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Species-specific responses to habitat conversion across scales synergistically restructure Neotropical bird communities

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Abstract. Ecologists are increasingly exploring methods for preserving biodiversity in agricultural landscapes. Yet because species vary in how they respond to habitat conversion, ecological communities in agriculture and more natural habitats are often distinct. Unpacking the heterogeneity in species responses to habitat conversion will be essential for predicting and mitigating community shifts. Here, we analyze two years of bird censuses at 150 sites across gradients of local land cover, landscape forest amount and configuration, and regional precipitation in Costa Rica to holistically characterize species responses to habitat conversion. Specifically, we used Poisson-binomial mixture models to (1) delineate groups of species that respond similarly to environmental gradients, (2) explore the relative importance of local vs. landscape-level habitat conversion, and (3) determine how landscape context influences species' local habitat preferences. We found that species fell into six groups: habitat generalists, abundant and rare forest specialists, and three groups of agricultural specialists that differed in their responses to landscape forest cover, fragmentation, and regional precipitation. Birds were most sensitive to local forest cover, but responses were contingent on landscape context. Specifically, forest specialists benefitted most when local forest cover increased in forested landscapes, while habitat generalists exhibited compensatory dynamics, peaking at sites with either local or landscape-level forest, but not both. Our study demonstrates that species responses to habitat conversion are complex but predictable. Characterizing species-level responses to environmental gradients represents a viable approach for forecasting the winners and losers of global change and designing interventions to minimize the ongoing restructuring of Earth's biota.

Key words: agro-ecology; avian habitat; countryside biogeography; deforestation; environmental gradient; fragmentation; habitat loss; landscape context; N-mixture model; tropical bird communities.

INTRODUCTION

Anthropogenic biomes are an ever-expanding component of Earth's ecosystems (Ellis et al. 2010) and ecologists are thus increasingly studying methods for improving biodiversity's prospects in human-modified landscapes (Daily et al. 2001, Perfecto et al. 2009). Though many species can persist in diversified agricultural landscapes (Karp et al. 2011, Melo et al. 2013), focusing on species numbers can mask the transformative shifts in communities that accompany habitat conversion. For example, even though individual studies report losses, no differences, and even gains in species richness between forests and agriculture (Mendenhall et al. 2014, Elsen et al. 2018, Nowakowski et al. 2018), the species that frequent the two habitats are usually highly distinct (Newbold et al. 2016, Socolar et al. 2016).

An approach that directly confronts the heterogeneity of species responses to habitat conversion is sorely needed if we are to anticipate and address the ongoing restructuring of Earth's communities. Conservationists, especially in the tropics, often take a top-down approach, dividing species into two groups, "forest specialists" and "habitat generalists," and comparing their diversity, richness, or abundance between land-cover types (e.g., Gibson et al. 2011, Carrara et al. 2015, Kormann et al. 2018). Focusing on forest specialists, which are often more range-restricted and vulnerable, most studies find that even small amounts of forest conversion or disturbance can be damaging (Gibson et al. 2011, Barlow et al. 2016). However, beyond the circularity of assessing the impacts of forest loss on "forest specialists," dividing communities into forest-specialist and habitat-generalist species overlooks the potential for more heterogeneity in species responses to habitat conversion. Indeed, tropical species can exist along a continuum from forest to agricultural affiliation, including everything in between (Lindell et al. 2004, Mendenhall

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et al. 2012, 2016), and the degree of habitat specialization can vary depending on where in a species range a population occurs (Frishkoff et al. 2015, 2016).

One path forward is to take a more bottom-up approach, quantifying individual species responses and how community composition emerges from those responses (Betts et al. 2014). By doing so, it may be possible to describe more natural, semi-discrete response groups that describe species reactions to global change. With respect to local habitat conversion, at least four groupings are possible: forest specialists, habitat generalists, agricultural specialists, and intermediate specialists (sometimes referred to as edge specialists). However, an even more accurate view would be to consider habitat conversion occurring, and species responding, at multiple spatial scales simultaneously.

