

Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species

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Summary

1. Worldwide loss of biodiversity necessitates a clear understanding of the factors driving population declines as well as informed predictions about which species and populations are at greatest risk. The biggest threat to the long-term persistence of populations is the reduction and changes in configuration of their natural habitat.

2. Inconsistencies have been noted in the responses of populations to the combined effects of habitat loss and fragmentation. These have been widely attributed to the effects of the matrix habitats in which remnant focal habitats are typically embedded.

3. We quantified the potential effects of the inter-patch matrix by estimating occupancy and colonization of forest and surrounding non-forest matrix (NF). We estimated species-specific parameters using a dynamic, multi-species hierarchical model on a bird community in southwestern Costa Rica.

4. Overall, we found higher probabilities of occupancy and colonization of forest relative to the NF across bird species, including those previously categorized as open habitat generalists not needing forest to persist. Forest dependency was a poor predictor of occupancy dynamics in our study region, largely predicting occupancy and colonization of only non-forest habitats.

5. Our results indicate that the protection of remnant forest habitats is key for the long-term persistence of all members of the bird community in this fragmented landscape, including species typically associated with open, non-forest habitats.

6. *Synthesis and applications.* We identified 39 bird species of conservation concern defined by having high estimates of forest occupancy, and low estimates of occupancy and colonization of non-forest. These species survive in forest but are unlikely to venture out into open, non-forested habitats, therefore, they are vulnerable to the effects of habitat loss and fragmentation. Our hierarchical community-level model can be used to estimate species-specific occupancy dynamics for focal and inter-patch matrix habitats to identify which species within a community are likely to be impacted most by habitat loss and fragmentation. This model can be applied to other taxa (i.e. amphibians, mammals and insects) to estimate species and community occurrence dynamics in response to current environmental conditions and to make predictions in response to future changes in habitat configurations.

Key-words: colonization, community dynamics, forest dependency, fragmentation, habitat loss, hierarchical model, matrix effects, occupancy modelling

Introduction

Determining how animal populations relate to their environment is the fundamental basis for understanding how popula-

tion processes are affected by changes in landscape characteristics (Kareiva & Wennergren 1995). Current declines in biodiversity, widely attributed to habitat loss and fragmentation, have motivated ecologists to improve predictions regarding the responses of wildlife populations to changes in the amount and configurations of available habitat (Wiens

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1996; Balmford, Green & Jenkins 2003). This requires identification of key environmental features that are directly linked to species' long-term probabilities of persistence in a landscape after a fragmentation event (Franklin & Noon 2002). Research on this topic has developed from a focus on metrics related to habitat patches (i.e. patch size, isolation) to a landscape-level approach (i.e. connectivity, % habitat cover), establishing a broad base of knowledge on how landscape characteristics can drive the dynamics of species' distributions at different scales (Haila 2002; Laurance 2008). Several decades of research have mainly focused on how the long-term persistence of a species in a given habitat patch is related to patch size and isolation (Andren 1994; Hanski 1999; Driscoll 2007).

There is no clear consensus on the roles that patch size and isolation play on the distribution of species in fragmented landscapes (Bender, Contreras & Fahrig 1998; Debinski & Holt 2000; Ewers & Didham 2006). A recent meta-analysis, using multiple taxa across different continents, concluded that patch size and isolation are 'poor predictors' of which species are likely to persist in a habitat patch (Prugh *et al.* 2008). Several reasons for the inconsistent predictive abilities of patch-related measures were tested. The composition of the inter-patch habitat matrix was found to be the strongest predictor of species' sensitivity to patch size and isolation. These results are consistent with mounting theoretical and empirical evidence suggesting that a significant number of species in heterogeneous landscapes might occupy, opportunistically use and even persist in the inter-patch habitat matrix (Vandermeer & Carvajal 2001; Bender & Fahrig 2005; Driscoll 2005; Debinski 2006; Revilla & Wiegand 2008). For these species, patch-related measures are highly unlikely to reflect sensitivity to habitat loss and fragmentation given that their habitat use is not restricted to a single 'habitat patch'. To date, most research addressing the effects of matrix habitat use has focused on species richness, or the presence or absence of a single or a subset of 'habitat specialist' species, for both focal and matrix habitats (i.e. Wethered & Lawes 2003; Antongiovanni & Metzger 2005).

To improve our understanding of how populations respond to changes in their environment, it is necessary to estimate how species dynamically use focal habitat together with the surrounding non-habitat matrix. This information is crucial for conservation and wildlife management (Blaum & Wichmann 2007; Fahrig 2007; Franklin & Lindenmayer 2009), especially in regions where it is more feasible to improve the quality of the matrix than to increase the proportion of focal habitat (Rudel 2006; Perfecto & Vandermeer 2008).

The impact of changes in the amount and configuration of available habitat are traditionally modelled by examining the probability that a habitat patch is occupied using two main approaches: the colonization-extinction (CE) approach widely used in metapopulation biology (Hanski 1992, 1999) and the birth-immigration-death-emigration (BIDE) approach, mainly applied in landscape ecology (Fahrig 2002). For the CE model, patch occupancy is dependent on population-level colonization and extinction dynamics. As habitat area decreases, colonization of unoccupied habitat patches decreases, and is assumed to be a function of the size and number of near-by

occupied patches (Hanski 1999). This approach assumes that only focal habitat patches are occupied and matrix habitats are used for dispersal, although recent work on matrix effects applying the CE framework have incorporated ease of movement through different matrix types (Hein *et al.* 2004; Ovaskainen 2004). In contrast, the BIDE model predicts that as habitat area decreases, colonization of the matrix by individuals increases, where mortality is assumed to be higher (Fahrig 2002). The result is an overall reduction in population size, decreasing immigration into and increasing emigration rates out of habitat patches (Fahrig 2002). Although the BIDE framework addresses matrix effects at an individual-level through assumed mortality in matrix habitats (similarly to the CE approach), it has yet to jointly incorporate occupancy dynamics of both focal and matrix habitats.

