantly negatively associated with patch size were edge specialists. These results were also reflected in emergent patterns of species richness. Predicted richness increased with patch size for interior specialists and decreased with patch size for edge specialists. We saw no strong trend for forest generalists or all species combined (Figure 4).

To ensure these results truly represented patch size effects and were not merely an artefact of the correlation between SIZE and EDGE, we followed the recommendations of Fletcher et al. (2007) and refit the model using only those point count stations located within 100 m of an edge ( $n = 306$ ). This reduced the correlation between these variables to 0.17, and yet, the model yielded a similar pattern (Supporting Information Appendix S1: Figure S1.3); the estimate of the mean patch size effect was significantly positive for interior specialists, and nearly significantly negative for edge specialists. Though the credible interval did slightly overlap zero for this latter group, this is most likely a function of the larger error stemming from a 38% reduction in the number of point count stations used in the model. These results thus provide conclusive evidence for patch size effects that cannot be attributed to effects of edge distance or habitat amount.

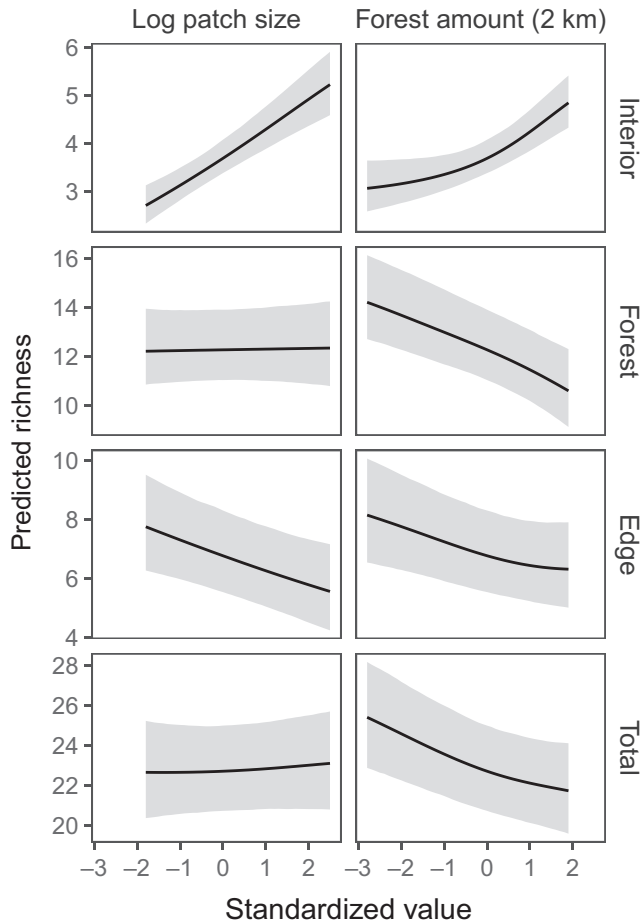
Support for the *forest amount hypothesis* was more variable within trait groups. Credible intervals for the average effect of forest amount overlapped zero for all groups (Figure 3). Nevertheless, a much greater proportion of interior species was significantly positively associated with forest amount (50%), when compared to the generalist (13%) and edge (14%) groups. Surprisingly, 16 total species were significantly negatively associated with forest amount within 2 km, including over half of the generalists. Of these 16 species, 11 (69%) are obligate primary (Downy Woodpecker [*Picoides pubescens*], Hairy Woodpecker [*Leuconotopicus villosus*], Red-bellied Woodpecker [*Melanerpes carolinus*], Red-headed Woodpecker [*Melanerpes erythrocephalus*], and Northern Flicker [*Colaptes auratus*]) or secondary (Carolina Chickadee [*Poecile carolinensis*], Prothonotary Warbler [*Protonotaria citrea*], Tufted Titmouse [*Baeolophus bicolor*], White-breasted Nuthatch [*Sitta carolinensis*], Carolina Wren [*Thryothorus ludovicianus*], and Great Crested Flycatcher [*Myiarchus crinitus*]) cavity nesters (Rodewald, 2015). Again, these results were reflected in emergent richness patterns; while predicted richness of interior species increased with increasing forest cover, the opposite pattern was noted for edge specialists, generalists and all species combined (Figure 4).