Whether local or landscape-level environmental characteristics are more important in structuring communities is hotly debated, as is the relative importance of habitat amount vs. configuration at the landscape scale (Fahrig 2003, 2013, Gonthier et al. 2014, Haddad et al. 2016, Kormann et al. 2016, 2018). As for local habitat conversion, responses to landscape-level changes vary dramatically among species. For example, a recent global analysis found significant variation in how 1,673 different vertebrate species responded to fragmentation (Pfeifer et al. 2017): 85% exhibited significant abundance responses with roughly an equivalent number of species responding positively and negatively. In this case, understanding species-level responses was critical, as edge-sensitive species tended to be the most threatened (Pfeifer et al. 2017), meaning forest fragmentation remains a conservation concern (Haddad et al. 2015).

Thus, a bottom-up approach that explicitly considers species-level responses to habitat conversion at multiple scales is needed to truly understand biodiversity patterns in human-modified environments. To date, identifying the scale at which organisms respond to their environments has proven difficult, as answers tend to vary between studies and taxa (Jackson and Fahrig 2015). But confronting this heterogeneity could lead to new insights; for example, variation in species mobility may underlie scale-dependence, with more vagile organisms influenced by habitat amount and configuration at larger scales (Gonthier et al. 2014).

Similarly, seminal theories and hypotheses that have addressed how landscape composition influences biodiversity patterns have either explicitly (theory of island biogeography; (MacArthur and Wilson 1967) or implicitly (intermediate landscape-complexity hypothesis; Tscharntke et al. 2005, 2012) treated all species equally. The intermediate landscape-complexity hypothesis, for example, posits that conservation interventions should be most effective in landscapes with intermediate levels of natural habitat. In heavily forested landscapes, conservation interventions are hypothesized to result in little community change because there is already sufficient surrounding habitat for species to exist everywhere (Tscharntke et al. 2012); in completely cleared landscapes, conservation interventions may be ineffective because source populations may not exist to send colonists to any restored sites (Duelli and Obrist 2003). It is also thought that species responses to local land cover may depend on landscape configuration, with species more likely to use agriculture in more fragmented landscapes (Boesing et al. 2018). The rationale underlying both hypotheses likely applies well to habitat generalists that can use both forested and cleared habitats. However, specialists may act in alternative ways, disproportionately benefiting from the combined presence (or absence) of unfragmented forest at both local and landscape scales (Fischer et al. 2010).

Given that species exhibit such varied responses to local land cover and that responses may change across different landscapes and regions, predicting the impacts of habitat conversion on biological communities remains a major challenge. Here, we seek to develop a framework for understanding variation in species-level responses to forest cover and configuration, at local and landscape scales, using hierarchical Poisson-binomial mixture models that account for variation in detection (Royle and Dorazio 2008, Karp et al. 2018). Specifically, we analyzed bird censuses conducted in 2016 and 2017 at 150 study sites arrayed across a regional precipitation gradient in Northwest Costa Rica that were selected such that local land cover, landscape forest amount, forest edge density (a measure of fragmentation), and regional precipitation varied independently (Appendix S1: Fig. S1). From these analyses, we sought to test three guiding questions regarding how species respond to complex human-dominated landscapes. First, is forest cover in the surrounding landscape or at the local scale more important for dictating species abundances? Second, do birds' responses to habitat conversion, at the most relevant spatial scale, actually cluster into the two commonly assumed groups, forest specialists and habitat generalists, or does this simplistic ontology obfuscate true, biologically meaningful delimitations of species responses? Finally, does the landscape composition at broad scales interact with conditions at the local scale to affect how species respond to forest cover locally? For example, are landscape-scale variables only important when the local environment is forested?

Methods

Study sites

We conducted bird surveys in northwest Costa Rica along independent environmental gradients of local land cover, landscape-level forest cover and configuration, and regional precipitation (Appendix S1: Figs. S1 and S2). Specifically, we conducted surveys in protected areas, privately-owned forests, fragments, pastures, and crop fields. Our surveys encapsulated the region's climatic heterogeneity. While average annual temperature and elevation did not appreciably vary (Karp et al. 2018), our sites spanned a precipitation gradient with tropical wet forests near the coast (~3,000 mm/yr rainfall) and dry forests more inland (~1,500 mm/yr; Appendix S1: Fig. S2).