These approaches are currently applied to make general predictions regarding the probability that a sample unit (patch) is occupied by an individual or species (i.e. occupancy) and the related dynamics: colonization (i.e. probability that a sample unit is occupied given it was unoccupied in the previous sampling period) and extinction (the probability that a sample unit is unoccupied given that it was occupied in the previous sampling period) (Hanski 1992; MacKenzie *et al.* 2006). However, most of the predictions based on occupancy dynamics in fragmented landscapes under the BIDE and CE models assume that an individual or species, respectively, was absent when not observed in a habitat patch (Moilanen 2002; MacKenzie 2006). Detectability of animals is less than perfect and can vary by habitat type: species can be present in a habitat patch, but not detected (Williams, Nichols & Conroy 2002; Mackenzie & Royle 2005). This separation of true occupancy from apparent absences is important in making predictions about the occupancy dynamics of contrasting habitat types; differences in occupancy rates between focal habitat patches and the surrounding matrix could be masked or biased by habitat-dependent differences in detectability (Boulinier *et al.* 1998; Moilanen 2002; Driscoll 2007). Current methodology in occupancy modelling accounts for the likelihood of false absences by incorporating detection probabilities, generating more accurate predictions with regards to the true state of occupancy and related dynamics (Royle & Link 2006; Nichols *et al.* 2008). Although much work on occupancy dynamics accounts for detectability (i.e. Boulinier *et al.* 2001; Hames *et al.* 2001; Ferraz *et al.* 2007; Radford & Bennett 2007; Francois, Alexandre & Julliard 2008), occupancy dynamics between habitat types is not contrasted specifically.

In this paper, we quantify differences in species' use of both focal and matrix habitat types by estimating probabilities of occupancy, colonization and detection in forest and intervening NF habitats, for a community of bird species in southwestern Costa Rica. We developed a multi-species hierarchical community model that estimates species and habitat-specific occupancy, colonization and detection. We tested *a priori* expectations on how occupancy and colonization of forest and non-forest habitats should vary among pre-determined categories of forest dependency (Stiles 1985). The framework we present can be applied to estimate species-specific and community

level use of multiple habitat types in a given region. The results from the model can help define which species are largely restricted to a focal habitat type of interest, meeting the assumptions of both CE and BIDE approaches, and are thus most likely to be adversely affected by habitat loss and fragmentation.

Materials and methods

STUDY SITE AND BIRD SURVEYS

The survey sites are situated within a 7 km radius of the Las Cruces Biological Station of the Organization for Tropical Studies in Coto Brus, southwestern Costa Rica. This once continuous forested region became heavily fragmented in the 1940s and 1950s as forests were cleared to make way for small-scale agriculture. The remnant forest fragments in this region are classified as mid-elevation tropical forests (Borgella & Gavin 2005). We surveyed 21, centrally located point count stations within the Las Cruces Forest Reserve (224 ha) and seven remnant forest patches (1.4–25 ha) situated between 900 and 1300 m in elevation. Previous work in the forest habitats of this region did not find significant differences in overall canopy height, diameter at breast height and basal area of trees between the forest fragments at the Forest Reserve used in this study (V. Ruiz-Gutierrez, unpublished data), and thus we classified both forest reserve and patches in a general 'forest' category. We also surveyed 10-point count stations in non-forest matrix (NF) habitat comprised of pasture, coffee and early stage secondary growth (charral). Point count surveys consisted of recording all birds seen and/or heard in 10 min within 50 m maximum detection distance. All surveys were conducted from sunrise (~5:30 am) until 9:00 am, by expert ornithologist J. R. Zook. Each point count station was visited on three consecutive days each year, rotating the daily order in which they were visited, during the months of May–September, from 2004 to 2008, although not all points were surveyed in 2004. These months fall within the time of year that most species in the region are known to reproduce (Stiles & Skutch 1989), which increases the likelihood that species were present within their breeding territories and thus reduces variability in estimates of occupancy. Within a given year, we assumed that the species pool was closed over the survey period, i.e. species were either present or absent for the duration of the 3-day survey.

CLASSIFICATION OF FOREST DEPENDENCY

Our categorization of forest dependency for each species was taken from the system developed by Stiles (1985), based on decades of natural history observations and research on the birds of Costa Rica. Species in the 'HIGH FD' category are considered highly forest dependent, or 'specialized' and mainly restricted to forest habitats. Species in the 'MED FD' category have a moderate degree of forest dependency, and are thought to use both forest and open habitats. Species in the 'LOW FD' are assumed to not need forest and are considered to be open habitat species, limited to deforested areas and agricultural habitats (Stiles 1985).

ANALYSIS

We used a recently developed hierarchical modelling approach that estimates community-level attributes through species-specific estimates of occupancy, detection and colonization (Dorazio & Royle

2005; Dorazio *et al.* 2006; Royle & Dorazio 2008; Kéry *et al.* 2009). Under this framework, occurrence models for all individual species are linked together in a multi-level, or hierarchical model, placing them in a context of related community-level responses to environmental factors (Link & Sauer 2002; Dorazio *et al.* 2006; Kéry & Royle 2008). Hierarchical community models postulate weak relationships among related parameters, in this case by assuming that species-specific parameter values are drawn from a common, community-level distribution (Link & Sauer 2002). Thus, for meaningful results, multi-species analyses should include only species that could conceivably come from a common distribution. Because we were interested in examining potential differences in occupancy dynamics among groups of species with variable forest dependency, we assumed each of the three forest-dependent species groups (i.e. HIGH, MED and LOW) had its own common group-level distribution (further details below). By sharing information across species, we were able to increase the precision of parameter estimates and enhance our understanding of both species-specific occupancy dynamics as well as the composite dynamics of each forest dependency group and thus the entire community. Our approach is especially useful for infrequently observed species for which estimates of occupancy, colonization and detection would otherwise be unattainable through individual species-level analyses (Zipkin, DeWan & Royle 2009).