#### 3.1 | Detection probability

Detection probabilities (and covariate effects) varied widely among species. Although we initially assumed detection probabilities would not differ among ecological trait groups, interior specialists



**FIGURE 3** Posterior means and 95% credible intervals for the effects of (a) edge distance, (b) amount of forest within 2 km and (c) log-transformed patch size on probability of occupancy for breeding forest bird communities. Species were divided into three ecological trait groups (interior specialist, forest generalist or edge specialist), and the mean effect of the covariate on members of each group was estimated along with individual effects. Within each trait group, species are listed from most common (top) to least common, or equivalently, from most influential on the group mean estimate, to least. Note that all covariates were standardized with a mean of 0 and standard deviation of 1 prior to model fitting

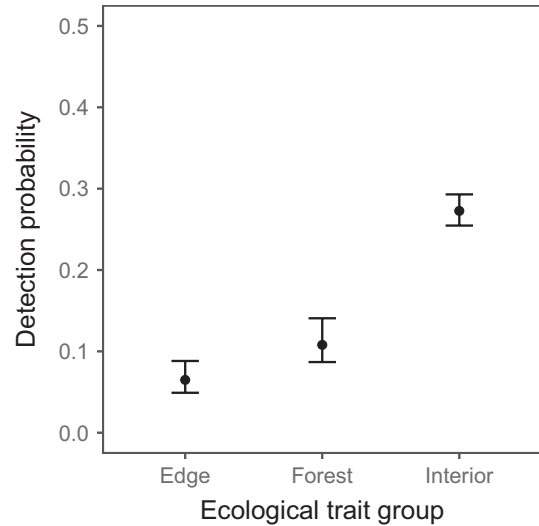


**FIGURE 4** Predicted richness ( $\pm 95\%$  credible intervals) of breeding forest birds occupying a 50 m radius forest plot varies as a function of forest patch size (left), local forest cover (right) and ecological trait group (interior specialists, forest generalists, and edge specialists). Predicted richness values were calculated from each of 6,000 draws from the posterior distributions of a community occupancy model, and represent the sum of the predicted occupancy probabilities of species when all other local and landscape variables are held constant at their means

tended to be more detectable. The average detection intercept for interior specialists was 2.5 times larger than the average intercept for forest generalists, and over four times larger than the average intercept for edge specialists (Figure 5). Detectability of 31 species (60%) was significantly influenced by at least one modelled covariate (Supporting Information Appendix S1: Table S1.4). Effects of tree basal area tended to be weak and non-significant, (posterior community mean = 0.02; 95% CI = -0.02, 0.06) while the effects of Julian date tended to be strong and negative (posterior community mean = -0.16; 95% CI = -0.26, -0.06).

## 4 | DISCUSSION

In this study, we tested for the independent effects of patch size and habitat amount on the distribution of forest breeding birds



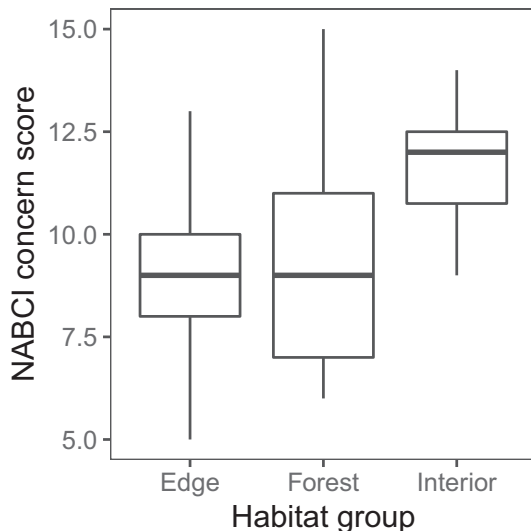
**FIGURE 5** The inverse logit (and 95% credible interval) of the average detection probability intercept for species classified as edge specialists, forest generalists and interior specialists. The values plotted are the means of the posterior distributions from a community occupancy model where intercepts represent the probability of detecting the species at a site with average tree basal area, sampled on the mean Julian date

while accounting for the confounding effects of edge distance, sample area and imperfect detection. Although we found little evidence for the *nonlinear patch size hypothesis*, both the *forest amount* and *patch size hypotheses* were supported for numerous species. These results bolster a substantial body of research highlighting the impact of landscape structure on species distribution patterns. Importantly, our results unequivocally demonstrate that patch size per se has a significant influence on the distribution of many species, beyond the amount of forest these patches contribute at landscape scales. Although we found that overall species richness varies little with patch size, community composition changes in ways that can be predicted by general ecological traits.