Across the precipitation gradient, we studied 25 focal landscapes, 20 in private lands at the forest-agriculture interface and 5 in forest reserves. Agricultural landscapes were composed of pasture ($N = 12$), rice ($N = 6$), sugarcane ($N = 1$), and Taiwan grass (a forage crop, $N = 1$). Reserves were located in tropical wet ($N = 2$) and dry ($N = 3$) forests. In each landscape, we surveyed birds at 6 sites ($N = 150$). In forest-agriculture landscapes, half the sites were located in agriculture and half were in adjacent forests, varying in landscape-level forest cover. In reserve landscapes, all sites were in forests, but two were placed near the forest edge to also vary landscape context.

To quantify regional precipitation, we compiled data from 29 regional weather stations, in operation for various periods between 1921 and 2015. We then modeled annual precipitation using a general additive mixed model with a spatial thin-plate spline (see Karp et al. 2018 for details). To quantify forest cover and configuration, we hand-classified tree cover within 1.5 km of each site from recent (2013–2017) Google Earth imagery (Karp et al. 2018). Classifications were ground-truthed at 600 locations (four per point count location). We then quantified the proportion of tree cover present within 50 m (local forest cover). Our sites also varied in landscape forest cover across scales (Appendix S1: Fig. S3), which we quantified as the proportion of tree cover in a series of “doughnuts,” with an inner radius always at 50 m and outer radii distributed from 60 m to 1.5 km in 10-m increments. In this way, local and landscape forest cover were decoupled. To measure forest fragmentation, we first reclassified the tree-cover map into a forest-cover map, removing all small clusters of trees <0.5 ha in size. We then quantified the perimeter of forest edge in concentric circles around each study site, also with radii spanning 60 m to 1.5 km in 10-m increments.

Bird surveys

We contracted the same expert observer (J. Zook) to conduct 20 min, 50 m radius bird point counts at each site within each landscape. Forest–agriculture landscapes were surveyed in 2016 and 2017 (120 sites, across 20 landscapes); five reserve landscapes were added in 2017 (for a total of 150 sites across 25 landscapes). Each year, one-half of the landscapes were sampled once (2016, $N_{\text{sites}} = 60$, $N_{\text{landscapes}} = 10$; 2017, $N_{\text{sites}} = 78$, $N_{\text{landscapes}} = 13$), and the other half were sampled three times (2016, $N_{\text{sites}} = 60$, $N_{\text{landscapes}} = 10$; 2017, $N_{\text{sites}} = 72$, $N_{\text{landscapes}} = 12$). All sites within a landscape were sampled within a 1-week period to accommodate binomial-mixture modeling. Sites were surveyed from May to July. One landscape (six sites) was surveyed each day, beginning at sunrise and continuing for ~5 h. In addition to recording the number of individuals of each species observed during the count, we also noted the following covariates: day of year, time of day, presence of disruptive noise, number of people observed nearby, wind speed (from a handheld anemometer), and distance to nearest river.

Poisson binomial mixture model

We used a multispecies Poisson-binomial mixture model to estimate how species respond to land-cover and precipitation gradients, while accounting for imperfect detection (Royle and Dorazio 2008, Kéry and Schaub 2011). The number of observed individuals ($Y_{i,j,k}$) of each species (i) at each site (j) during each visit (k) in each year (t) was assumed to result from detection and abundance processes such that

$$Y_{i,j,k,t} \sim \text{Binomial}\left(A_{i,j,t}\ ,\ P_{i,j,k,t}\right)$$

where A is the true number of individuals, and P is the detection probability of an individual. The detection process was modeled as

$$\begin{aligned}\text{logit}\left(P_{i,j,k}\right) = {} & \alpha 0_{\text{LU}[j]} + \alpha 1 \times \text{time}_{j,k} \\ & + \alpha 2 \times \text{noise}_{j,k} + \alpha 3 \times \text{ppl}_{j,k} + \alpha 4 \times \text{wind}_{j,k} \\ & + \theta 1_i \times \text{date}_{j,k} + \delta 0_i + \delta 1_{i,j,k,t}\end{aligned}$$

where LU indicated whether a site was forested or agriculture, time expressed time of day, noise indicated whether loud noises occurred during the count (e.g., farm equipment, cicadas, etc.), ppl was log(number of humans) (e.g., farmworkers) within the count radius, wind was the wind speed at the beginning of the survey, and date was the day of year that a survey took place.