MODEL

We developed a multi-species hierarchical community model based on survey-specific detection/non-detection records to estimate occupancy dynamics of bird species in forest vs. non-forest habitats. The observations, $x(i, j, t, k)$, denote detection ($x = 1$) or non-detection ($x = 0$) of species i (1, 2, ..., 212) at site j (1, 2, ..., 31) in year t (1, 2, ..., 5) during sampling occasion k (1, 2, 3). We formulated our model by first assuming that occupancy and colonization were species-specific processes that were dependent on habitat type (i.e. forest vs. non-forest). As in previous applications of this method (e.g. Kéry & Royle 2008) we assumed that occupancy for species i at site j in year t , denoted $z(i, j, t)$, was a latent variable (i.e. imperfectly observed) such that $z(i, j, t) = 1$ when species i was present and zero otherwise. If a species in a given location and year was detected, then the species was in fact present. However, if a species was not observed, it could be because either the species was present and went undetected or the species was truly absent. Thus, our repeated sampling protocol ($k > 1$) was designed explicitly to differentiate non-detection from true absences by estimating detection probability.

We tested for differences in occupancy, colonization and detectability between forest and non-forest habitats by including habitat type (hab) as a binary covariate dependent on whether the sampled site (j) was in forest (hab = 1) or non-forest (hab = 0) (Russell *et al.* 2009; Zipkin *et al.* 2010). The topography in this pre-montane region of Costa Rica is highly variable, with many species showing both upper and lower distributional limits along the elevational continuum. In regions with similar topography and species distributions along elevational gradients, elevation has been successfully applied as a surrogate for key habitat variables that influence distribution and abundance (Kéry & Royle 2009). We included linear and quadratic covariate terms for elevation in our occupancy model which allowed us to incorporate species elevational preferences.

We specified the species-specific occurrence model by assuming that occupancy was a Bernoulli random variable, $z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t})$, with probability $\psi_{i,j,t}$, for species i in site j , during year t . For the first year of sampling ($t = 1$), we assumed that species-specific occupancy probabilities were linearly related to the above-mentioned habitat

covariates, forest habitat and elevation, on the logit scale (Kéry & Royle 2009):

$$\text{logit}(\psi_{i,j,t}) = u_{1i}\text{hab}_j + u_{2i}(1 - \text{hab}_j) + \alpha_{1i}\text{elev}_j + \alpha_{2i}\text{elev}_j^2$$

where, $\text{hab}_j = 1$ if site j is in a forest and $\text{hab}_j = 0$ otherwise, thus allowing for species-specific occupancy to vary by habitat type. We standardized elevation covariates so that mean elevation was zero. Under this model, u_{1i} is the probability of occupancy for species i in forested sites at mean elevation, and likewise, u_{2i} is the occupancy probability in non-forest sites (both on the logit scale). The coefficients α_{1i} and α_{2i} are the linear and squared effects of elevation on species i respectively. For $t = 2, \dots, 5$, we modified the occupancy model, such that the probability of occupancy for species i in site j was also dependent upon whether or not that species was present the previous year:

$$\begin{aligned} \text{logit}(\psi_{i,j,t \geq 2}) = & u_{1i}z_{i,j,t-1}\text{hab}_j + u_{2i}z_{i,j,t-1}(1 - \text{hab}_j) \\ & + w_{1i}(1 - z_{i,j,t-1})\text{hab}_j + w_{2i}(1 - z_{i,j,t-1})(1 - \text{hab}_j) \\ & + \alpha_{1i}\text{elev}_j + \alpha_{2i}\text{elev}_j^2. \end{aligned}$$

Thus, w_{1i} and w_{2i} are the occupancy probabilities (on the logit scale) for species i in forest and non-forest, respectively, when species i was not present in the previous year ($z_{i,j,t-1} = 0$). When a species was in fact present in the previous year ($z_{i,j,t-1} = 1$) then the probability of occupancy simplifies to the original model for the first year of sampling. Thus, we define the probability of occupancy (μ_{1i} and μ_{2i}) as a combination of initial occupancy (the probability that species i was present at site j in the first year of sampling), and continued occupancy (the probability that species i was present at site j given it was present the previous year) (Royle & Kéry 2007). Occupancy is therefore the probability of persistence from one year to the next for a given species in forest and non-forest habitats. The probability of colonization (w_{1i} and w_{2i}) is defined as the probability that species i was present at site j in year t , given that it was absent at site j in year $t-1$. Colonization, in turn, is the probability of colonizing available forest and non-forest habitats for a given species.

The detection model was similarly assumed to be a Bernoulli random variable, $x(i, j, t, k) \sim \text{Bern}(p_{i,j,t,k} \cdot z_{i,j,t})$, where, $p_{i,j,t,k}$ is the detection probability of species i for the k th sampling period in year t at site j , given that species i was in fact present at site j . When species i was not present, detection was a fixed zero since $z_{i,j,t} = 0$. We assumed that species identity and the habitat type (forest or non-forest) were the only effects on detection:

$$\text{logit}(p_{i,j,t,k}) = v_{1i}\text{hab}_j + v_{2i}(1 - \text{hab}_j).$$

In the community hierarchical level of the model, the species-specific parameters were linked together through a common distribution (Royle & Dorazio 2008). To test the *a priori* hypothesis that species estimates of occupancy, colonization and detection were associated with their prior categorization of forest dependency, we assumed that species parameter estimates (i.e. occupancy, colonization and detection) were related only to other species within their category and were also stratified by habitat type. For example, all species in the HIGH FD category were linked together by assuming that their parameter values for occupancy (and similarly for colonization and detection) were drawn from a common distribution dependent on habitat type. Specifically, we assumed that $u_{1i \in \text{high}} \sim N(\mu_{1_high}, \sigma_{u_{1_high}})$ where, μ_{1_high} is mean occupancy across the HIGH FD species in forests and $\sigma_{u_{1_high}}$ is the standard deviation (among HIGH FD species in forests) and that $u_{2i \in \text{high}} \sim N(\mu_{2_high}, \sigma_{u_{2_high}})$ is the distribution for HIGH FD species in non-forest sites. We similarly defined the hyperparam-