The primary goal of our study was to separate the independent effects of patch size and habitat amount on breeding bird communities. To ensure minimal correlation between these covariates, we had to define them prior to sampling using definitions we expected would be relevant to most members of the community. In designing this study, we thus made two explicit assumptions. The first is that a 2 km landscape is a biologically relevant scale for measuring habitat for most species. The second is that “forest” is a reasonable proxy for “habitat” for those species. Unfortunately, designing multispecies studies that account for idiosyncrasies in habitat requirements and perceptual range while minimizing correlation between composition and configuration variables for all species would require an extraordinary logistical effort that was beyond our scope. Thus, our study does not constitute a rigorous “species-centred” test of any of our hypotheses (Betts et al., 2014; Fahrig, 2013; Hanski, 2015), and it is critical to interpret our results within this context.

We found support for the *forest amount hypothesis* for <20% of species in our study, a result that notably contrasts with results from





**FIGURE 6** The distribution of conservation concern scores for 52 species classified as edge specialists, forest generalists or interior specialists (North American Bird Conservation Initiative, 2016). Results from a linear model showed interior specialists, which tend to be positively associated with forest patch size, are of greater conservation concern than forest edge ( $t = 2.92$ ,  $p = 0.005$ ) or generalist ( $t = 2.81$ ,  $p = 0.007$ ) species

other published research (Andr n, 1994; De Camargo et al., 2018; Fahrig, 2003, 2013, 2017; McGarigal & Cushman, 2002; Trzcinski et al., 1999). Given that different species are known to respond to landscape metrics at different spatial scales (e.g., Melo et al., 2017; Mitchell et al., 2001), one logical explanation is that we did not measure this variable at the appropriate scale for all species. We did refit our model using forest amount variables measured at eight alternative spatial scales (250 m–5 km), and the main results from these analyses are presented in Supporting Information Appendix S1: Figure S1.4. However, we chose not to focus on these results for three reasons. First, between 750 m and 5 km, the forest amount measures were highly correlated ( $r > 0.8$ ) with forest cover at 2 km (Supporting Information Appendix S1: Table S1.5) and using them in the model had very little impact on parameter estimates (Supporting Information Appendix S1: Figure S1.4). Secondly, when we measured forest cover at finer spatial scales (250 m–500 m), correlation with patch size increased dramatically ( $r \geq 0.53$ ; Supporting Information Appendix S1: Table S1.5), undermining our original sampling goal of separating the independent effects of these variables. Lastly, a post hoc analysis of natal dispersal distances supported the validity of our original decision. When we converted the range in reported home range sizes for our study species (Rodewald, 2015) to dispersal distances (Bowman, 2003), the estimated dispersal range for 94% of species included or was <2 km. Therefore, our forest amount metric likely encompassed ecologically relevant scales for most members of the community (Supporting Information Appendix S1: Figure S1.5).

An alternative explanation, then, is that the amount of forest does not adequately represent the amount of “habitat” for all species. This idea is supported by the fact that many cavity nesters were

negatively associated with forest cover (Figure 3). We speculate this may be because availability of cavity trees is inversely related to forest cover in our study region. Tree mortality tends to be greater near forest edges (e.g., Esseen, 1994), and it is possible that landscapes with lower forest cover tended to have greater edge-to-area ratios. It is also possible that cavity nesters exhibit preferences for certain tree species (e.g., Martin, Aitken, & Wiebe, 2004) that are less prevalent in heavily forested landscapes. Though we are unable to identify the exact mechanism, failure to account for the distribution of cavity trees at the landscape scale likely meant that forest cover was a poor measure of habitat amount, even for many of our generalist species.

Yet regardless of whether we accurately measured “habitat” for any particular species, our results clearly show that forest patch size does influence the distribution of many species. The average patch size effect was significantly positive for interior specialists, significantly negative for edge specialists and approximately zero for forest generalists (Figure 3). Moreover, our results suggest these patterns cannot be attributed to the correlation ( $r = 0.62$ ) between patch size and edge distance in our full model. First, because edge distance was also included in the model, this correlation would likely increase the variability in the patch size parameter estimates (Dormann et al., 2013), making our test conservative. Secondly, the pattern held even after excluding point count stations further than 100 m from an edge (Supporting Information Appendix S1: Figure S1.3). In fitting this latter model, we effectively measured the community response at similar edge distances in large and small patches which is recommended for separating patch size effects from edge effects (Fletcher et al., 2007). Thus, we consider our results regarding patch size effects to be strong and conclusive.