The true number of individuals (A) was assumed to come from a Poisson distribution, based on the expected number of individuals (Λ), which was modeled according to

$$\begin{aligned}\log\left(\Lambda_{i,j,t}\right) = {} & \beta 0_i + \beta 1_i \times \text{local}_j + \beta 2_i \times \text{local}_j^2 \\ & + \beta 3_i \times \text{precip}_j + \beta 4_i \times \text{precip}_j^2 + \beta 5_i \times \text{landscape}_j \\ & + \beta 6_i \times \text{edge}_j + \beta 7_i \times \text{local}_j \times \text{precip}_j \\ & + \beta 8_i \times \text{local}_j \times \text{landscape}_j + \beta 9_i \times \text{local}_j \times \text{edge}_j \\ & + \beta 10_i \times \text{river}_j + \eta 1 \times \text{year}_t + \gamma 0_j + \gamma 1_{i,j} \\ & + \gamma 2_{i,\text{farm}[j]}\end{aligned}.$$

Local describes the fraction of forest cover within 50 m and precip is the mean annual precipitation of the site. Landscape and edge refer to the amount of forest cover and the edge density in the landscape, at a spatial scale selected by the model. River refers to the distance to the nearest river or stream and year indicated the first or second year of sampling. All variables were standardized to mean 0 and unit variance prior to analysis. We included quadratic effects of local forest cover and precipitation, but not landscape forest cover or edge, because preliminary analyses indicated that the latter were nonsignificant. Pairwise correlation coefficients between predictor variables were all below 0.6, suggesting that collinearity is not severely inflating uncertainty in parameter estimates (Appendix S1: Fig. S1).

Parameters in the α and η families were simple fixed effect terms. All parameters in the β and θ families were estimated for each species, with species terms drawn from a normal distribution of mean (μ) and variance (σ^2) estimated from the data. γ and δ terms were random intercepts (variance estimated from data around a mean of 0) designed to incorporate additional variation for each species, site, or replicate that could not be explained by other fixed and random effects.

The spatial scale at which landscape-level variables (i.e., landscape and edge) affect biological communities is unknown a priori. We therefore integrated over the uncertainty in spatial scale directly within the Markov chain Monte Carlo (MCMC) (Frishkoff et al. 2017). Briefly, along each iteration of the MCMC, a spatial scale (s) was drawn from a uniform prior, stretching from the smallest (60 m) to the largest scale (1,500 m). Then, the amount of landscape forest cover and edge were interpolated linearly, from a matrix of these values calculated at 10-m increments (after subtracting the amount in the core 50-m point count radius), and used in the fitting process. The result is a posterior distribution of s that describes the spatial scales at which the community responds to landscape variables. This method assumes that there is a single spatial scale at which landscape forest cover and edge density affect all species in the community. While this assumption is statistically expedient, it is unlikely to be true in real biological communities (though our model somewhat relaxes this assumption by partitioning effect of local and landscape factors). To evaluate this assumption, we also implemented a model in which spatial scale of response was allowed to vary by species, but this more complex model was not supported according to model comparisons using Deviance Information Criteria (DIC).

We did not explicitly account for x–y spatial autocorrelation between point count sites. Instead, we minimized the potential for autocorrelation across landscapes by using a random landscape effect in the models. Further, we designed our study to minimize problems with spatial autocorrelation, by placing point count locations within landscapes to stratify local forest cover and landscape context, and to ensure that distance between points within a habitat type is not systematically closer together than points between habitat types.