eters (the mean and standard deviations – across species in a given group – of occupancy, colonization and detection) for MED FD and LOW FD species categories. We assumed that species-specific elevation effects were related across all species (independent of forest dependency classification) and accordingly defined common distributions for the linear and squared effects respectively. We analysed the model using a Bayesian approach with non-informative priors. Model specifications, including WinBUGS code, and implementation details are provided in Appendix S1 (Supporting information).

PREDICTIONS BASED ON PRIOR ECOLOGICAL CLASSIFICATION

We predicted that mean forest occupancy across species would be highest for the HIGH FD category followed by MED FD category, and lowest for the LOW FD category (i.e. $\mu_{u1_high} > \mu_{u1_med} > \mu_{u1_low}$), and we expected the opposite pattern for non-forest habitats (i.e. $\mu_{u2_high} < \mu_{u2_med} < \mu_{u2_low}$). We predicted forest colonization to be higher relative to non-forest for the HIGH FD category (i.e. $\mu_{w1_high} > \mu_{w2_high}$), but did not expect a difference for the MED FD category (i.e. $\mu_{w1_med} \approx \mu_{w2_med}$). For the LOW FD category, we expected colonization to be higher in non-forest relative to forest (i.e. $\mu_{w1_low} < \mu_{w2_low}$). Our null hypothesis was that detection be equal across species and habitat types.

To test our predictions and assess potential differences in occupancy, colonization and detection between categories of forest dependency, we compared posterior distributions of the group-level hyperparameters. We investigated whether values of given parameters were equal, which we estimated by computing the proportion of iterations in which one parameter is greater than another. For example, to compare colonization for the HIGH FD in forest (μ_{w1_low}) to non-forest habitat (μ_{w2_high}), we sum the number of markov chain Monte Carlo (MCMC) iterations in which $\mu_{w1_high} > \mu_{w2_high}$ and divide that by the total number of iterations. If this probability is close to 0.5, that suggests no difference in the parameter values. More extreme differences imply comparatively less overlap in posterior distributions. A major benefit of a Bayesian approach to model analysis is the ease of interpretation of parameters. A probability of 0.95 is interpreted as a 95% probability that $\mu_{w1_high} > \mu_{w2_high}$.

Results

AVIAN COMMUNITY

We observed 212 diurnal species in 31 sites on at least one occasion over the 5 years of sampling. We did not have sufficient data to estimate occupancy, colonization and detection for 139 of the 212 species (i.e. inclusion of too many rare species resulted in unsubstantiated parameter estimates). Even though we were unable to obtain information about a large portion of the observed species, our hierarchical community model was able to produce parameter estimates for many more species than if we had modelled each species separately (Zipkin *et al.* 2009). However, as we focused on a subset of the most frequently observed species, estimates of occupancy were fairly high overall and are unlikely to be indicative of the excluded species. Posterior summaries of species-specific estimates of occupancy are presented in Table S1 (Supporting information), for colonization in Table S2 (Supporting information) and detection in Table S3 (Supporting information).

OCCUPANCY OF FOREST VS. NON-FOREST

Estimates of mean group occupancy of forest habitat (μ_{u1}) for the HIGH ($n = 13$), MED ($n = 39$) and LOW FD ($n = 21$) were fairly high across all categories [0.84(SD 0.06), 0.77(SD 0.04), 0.72(SD 0.09) respectively]. Contrary to our predictions, the posterior distributions of group-level forest occupancy had high overlap among categories ($\Pr(\mu_{u1_high} > \mu_{u1_med} > \mu_{u1_low}) = 0.055$; $\Pr(\mu_{u1_high} > \mu_{u1_med}) = 0.84$; $\Pr(\mu_{u1_high} > \mu_{u1_low}) = 0.67$; $\Pr(\mu_{u1_high} > \mu_{u1_low}) = 0.87$) (Fig. 1a; ($\mu_{u1_high} \approx \mu_{u1_med} \approx \mu_{u1_low}$), suggesting limited differences in forest occupancy by forest-dependent categorization (Fig. 1a). Estimates of species-specific occupancy (u_{1i}) were similarly not dependent on prior categorization of forest dependency (Fig. 2a–c; Table S1, Supporting information). Posterior distributions of mean group occupancy among forest-dependent categories in non-forest overlapped less than in the forest habitat and were more consistent with our predictions ($\Pr(\mu_{u2_high} < \mu_{u2_med} < \mu_{u2_low}) = 0.88$) (Fig. 1b). As predicted, mean occupancy in non-forest was highest for the LOW FD category and did not have high overlap MED FD ($\Pr(\mu_{u2_med} < \mu_{u2_low}) = 0.96$) and HIGH FD ($\Pr(\mu_{u2_high} < \mu_{u2_low}) > 0.99$) categories. The distributions for the MED and HIGH FD categories had a slightly greater proportion of overlap ($\Pr(\mu_{u2_high} < \mu_{u2_med}) = 0.92$) (Fig. 1b). This pattern was also evident in species-specific estimates of non-forest occupancy (Fig. 2a–c).