Bender et al. (1998) identified a similar pattern in their review of patch size effects on animal densities, pointing out that the amount of habitable area is overestimated for interior species at low patch sizes, and for edge species at large patch sizes. Our results may have been driven by a similar geometric pattern; the size of a contiguous habitable interior patch would increase with forest patch size, while small patches have a greater edge-to-area ratios. This prompted us to test whether interior and edge species distributions were positively associated with core patch size and edge patch size, respectively. However, our results did not differ markedly from the model presented because all three measures of patch size were highly correlated (Supporting Information Appendix S1: Figure S1.6).

Theoretical and empirical studies with diverse species have demonstrated that there is often a landscape threshold around 30% habitat cover, below which community composition shifts most drastically (e.g., Andr n, 1994; Banks-Leite et al., 2014; Pardini et al., 2010). Due to generally high forest cover in our study region, only about 4% ( $n = 21$ ) of our study sites had <30% forest cover within 2 km (Supporting Information Appendix S1: Figure S1.1). As a result, our study likely had low statistical power to detect an interaction between patch size and habitat amount, and perhaps even effects of habitat amount themselves (Banks-Leite et al., 2014; Pardini et al., 2010). For this reason, we cannot rule out the possibility that some of our study species have nonlinear responses to habitat loss or

fragmentation. This does not, however, negate the general pattern of our results, but perhaps implies that we may have found even more extreme patch size effects had we sampled a broader range in habitat amount.

Like previous studies, we did not find that total species richness increased with increasing patch size (Fahrig, 2013). Though we excluded 22 habitat generalist species from our analysis, this pattern would not have changed had they been included, as occupancy probability for most habitat generalists decreased (non-significantly) with increasing patch size (Supporting Information Appendix S1: Figure S1.7). Such evidence has prompted calls to dismiss patch size as a useful metric because its effects do not conform with IBT (MacArthur & Wilson, 1967) or metapopulation theory (Hanski, 1998; Levins, 1969). In fact, in a recent review, Fahrig (2017) found that the distributions of individual species are far more likely to increase, rather than decrease, with fragmentation. Yet, the ratio of interior ( $n = 8$ ) to edge ( $n = 21$ ) specialists in our study may help explain these results; if edge specialists are simply more common, one would expect to find negative patch size effects more often, and therefore no positive patch size effect on richness.

More importantly, our results notably contrast with one of Fahrig's (2017) main conclusions that "there is no justification for assigning lower conservation value to a small patch than to an equivalent area within a large patch..." Our interior specialists are of significantly greater conservation concern than forest edge ( $t = 2.92$ ,  $p = 0.005$ ) or generalist ( $t = 2.81$ ,  $p = 0.007$ ) species (Figure 6). These results are based on a comparison of North American Bird Conservation Initiative (2016) concern scores, which have greater precision than coarse IUCN population trends on which similar assessments have been made (e.g., Fahrig, 2017). In our study region then, larger patches do have greater conservation value for those species in greatest need of conservation efforts.

There are numerous potential mechanisms that could explain the sensitivity of interior specialists to fragmentation. These species may actively avoid choosing territories in small habitat patches due to altered biophysical properties (Fletcher et al., 2007) or may be more sensitive to the mechanisms driving extinction or dispersal limitation in fragmented landscapes (Stratford & Robinson, 2005). Alternatively, interior species may be particularly reliant on conspecific attraction during habitat selection, which can manifest as area sensitivity (Fletcher, 2009). Unfortunately, isolating these mechanisms was beyond the scope of this study and is left to future work.

Finally, our results demonstrate the benefit of a hierarchical approach to modelling community structure. In our study, species which tended to be negatively associated with patch size (edge specialists) also tended to have lower detection probabilities than those positively associated with patch size (interior specialists, Figure 5). Territories of edge specialists may encompass non-forested habitats, and our point counts were specifically designed to exclude these areas. As such, we hypothesize that edge specialists had lower detectability due to higher rates of temporary emigration from our

point count stations (Valente et al., 2017), though that also requires further study. Regardless of the mechanism, when patch sizes were large, we were likely detecting a greater proportion of the species in the community during a survey than when patch size was small. Failing to account for this could therefore artificially inflate the positive association between species richness and patch size. Thus, ignoring detection heterogeneity does not necessarily explain the general lack of empirical support for fragmentation effects (Fahrig, 2013, 2017).