The binomial mixture model was implemented in JAGS V4.2.0 (Plummer 2003). Non-informative priors were used throughout. Specifically, means and fixed effects were drawn from a normal(0, 100) distribution, and sigma terms from a uniform(0, 10) distribution. We ran the model with eight chains for 100,000 iterations, a thinning interval of 400, and 20,000 iterations discarded as burn-in, resulting in 1,600 samples of the posterior. We checked convergence by visually inspecting trace plots and through the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992), ensuring that all values were less than 1.1.

Post-hoc community analyses

We extracted the posterior distribution for all parameter estimates detailing how each species responded to each environmental gradient and interactions between them (i.e., $\beta1$–$\beta9$). Environmental gradients and interactions were considered to significantly affect species on average when the 95% Bayesian credible interval (BCI) for the mean (μ) of the random effect distribution governing species' responses did not overlap 0. We considered there to be significant variability among species in their responses when the corresponding σ of the distribution was greater than 0. Because σ parameters are bounded by 0, we estimated the BCI using a truncated kernel density function of the posterior, using the 95% highest posterior density (HPD) interval rather than the equal-tails interval. Finally, to balance type I and type II error, individual species were considered to exhibit "significant" responses to environmental gradients and interactions when the 90% BCI did not overlap 0. We also recorded significance at the 95% BCI level (Appendix S1: Table S1). Results were similar when using a 95% cut off, except that fewer species were deemed significant, limiting the number for which we could choose as examples to illustrate general community-wide patterns. For visualization purposes, we calculated the mean species response to each gradient and interaction across posteriors. We also calculated each species' optimal local forest cover and precipitation as the value for which the species' abundance was maximized.

We used the posterior mean for each species' response to each environmental gradient ($\beta1$–$\beta9$), along with the species' intercept ($\beta0$), to cluster species into response groups. First, we used a hierarchical clustering algorithm based on Gaussian mixture modeling (mclust package; Scrucca et al. 2016) to define clusters of species based on their predicted abundance intercept and response to local forest cover, using BIC to choose the number of clusters supported by the data. Note that because the binomial mixture models pull species responses from shared normal distributions, our secondary clustering analysis will be inherently biased towards uncovering fewer response groups than exist in nature. The number of response groups we present is therefore conservative.

For visualizing the distribution of response groups in parameter space, we used a principal component analysis to determine the major axes along which β parameter estimates varied. To further explore how species within each cluster varied in their responses to environmental gradients and interactions, we examined how β

parameter values differed between each response group, assessing uncertainty in these values through bootstrapping (function MclustBootstrap). We then repeated this procedure to cluster species according to their responses not only to local land cover, but to all modeled environmental gradients and interactions.

We also characterized species' local habitat affinities and breadths to determine if forest specialists, agricultural specialists, and habitat generalists differed in their responses to habitat conversion at larger scales. First, we extracted $A_{i,j,t}$ (the predicted abundance of each species at each site in each year) along each iteration of the MCMC (Karp et al. 2018). Then, for each sample of the posterior, we compiled the local forest cover values of each site where each individual of each species was present. A species' local forest affinity was defined as the mean local forest cover value associated with all the individuals of the species. A species' local habitat breadth was defined as the standard deviation in local forest cover values across all individuals. In this way, we quantified local forest affinity and habitat breadth for each species in each posterior draw. Species' "local forest affinities" (defined from the posterior) tightly correlated with their predicted responses to local forest cover (estimated directly from the binomial-mixture model; Appendix S1: Fig. S4). We restricted our analyses to species with a mean predicted abundance (across all 1600 posterior draws) of at least 10 individuals across all sites. We did so because standard deviation calculations needed to estimate habitat breadth become 0 if species only occupy a single site: a biologically unrealistic result. This fraction of the analysis was therefore limited to the 106 most common species. Because dropping rare species risks biasing our analysis (if say, rare species are more likely to be forest affiliated), we checked the parameter estimates of the binomial mixture model. In no case did rare species respond to environmental gradients differently from common species, indicating that potential bias from dropping rare species was minimal (Appendix S1: Fig. S5).