Occupancy was generally higher in forests compared with non-forests for HIGH ($\Pr(\mu_{u1_high} > \mu_{u2_high}) > 0.99$) and MED ($\Pr(\mu_{u2_med} < \mu_{u2_med}) = 0.98$) FD groups but more similar among forest and non-forest habitat types for the LOW forest-dependent category ($\Pr(\mu_{u1_low} > \mu_{u2_low}) = 0.41$) (Fig 1a,b).

COLONIZATION OF FOREST VS. NON-FOREST

Compared with non-forest habitats, forest habitats had higher colonization probabilities across all groups of species ($\Pr(\mu_{w1_high} > \mu_{w2_high}) = 0.99$); ($\Pr(\mu_{w1_med} > \mu_{w2_med}) > 0.99$); ($\Pr(\mu_{w1_low} > \mu_{w2_low}) = 0.93$); Fig. 1c,d and Table S2, Supporting information). Within non-forested habitat, the LOW FD category had higher colonization probabilities compared with the MED FD ($\Pr(\mu_{w2_med} < \mu_{w2_low}) > 0.98$) and HIGH FD ($\Pr(\mu_{w2_high} < \mu_{w2_low}) > 0.98$) categories yet there was no difference between the MED and HIGH FD groups ($\Pr(\mu_{w2_high} < \mu_{w2_med}) > 0.51$) (Fig. 1d; $\mu_{w2_high} \approx \mu_{w2_med} < \mu_{w2_low}$). Species-specific estimates of colonization were similarly low in non-forest habitats compared with forest habitats (Fig. 2d–f).

COLONIZATION AS A FUNCTION OF OCCUPANCY

Mean species-specific estimates of forest and non-forest colonization probabilities were not correlated with their respective occupancy probabilities for either habitat type (Fig. 3a,b). Thus, the probability of persisting from one year to the next in forest or non-forest was a poor indicator of the probability of

colonizing the same. We found high variability in species-specific forest colonization probabilities within the small range of forest occupancy probabilities (Fig. 3a). Species-specific colonization probabilities of non-forest appeared to increase in variability as the probability of non-forest occupancy increased (Fig. 3b).

DETECTION

Mean species-specific estimates of detection were < 0.80 for all species in both forest and non-forest habitats (Table S3, Supporting information). Distributions of mean group-level detection probabilities in forest habitats for the HIGH and MED FD categories overlapped ($\Pr(\mu_{v2_high} > \mu_{v2_med}) = 0.68$) and were generally higher than the LOW FD category ($\Pr(\mu_{v1_high}, \mu_{v1_med} > \mu_{v1_low}) = 0.01$) (Fig. 1e;

$$\mu_{v1_high} \approx \mu_{v1_med} > \mu_{v1_low}).$$

In non-forest habitats, the LOW FD category had higher detection probabilities than the MED ($\Pr(\mu_{v2_low} > \mu_{v2_med}) > 0.99$) or HIGH ($\Pr(\mu_{v2_low} > \mu_{v2_high}) = 0.95$) FD groups. Yet, the distributions of mean group-level detection probabilities for HIGH and MED FD species group were again overlapping ($\Pr(\mu_{v2_high} > \mu_{v2_med}) = 0.52$) (Fig. 1f; $\mu_{v2_high} \approx \mu_{v2_med} < \mu_{v2_low}$). This suggests that our analyses of occupancy and colonization across habitat types at the species and group level would have been biased had we not accounted for imperfect detection of species.

Discussion

We applied a dynamic, multi-species hierarchical community model to estimate probabilities of occupancy and colonization of both focal and intervening matrix habitat types, which accounted for potential differences in detectability. Our results showed that prior categorizations of species by degree of forest dependency was a poor indicator of occupancy and colonization dynamics, and instead found forest habitats were generally favoured across all species groups. Most importantly, our model provides pertinent information on the dynamic use of forest and non-forest habitats, which we used to identify those species, specific to this region, that were highly vulnerable to habitat loss and fragmentation.

OCCUPANCY AND COLONIZATION: FOREST IS FAVOURED INDEPENDENT OF FD CATEGORY

We found higher overlap in the distributions of mean forest occupancy and colonization among the HIGH, MED and LOW FD categories compared with non-forest habitat types (Fig. 1a–d). Only the distributions of occupancy in non-forest habitats resembled the predicted patterns for forest dependency categories (Fig. 1b). Species-specific estimates of forest colonization were also higher compared with non-forest (Fig. 1d–f), and were not correlated with their respective estimates of occupancy (Fig. 3a,b). This indicates a higher than expected level of forest colonization across species, especially