Many argue for abandoning the patch-island paradigm in fragmentation research because patch boundaries and matrix characteristics do not conform with existing theory. That is, larger patches do not tend to have greater species richness as predicted by IBT (e.g., Fahrig, 2013; Mendenhall et al., 2014), boundaries between patches and matrix may not delineate demographically distinct metapopulation units (Baguette, 2004; Fahrig, 2013; Manning et al., 2004), and habitat amount is vastly more important than the size of a patch (Andr n, 1994; Fahrig, 2003, 2013, 2017; McGarigal & Cushman, 2002; Trzcinski et al., 1999). Yet, some species require large forest patches to have any habitat available to them at all. A conservation strategy focused on maintaining large forest patches will not necessarily be beneficial for all or even most species (Fahrig, 2017). Yet given that core forest area has become extremely scarce worldwide (Haddad et al., 2015), and that many species of conservation concern depend upon it (Betts et al., 2017), protecting large forest patches may provide additional benefit beyond the amount of habitat they contribute to the landscape.

## ACKNOWLEDGEMENTS

This research was supported by the Department of Defense Strategic Environmental Research and Development Program grant number RC-2121. We thank L. Ganio, A. Hadley, C. LeGrande, K. McCune and J. Northrup for their intellectual contributions.

## DATA ACCESSIBILITY

All data are available in the supporting information for this article. Code for analyzing these data can be found in Appendix S3.

## ORCID

Jonathon J. Valente  <http://orcid.org/0000-0002-6519-3523>

Matthew G. Betts  <http://orcid.org/0000-0002-7100-2551>

## REFERENCES

- Andr n, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos*, 71, 355–366. <https://doi.org/10.2307/3545823>
- Baguette, M. (2004). The classical metapopulation theory and the real, natural world: A critical appraisal. *Basic and Applied Ecology*, 5, 213–224. <https://doi.org/10.1016/j.baae.2004.03.001>
- Bailey, L. L., Reid, J. A., Forsman, E. D., & Nichols, J. D. (2009). Modeling co-occurrence of northern spotted and barred owls: Accounting for