Using our metrics of forest affinities and breadths, we then tested whether species' responses to local forest cover were correlated with their responses to habitat conversion at broader spatial scales. To do so, we regressed species' local habitat affinities (or habitat breadth) against their model-estimated responses to landscape forest amount, configuration, and interactions in each posterior. Both linear and quadratic effects of local habitat affinities were included. We then extracted the model slope terms and determined if there was a significant relationship (i.e., the 95% quantiles across all posteriors did not overlap 0). For visualization purposes, we used the slope terms across all posteriors to graph relationships.

RESULTS

We detected 9,215 individuals of 150 species across two years of sampling. The Poisson-binomial mixture model indicated that detection varied between species, land-cover types, and replicate site visits (Appendix S1: Table S1). Detection was higher when it was quiet, earlier in the morning, and less windy but detection was not affected by the number of people near the count (Appendix S1: Table S1). Species also varied in their detectability by date, but detection did not systemically decline or increase across all species over the field season.

What is the relative impact of different environmental gradients on species abundances?

Species' abundances responded to environmental gradients in continuous manners, with some species increasing, others decreasing, and others unaffected by any given gradient. Investigating the characteristics of the distribution of these responses (i.e., means and standard deviations) sheds light on how community change occurs. For example, species richness increases along a gradient if the mean abundance response is strongly positive, whereas community turnover is heightened if the standard deviation in response to a gradient is large.

Across all species in the metacommunity, the average abundance responses with respect to precipitation and landscape forest cover were positive. In other words, the "average" species increased in abundance in wetter regions and in landscapes with more forest. But the average species did not significantly respond to forest edge density (Fig. 1; Appendix S1: Table S1). After accounting for local effects, the most predictive scale for landscape forest cover and edge was 710 m (95% BCI, 620–850 m) from bird census stations (Appendix S1: Fig. S6). The "average" species did not significantly increase or decrease with local forest cover; however, 41% of the 150 species surveyed exhibited significant quadratic responses (90% BCI did not overlap 0), 29% responded linearly, and 30% did not exhibit a significant response (Appendix S1: Fig. S7). We also detected a significant quadratic response to precipitation, with the average species reaching peak abundance in regions with 2.37 m of annual precipitation (Appendix S1: Fig. S7). Fewer individual species exhibited significant quadratic responses, however (quadratic, 12%; linear, 32%; no response, 57%).

Despite the absence of an average directional response across all species, local forest cover was more important in structuring bird communities than landscape forest and edge (i.e., the local forest response distribution had a larger standard deviation). As a result, for most species, the predicted change in species abundances between locally forested vs. deforested sites was larger than the predicted change between sites with the maximal and minimal amounts of landscape forest cover (71% of species responded more strongly to local forest cover) and edge (87% of species). Between landscape forest cover and edge, landscape forest cover proved more influential for 75% of species. Interestingly, most species were more responsive to precipitation than to local forest cover (54% of species), landscape forest (74%), and edge