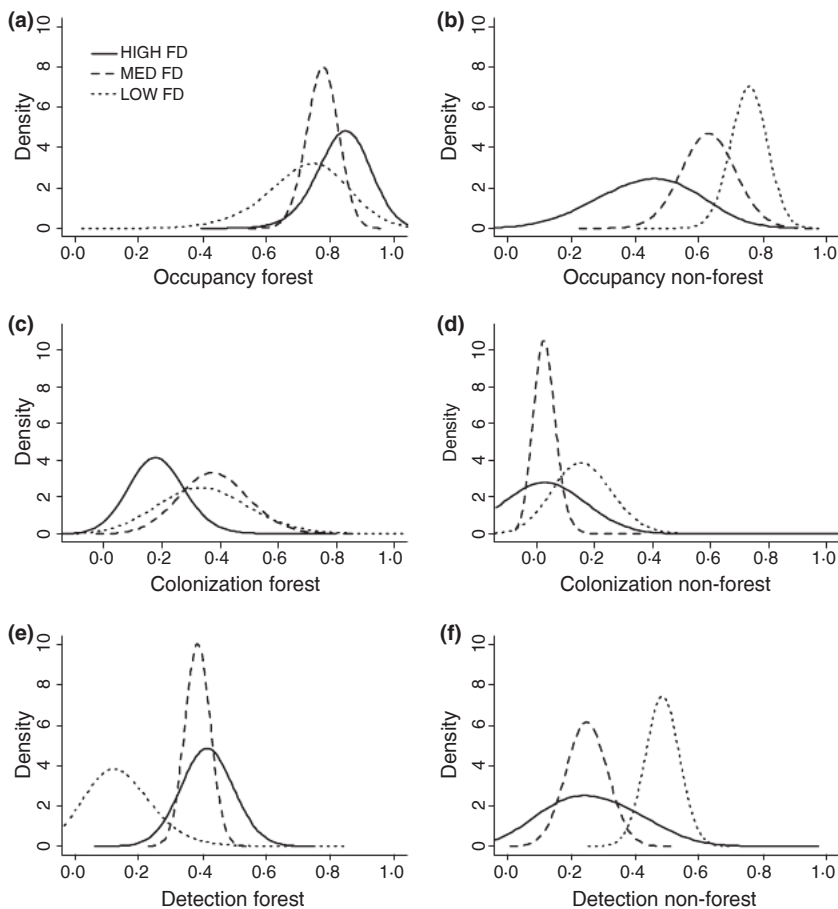


Fig. 1. Density plots of the posterior distributions for the group-level hyper parameters of mean occupancy (a and b), colonization (c and d) and detection (e and f) of forest and non-forest, respectively, as estimated using the hierarchical community model. Each plot shows the distribution of the estimated mean across species within each forest dependency category: HIGH, MED and LOW FD.

for species categorized as favouring open habitat and generally regarded as not needing forest to persist. Because our point count stations were centrally located within fragments and colonization rates were generally higher in forest vs. non-forest for all species, including LOW FDs, we believe that edge effects did not have a significant influence on our estimates of occupancy and colonization. As further evidence, we detected species from all three forest dependency categories across the size range of forest fragments and Las Cruces Forest Reserve. Edge effects are highly variable in tropical systems (Laurance 2000; Laurance *et al.* 2007) and likely to be confounded by the steepness of the slope in montane forests (Harper *et al.* 2005).

A high affinity to forest was found regardless of the habitat type in which a species is likely to persist over the years (i.e. occupancy). Most importantly, distributions of mean occupancy and colonization of forest habitat for the HIGH FD category overlapped with distributions for the MED and LOW FD categories (Fig. 3a). This suggests that forest dependency for species in the latter categories is likely to be underestimated when it is based simply on prior categorization of forest dependency.

Species classified with lower degrees of forest dependency, considered to be resilient to reductions in forest habitat based on high association with open habitat types, are also likely to use and persist in forest habitats, with higher than expected occupancy and colonization probabilities in forest. This highlights the importance of remnant forest habitats for the long-term persistence of all members of the bird community in

fragmented landscapes, even for species typically associated with open and degraded land uses.

HABITAT-SPECIFIC DETECTABILITY

All species that we analysed had detection probabilities that were < 80% per sampling occasion (Table S3, Supporting information). Detectability differed widely between habitats by category of forest dependency (Fig. 1e,f), showing great variability in species-specific estimates of detection within habitat types (Table S3, Supporting information). Our comparison of occupancy dynamics would have been severely biased had we not corrected for differences in detectability between species and habitat types. We suggest that future work account for differences in detection among species and habitat types, especially in species-rich regions. This is even more strongly recommended for work contrasting occupancy, species richness or abundance between different habitat types, as any significant contrasts could merely be artefacts of differences in detectability.

IMPLICATIONS FOR CE AND BIDE APPROACHES

We found that occupancy probabilities of forest and non-forest habitats were not strong indicators of colonization probabilities of either habitat type (Fig. 3). In other words, opportunistic use of available habitat types (i.e. colonization) cannot simply be determined by looking at the habitats with