- detection probability differences. *Biological Conservation*, 142, 2983–2989. <https://doi.org/10.1016/j.biocon.2009.07.028>
- Banks-Leite, C., Pardini, R., Tambosi, L. R., Pearse, W. D., Bueno, A. A., Bruscatin, R. T., ... Metzger, J. P. (2014). Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science*, 345, 1041–1045. <https://doi.org/10.1126/science.1255768>
- Bélisle, M., & Desrochers, A. (2002). Gap-crossing decisions by forest birds: An empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology*, 17, 219–231. <https://doi.org/10.1023/A:1020260326889>
- Bender, D. J., Contreras, T. A., & Fahrig, L. (1998). Habitat loss and population decline: A meta-analysis of the patch size effect. *Ecology*, 79, 517–533. [https://doi.org/10.1890/0012-9658\(1998\)079\[0517:HLAPDA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0517:HLAPDA]2.0.CO;2)
- Betts, M. G., Fahrig, L., Hadley, A. S., Halstead, K. E., Bowman, J., Robinson, W. D., ... Lindenmayer, D. B. (2014). A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, 37, 517–527. <https://doi.org/10.1111/ecog.00740>
- Betts, M. G., Forbes, G. J., & Diamond, A. W. (2007). Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology*, 21, 1046–1058. <https://doi.org/10.1111/j.1523-1739.2007.00723.x>
- Betts, M. G., Forbes, G. J., Diamond, A. W., & Taylor, P. D. (2006). Independent effects of fragmentation on forest songbirds: An organism-based approach. *Ecological Applications*, 16, 1076–1089. [https://doi.org/10.1890/1051-0761\(2006\)016\[1076:IEFOF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1076:IEFOF]2.0.CO;2)
- Betts, M. G., Wolf, C., Ripple, W. J., Phalan, B., Millers, K. A., Duarte, A., ... Levi, T. (2017). Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature*, 547, 441–444. <https://doi.org/10.1038/nature23285>
- Boulinier, T., Nichols, J. D., Sauer, J. R., Hines, J. E., & Pollock, K. H. (1998). Estimating species richness: The importance of heterogeneity in species detectability. *Ecology*, 79, 1018–1028. [https://doi.org/10.1890/0012-9658\(1998\)079\[1018:ESRTIO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1018:ESRTIO]2.0.CO;2)
- Bowman, J. (2003). Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology*, 81, 195–202. <https://doi.org/10.1139/z02-237>
- Cam, E., Nichols, J. D., Sauer, J. R., & Hines, J. E. (2002). On the estimation of species richness based on the accumulation of previously unrecorded species. *Ecography*, 25, 102–108. <https://doi.org/10.1034/j.1600-0587.2002.250112.x>
- Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J. H., Schondube, J. E., de Freitas, S. M., & Fahrig, L. (2015). Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biological Conservation*, 184, 117–126. <https://doi.org/10.1016/j.biocon.2015.01.014>
- Cook, W. M., Lane, K. T., Foster, B. L., & Holt, R. D. (2002). Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, 5, 619–623. <https://doi.org/10.1046/j.1461-0248.2002.00366.x>
- De Camargo, R. X., Boucher-Lalonde, V., & Currie, D. J. (2018). At the landscape level, birds respond strongly to habitat amount but weakly to fragmentation. *Diversity and Distributions*, <https://doi.org/10.1111/ddi.12706>
- Debinski, D. M., & Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14, 342–355. <https://doi.org/10.1046/j.1523-1739.2000.98081.x>
- Didham, R. K., Kapos, V., & Ewers, R. M. (2012). Rethinking the conceptual foundations of habitat fragmentation research. *Oikos*, 121, 161–170. <https://doi.org/10.1111/j.1600-0706.2011.20273.x>
- Dondina, O., Orioli, V., D'Occhio, P., Luppi, M., & Bani, L. (2017). How does forest species specialization affect the application of the island biogeography theory in fragmented landscapes? *Journal of Biogeography*, 44, 1041–1052. <https://doi.org/10.1111/jbi.12827>
- Dorazio, R. M. (2007). On the choice of statistical models for estimating occurrence and extinction from animal surveys. *Ecology*, 88, 2773–2782. <https://doi.org/10.1890/07-0006.1>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Esseen, P.-A. (1994). Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation*, 68, 19–28. [https://doi.org/10.1016/0006-3207\(94\)90542-8](https://doi.org/10.1016/0006-3207(94)90542-8)
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663. <https://doi.org/10.1111/jbi.12130>
- Fahrig, L. (2015). Just a hypothesis: A reply to Hanski. *Journal of Biogeography*, 42, 993–994. <https://doi.org/10.1111/jbi.12504>
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48, 1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Fletcher, R. J. (2009). Does attraction to conspecifics explain the patch-size effect? An experimental test. *Oikos*, 118, 1139–1147. <https://doi.org/10.1111/j.1600-0706.2009.17342.x>
- Fletcher, R. J., Ries, L., Battin, J., & Chalfoun, A. D. (2007). The role of habitat area and edge in fragmented landscapes: Definitively distinct or inevitably intertwined? *Canadian Journal of Zoology*, 85, 1017–1030. <https://doi.org/10.1139/Z07-100>
- Fry, J., Zian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., ... Wickham, J. (2011). Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing*, 77, 858–864.
- Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2004). *Bayesian data analysis* (2nd ed.). Boca Raton, FL: CRC/Chapman and Hall.
- Gilpin, M. E., & Diamond, J. M. (1976). Calculation of immigration and extinction curves from the species area distance relation. *Proceedings of the National Academy of Sciences of the USA*, 73, 4130–4134. <https://doi.org/10.1073/pnas.73.11.4130>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052.
- Hadley, A. S., & Betts, M. G. (2016). Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports*, 1, 55–66. <https://doi.org/10.1007/s40823-016-0007-8>
- Haila, Y. (1983). Land birds on northern islands: A sampling metaphor for insular colonization. *Oikos*, 41, 334–351. <https://doi.org/10.2307/3544092>
- Haila, Y. (2002). A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications*, 12, 321–334.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396, 41–49. <https://doi.org/10.1038/23876>
- Hanski, I. (2015). Habitat fragmentation and species richness. *Journal of Biogeography*, 42, 989–994. <https://doi.org/10.1111/jbi.12478>
- Hanski, I., & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conservation Biology*, 16, 666–673. <https://doi.org/10.1046/j.1523-1739.2002.00342.x>
- Henle, K., Davies, K. F., Kleyer, M., Margules, C., & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, 13, 207–251. <https://doi.org/10.1023/B:BIOC.0000004319.91643.9e>
- Iknayan, K. J., Tingley, M. W., Furnas, B. J., & Beissinger, S. R. (2014). Detecting diversity: Emerging methods to estimate species diversity.