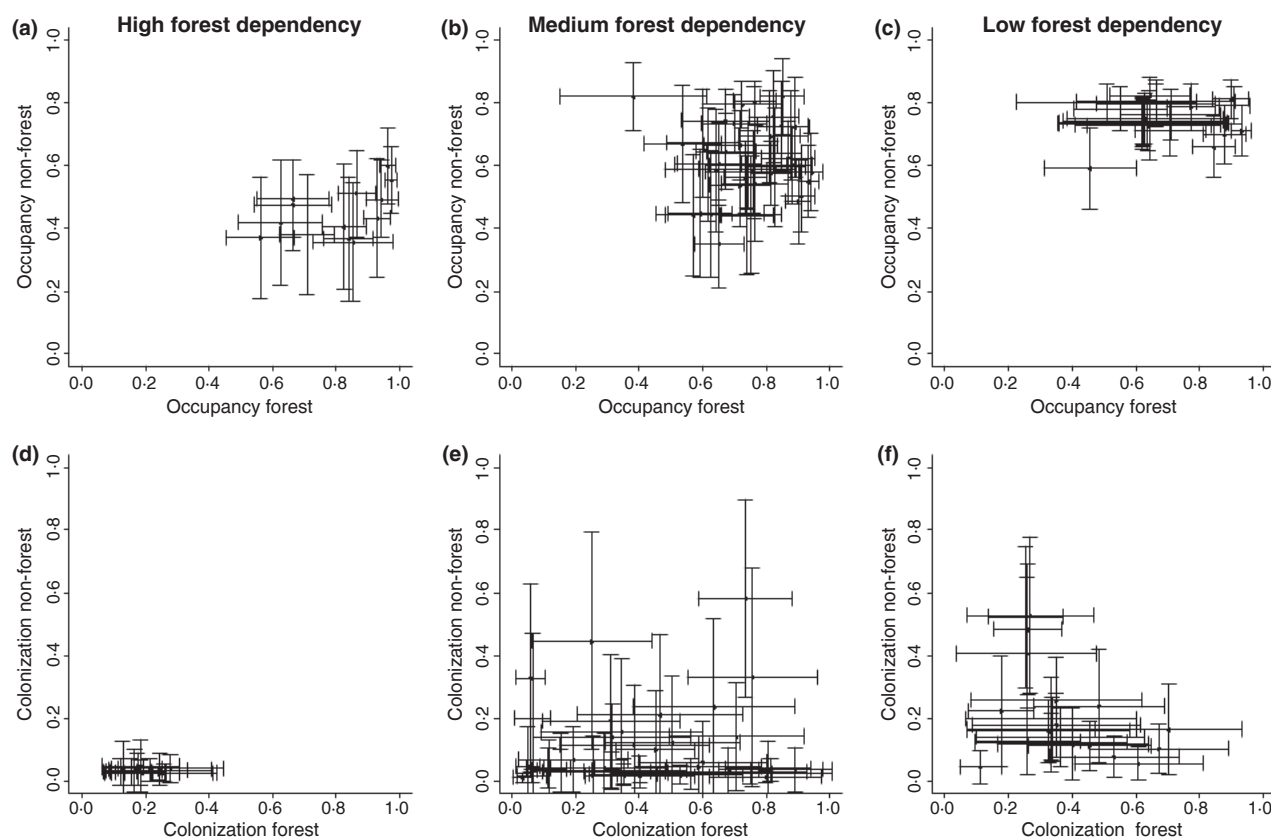


Fig. 2. Species-specific mean estimates of occupancy (a and c) and colonization (d and f), of forest and non-forest. The estimates are plotted by prior categorization of degree of forest dependency: HIGH FD, MED FD and LOW FD. The bars represent the standard deviations (SD) of each posterior mean estimate.

which a species is most associated (i.e. occupancy). The large amount of variability in colonization rates of forest habitats also indicates that an effective patch size is difficult to estimate for all but a few species (Fig. 3a,c). For these species, colonization is likely to be a function of both nearby occupied focal and matrix habitats. The 'island system' assumed under the CE approach will probably be most valid only for species with high occupancy of forest habitats, and low probabilities of occupancy and colonization for non-forest.

Our results also suggest that colonization of matrix habitats in a heterogeneous landscape is not directly related to how likely a species is to remain in that habitat type long term (Fig. 3b), a factor usually attributed to focal patch area under the BIDE approach. If this is true, commonly used landscape metrics like patch area or isolation might not be good indicators of the likelihood of matrix colonization by individuals of a species. Some species were also found to occupy both forest and matrix habitats, hence colonization of the matrix by individuals of these species may not necessarily be detrimental, which is an assumption of the BIDE approach. Similarly, to the CE approach, individuals for which BIDE would accurately predict occupancy dynamics in a patchy environment would belong to species with high occupancy probabilities of focal habitat, and low occupancy and colonization probabilities of NF habitats.

Our model can be used to define which species or individuals in the community are unlikely to use matrix habitats (i.e.

occupy and colonize) and are largely restricted to a focal habitat of interest. These species will meet the assumptions of both CE and BIDE approaches, and thus be most vulnerable to changes in the amount and configuration of available habitat.

VALIDITY OF FOREST DEPENDENCY CATEGORIES

Current research on the effects of habitat loss and fragmentation is largely based on ecological classifications of species into habitat specialists/generalists derived from prior published work (Boulinier *et al.* 2001; Gil-Tena, Saura & Brotons 2007), observations and distributional data not corrected for detectability (Lindell, Chomentowski & Zook 2004; Azeria *et al.* 2007; Caplat & Fonderflick 2009), or expert opinions (Petit & Petit 2003; Ferraz *et al.* 2007). The resulting classes and categories of species are widely used to subset species from a community with which to test hypotheses (Puettker, Meyer-Lucht & Sommer 2008), as well as for use in presence/absence observations to assess the conservation value of agricultural land uses (Ranganathan *et al.* 2008; Pardini *et al.* 2009). Radford & Bennett (2007) and Schlossberg & King (2008) found that these broad ecological classifications of avian species did not coincide with their observations on edge and forest specialists, and highlighted the need to test these types of widely accepted, potentially unreliable indicators of habitat specialization.

Our measures of occupancy of forest and non-forest habitats displayed predicted trends across species only for HIGH

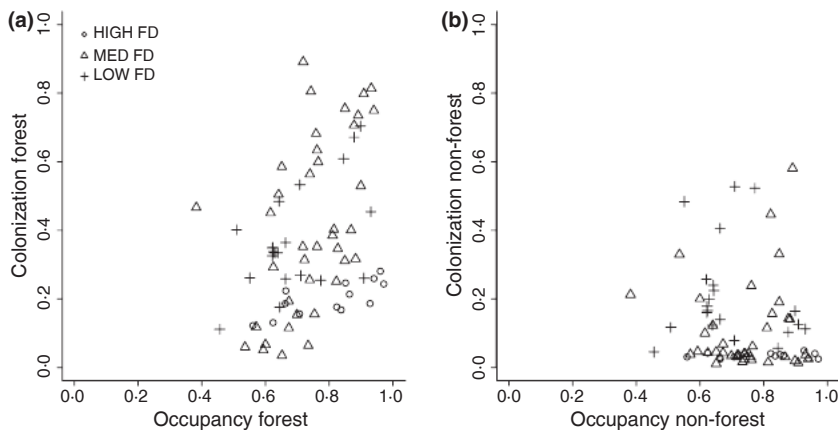


Fig. 3. Species-specific estimates of mean forest and non-forest colonization plotted against mean estimates of occupancy in forest and non-forest respectively. The symbols represent prior categorization of degree of forest dependency: HIGH FD, MED FD and LOW FD.

FD species, but had poor predictive power for species in the MED and LOW FD categories (Figs 1a,b and 2a–c). Colonization of forest and non-forest habitats was also inconsistent for species in these categories (Fig. 1c,d). Our results indicate that the classification system we tested, posed by Stiles (1985) and widely used by scientists focusing on avian communities in Costa Rica (Daily, Ehrlich & Sanchez-Azofeifa 2001; Borgella & Gavin 2005; Ranganathan, Chan & Daily 2007; Sekercioglu *et al.* 2007; Gillies & Clair 2008), should not be applied to make predictions for the avian community in our study region, and is likely to yield inaccurate estimates of habitat requirements for other regions of the country as well.

We conclude that prior ecological classification of species into habitat specialists/generalists may have poor predictive power with regards to how individuals or species respond to fragmentation, and thus should be used cautiously to identify which species will be most affected by habitat loss.

IMPLICATIONS FOR CONSERVATION: IDENTIFICATION OF VULNERABLE SPECIES

A classification system based on species presence or absence in matrix habitats has been used previously to predict which species will be most vulnerable to the combined effects of habitat loss and fragmentation, and has improved the predictive power of patch occupancy models across species (Donald & Evans 2006; Umetsu, Metzger & Pardini 2008). However, occupancy dynamics have also been shown to be highly landscape-specific, and to vary by region (Castellon & Sieving 2006; Rhodes *et al.* 2008; Watson *et al.* 2008). Matrix habitat use could also be spatially explicit, change at different scales and/or be dependent on the relative proportions of habitat (Flather & Bevers 2002; Tubelis, Lindenmayer & Cowling 2004). We suggest jointly estimating occupancy dynamics of focal and matrix habitats as a potential classification system of species most likely to be negatively affected by habitat loss and fragmentation. Consistent with CE and BIDE approaches, the most vulnerable species would be those with relatively high estimates of occupancy of forest and low estimates of occupancy and colonization of non-forest; namely, species or individuals who persist in forest habitats year after year, and are not likely to venture out into open, non-forested habitats. Under these criteria, species of highest conservation concern

make up 53% of the species in our analysis ($n = 39$), including all of the species classified as highly forest dependent, as well as 22% of our species with a medium degree of forest dependency ($n = 16$) (see Table S4, Supporting information).

STRENGTHS AND APPLICABILITY OF MODELLING APPROACH

We were not able to obtain estimates for 139 species for which we had insufficient information (< 30 observations across 5 sampling years). The proportions of modelled and non-modelled species were similar in each forest dependency category. Of the 73 modelled species, 17% ($n = 13$) were in the HIGH forest dependency category, 53% ($n = 39$) in the MED FD, and 29% ($n = 21$) in the LOW FD, compared with 28% ($n = 39$) in the HIGH FD, 50% ($n = 69$) in the MED FD, and 24% ($n = 34$) in the LOW FD for the 139 unmodelled species. We suspect that our inferences regarding occupancy dynamics of our subsample of the bird community in this region may be representative of the community as a whole, although we believe that overall estimates of occupancy, colonization, and detection for the unmodelled species are likely to be much lower. A large proportion of the 73 species about which we were able to make inferences using our community-level approach, would otherwise have not been possible under more widely used single-species approaches (Zipkin *et al.* 2009).

Conclusions

Regardless of prior categorization of forest dependency we found a higher than expected level of forest occupancy and colonization across species, including those categorized as open habitat species and currently considered not to need forest to persist. Adequate protection of both extensive and remnant forest habitats will be crucial for the long-term persistence of the avifauna in this region, including those species that are not currently considered to be negatively influenced by land-use changes. All of the species in our community had detection probabilities below 80%, and our comparison of occupancy dynamics between forest and non-forest would have been biased low had we not corrected for detection. Given that only occupancy and colonization of non-forest corresponded

closely to species' prior categorizations of forest dependency, we also consider these categories as poor indicators of overall occupancy dynamics. Consistent with CE and BIDE approaches, species or individuals that are restricted to forest and unlikely to use the surrounding NF (i.e. high occupancy in forest, and low occupancy and colonization in non-forest), are likely to be the most vulnerable to the effects of habitat loss and fragmentation. For our subset of the community, we found that 53% of the species in our analysis ($n = 39$) fall into this category, compared with 31% ($n = 23$) if we were only to focus on species classified as highly forest dependent. We believe that our approach using a community hierarchical model to estimate species-specific and group-level occupancy dynamics of focal and surrounding matrix habitats is a powerful method to identify which species, specific to a region of interest, are likely to be most vulnerable to the effects of habitat loss and fragmentation, at an appropriate scale of inference. The model reported here can similarly be applied to estimate the occupancy dynamics of other taxa and used to identify which species within a community are most likely to be impacted by projected changes in environmental conditions.

Acknowledgements

We acknowledge James R. Zook who carried out the bird point counts for this study. We are indebted to Andy Royle for his collaboration and support in the development of this work. We thank Thomas Gavin, Evan Cooch, Wesley Hochachka and the Dhondt Lab group their intellectual contribution throughout this project. We also thank Paul Doherty and his Lab group, Larissa Bailey, Gonçalo Ferraz and an anonymous reviewer for their helpful comments on earlier drafts of this manuscript. We are grateful for the assistance of the staff at the Las Cruces Biological Station, Michael Atencio, Jeisson Figueroa and the Cedeño and Gamboa families. This project was funded by the Guani Family Fellowship in Conservation Biology, the Cornell Latin American Studies Program Tinker Foundation Research Grant, and an NSF-DDEP (number OISE-0631735) to VRG.

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Received 16 December 2009; accepted 8 March 2010

Handling Editor: Jos Barlow

Supporting Information

Additional Supporting Information may be found in the online version of this article

Appendix S1. WinBUGS model code and specifications, for our multi-species hierarchical community model based on survey-specific detection/non-detection records for three sampling occasions per year, for 5 years.

Table S1. Posterior summaries of species-specific estimates of occupancy

Table S2. Posterior summaries of species-specific estimates of colonization

Table S3. Posterior summaries of species-specific estimates of detection

Table S4. List of species of conservation concern

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