- Trends in Ecology and Evolution*, 29, 97–106. <https://doi.org/10.1016/j.tree.2013.10.012>
- Indiana State Climate Office (2002). *About Indiana climate*. Retrieved from <https://climate.agry.purdue.edu/climate/narrative.asp>
- Kellner, K. (2016). *jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses*. R package version 1.4.2. Retrieved from <http://CRAN.R-project.org/package=jagsUI>
- Kéry, M., & Royle, J. A. (2008). Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, 45, 589–598. <https://doi.org/10.1111/j.1365-2664.2007.01441.x>
- Kéry, M., Royle, J. A., & Schmid, H. (2008). Importance of sampling design and analysis in animal population studies: A comment on Sergio et al. *Journal of Applied Ecology*, 45, 981–986.
- Laurance, W. (2008). Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*, 141, 1731–1744. <https://doi.org/10.1016/j.biocon.2008.05.011>
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15, 237–240. <https://doi.org/10.1093/besa/15.3.237>
- Lomolino, M. V. (1990). The target area hypothesis: The influence of island area on immigration rates of non-volant mammals. *Oikos*, 57, 297–300. <https://doi.org/10.2307/3565957>
- Lynch, J. F., & Whigham, D. F. (1984). Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation*, 28, 287–324. [https://doi.org/10.1016/0006-3207\(84\)90039-9](https://doi.org/10.1016/0006-3207(84)90039-9)
- MacArthur, R. G., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84, 2200–2207. <https://doi.org/10.1890/02-3090>
- Manning, A. D., Lindenmayer, D. B., & Nix, H. A. (2004). Continua and Umwelt: Novel perspectives on viewing landscapes. *Oikos*, 104, 621–628. <https://doi.org/10.1111/j.0030-1299.2004.12813.x>
- Martin, K., Aitken, K. E. H., & Wiebe, K. L. (2004). Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *The Condor*, 106, 5–19. <https://doi.org/10.1650/7482>
- McGarigal, K., & Cushman, S. A. (2002). Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, 12, 335–345. [https://doi.org/10.1890/1051-0761\(2002\)012\[0335:CEOEAT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2)
- Melo, G. L., Sponchiado, J., Cáceres, N. C., & Fahrig, L. (2017). Testing the habitat amount hypothesis for South American mammals. *Biological Conservation*, 209, 304–314. <https://doi.org/10.1016/j.biocon.2017.02.031>
- Mendenhall, C. D., Karp, D. S., Meyer, C. F. J., Hadly, E. A., & Daily, G. C. (2014). Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, 509, 213–217. <https://doi.org/10.1038/nature13139>
- Mitchell, M. S., Lancia, R. A., & Gerwin, J. A. (2001). Using landscape-level data to predict the distribution of birds on a managed forest: Effects of scale. *Ecological Applications*, 11, 1692–1708. [https://doi.org/10.1890/1051-0761\(2001\)011\[1692:ULLDTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1692:ULLDTP]2.0.CO;2)
- National Climatic Data Center (2011). *NOAA's 1981–2010 climate normals*. Retrieved from <http://www.ncdc.noaa.gov/oa/climate/normals/usnormals.html>
- Norris, D. R., & Stutchbury, B. J. M. (2001). Extraterritorial movements of a forest songbird in a fragmented landscape. *Conservation Biology*, 15, 729–736. <https://doi.org/10.1046/j.1523-1739.2001.015003729.x>
- North American Bird Conservation Initiative (2016). *The state of North America's birds 2016*. Ottawa, ON, Canada: Environment and Climate Change Canada.
- Pardini, R., Bueno, A. D. A., Gardner, T. A., Prado, P. I., & Metzger, J. P. (2010). Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*, 5, e13666. <https://doi.org/10.1371/journal.pone.0013666>
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In K. Hornik, F. Leisch & A. Zeileis (Eds.), *Proceedings of the 3rd International Workshop on Distributed Statistical Computing* (pp. 1–10). Vienna, Austria: Technische Universität Wien.
- Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the USA*, 105, 20770–20775. <https://doi.org/10.1073/pnas.0806080105>
- Püttker, T., Bueno, A. A., de Barros, C. S., Sommer, S., & Pardini, R. (2013). Habitat specialization interacts with habitat amount to determine dispersal success of rodents in fragmented landscapes. *Journal of Mammalogy*, 94, 714–726. <https://doi.org/10.1644/12-MAMM-A-119.1>
- R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Ries, L., Fletcher, R. J., Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, 35, 491–522. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130148>
- Robbins, C. S., Dawson, D. K., & Dowell, B. A. (1989). Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs*, 103, 3–34.
- Rodewald, P. (2015). *The birds of North America*. Ithaca, NY: Cornell Lab of Ornithology. Retrieved from <https://birdsna.org>
- Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology*. Boston, MA: Academic Press.
- Samu, F., Csontos, P., & Szinetar, C. (2008). From multi-criteria approach to simple protocol: Assessing habitat patches for conservation value using species rarity. *Biological Conservation*, 141, 1310–1320. <https://doi.org/10.1016/j.biocon.2008.03.015>
- Stratford, J. A., & Robinson, W. D. (2005). Gulliver travels to the fragmented tropics: Geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and the Environment*, 3, 91–98. <https://doi.org/10.2307/3868515>
- Thornton, D. H., Branch, L. C., & Sunquist, M. E. (2011). The influence of landscape, patch, and within-patch factors on species presence and abundance: A review of focal patch studies. *Landscape Ecology*, 26, 7–18. <https://doi.org/10.1007/s10980-010-9549-z>
- Trzcinski, M. K., Fahrig, L., & Merriam, G. (1999). Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications*, 9, 586–593. [https://doi.org/10.1890/1051-0761\(1999\)009\[0586:IEOFCA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0586:IEOFCA]2.0.CO;2)
- Valente, J. J., Hutchinson, R. A., & Betts, M. G. (2017). Distinguishing distribution dynamics from temporary emigration using dynamic occupancy models. *Methods in Ecology and Evolution*, 8, 1707–1716. <https://doi.org/10.1111/2041-210X.12840>
- Villard, M.-A. (1998). On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *The Auk*, 115, 801–805.
- Villard, M.-A., & Metzger, J. P. (2014). Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, 51, 309–318. <https://doi.org/10.1111/1365-2664.12190>
- Villard, M.-A., Trzcinski, M. K., & Merriam, G. (1999). Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology*, 13, 774–783. <https://doi.org/10.1046/j.1523-1739.1999.98059.x>
- Zipkin, E. F., DeWan, A., & Royle, J. A. (2009). Impacts of forest fragmentation on species richness: A hierarchical approach to community modelling. *Journal of Applied Ecology*, 46, 815–822. <https://doi.org/10.1111/j.1365-2664.2009.01664.x>
- Zuckerberg, B., Desrochers, A., Hochachka, W. M., Fink, D., Koenig, W. D., & Dickinson, J. L. (2012). Overlapping landscapes: A persistent, but misdirected concern when collecting and analyzing ecological data. *Journal of Wildlife Management*, 76, 1072–1080. <https://doi.org/10.1002/jwmg.326>

## BIOSKETCHS

**Jonathon J. Valente** is a quantitative ecologist who focuses on understanding the factors influencing species distribution patterns and the mechanisms driving them. He is particularly interested in evaluating how biological and statistical assumptions influence the way we perceive these patterns.

**Matthew G. Betts** is a professor of Landscape Ecology in the Department of Forest Ecosystems and Society at Oregon State University and the Director of the Forest Biodiversity Research Network (<https://www.forestbiodiversity.org>). His group studies drivers and consequences of species diversity and distributions in tropical and temperate systems.

Authors' contributions: M.G.B. conceived the original research idea. J.J.V. developed the study design, and conducted the data collection and analysis with input from M.G.B. Both authors wrote the manuscript.

## SUPPORTING INFORMATION

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

**How to cite this article:** Valente JJ, Betts MG. Response to fragmentation by avian communities is mediated by species traits. *Divers Distrib*. 2019;25:48–60. <https://doi.org/10.1111/ddi.12837>