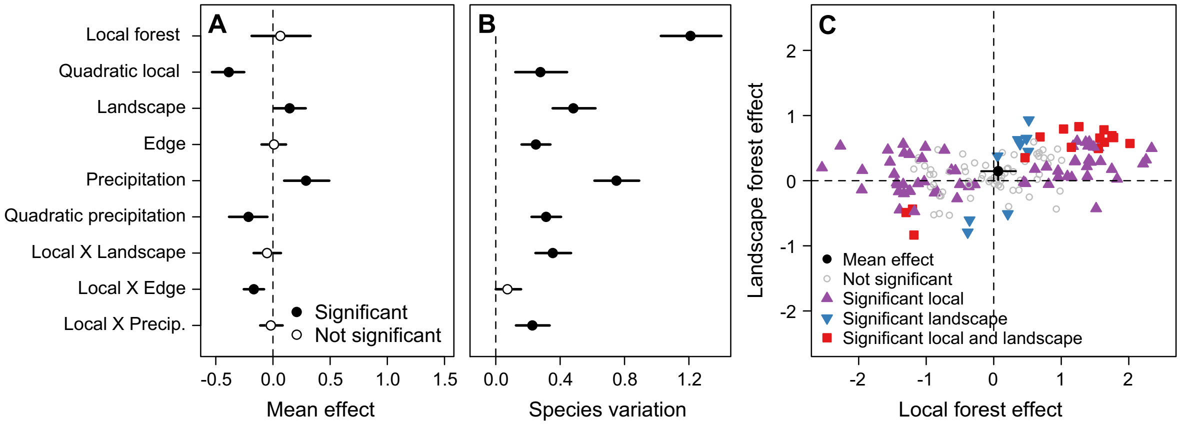

Fig. 1. Species' abundance responses to environmental gradients. (A) Points depict responses of the average species' abundance (slope term) to habitat gradients, regional precipitation, and interactions, estimated from the Poisson-binomial mixture model. On average, species abundance increased with precipitation and landscape forest cover. Responses to local forest cover and precipitation were quadratic. Species in more fragmented landscapes (more forest edge) were more likely to decline in abundance with local forest loss (significant negative interaction). (B) Points depict variation in species responses to environmental gradients (standard deviation in slope terms). Species varied considerably in their responses to each environmental gradient; however, all species exhibited the same negative interaction between local forest cover and landscape forest edge. In panels A and B, filled circles depict significant responses; lines depict 95% Bayesian credible intervals (BCIs). (C) Points depict individual species' responses to local and landscape forest amount. Black point and lines depict the "average" species response and BCI. A significant "average" species response to landscape but not local forest masks the importance of local forest in structuring communities. Species exhibited much more variation in how they responded to local forest: 41 species exhibited significant positive responses and 35 significant negative responses, compared to only 18 species responding positively and 6 negatively to landscape forest amount (90% BCI did not overlap 0).

(81%). Correspondingly, variation among species in how they responded to precipitation and local forest cover was larger than the variation in species responses to landscape forest cover or edge (though interspecific variation was significant for every gradient; Fig. 1).

How do species group based on their responses to environmental gradients?

We found strong evidence for the community clustering into natural response groups. Three well-defined groups of species emerged based on responses to local forest cover (Appendix S1: Table S2; Fig. 2), which we term habitat generalists ($N = 85$), forest specialists ($N = 44$), and agriculture specialists ($N = 21$). Habitat generalists were more abundant than forest and agriculture specialist (Appendix S1: Fig. S8). We found no evidence for "intermediate specialists" (i.e., species that maximized their abundances at forest edges with intermediate amounts local forest cover; Fig. 2A). Examining species based on their responses to all environmental gradients and interactions resulted in strong support for further division beyond the three categories listed above (minimum BIC, six groups; six groups vs. one group $\Delta\text{BIC} = 342.4$, $P < 0.001$; six groups vs. three groups $\Delta\text{BIC} = 58.7$, $P < 0.001$; the model for seven groups was within 2 BIC units of the best model indicating potential existence of further natural response groups). In addition to habitat generalists, the most favored model divided forest species into two groups (of higher and lower abundances) and agricultural species into three groups that differed in their responses to landscape forest cover, forest edge, and regional precipitation (Fig. 2C, D; Appendix S1: Fig. S9; Appendix S1: Table S2). These abundance responses at the level of individual species reverberated to the community level. Species richness of the six groups shifted along land cover and climate gradients as expected based on their abundance responses (Fig. 3; Appendix S1: Fig. S10). Habitat generalists made up the majority of species across all gradients, and a small number of forest specialist birds were able to persist in agricultural sites.

In general, species responses to local forest cover were strongly associated with their responses to forest cover and configuration at a landscape scale (Fig. 4; Appendix S1: Table S3). We detected a significant nonlinear relationship between local forest affinity and species responses to landscape forest cover, with only the strong local forest specialists consistently increasing in more forested landscapes (Fig. 4A, B). Unlike habitat generalists, both forest specialists and agricultural specialists declined in fragmented landscapes (Fig. 4C, D).

Are species-level responses to local gradients contingent on surrounding landscapes?

We found that the amount and configuration of forest in the surrounding landscape influenced how species responded to forest cover locally, but in fundamentally different ways for different species (Fig. 5; Appendix S1: Table S3). In general, habitat specialists tended to exhibit more synergistic patterns, while generalists exhibited

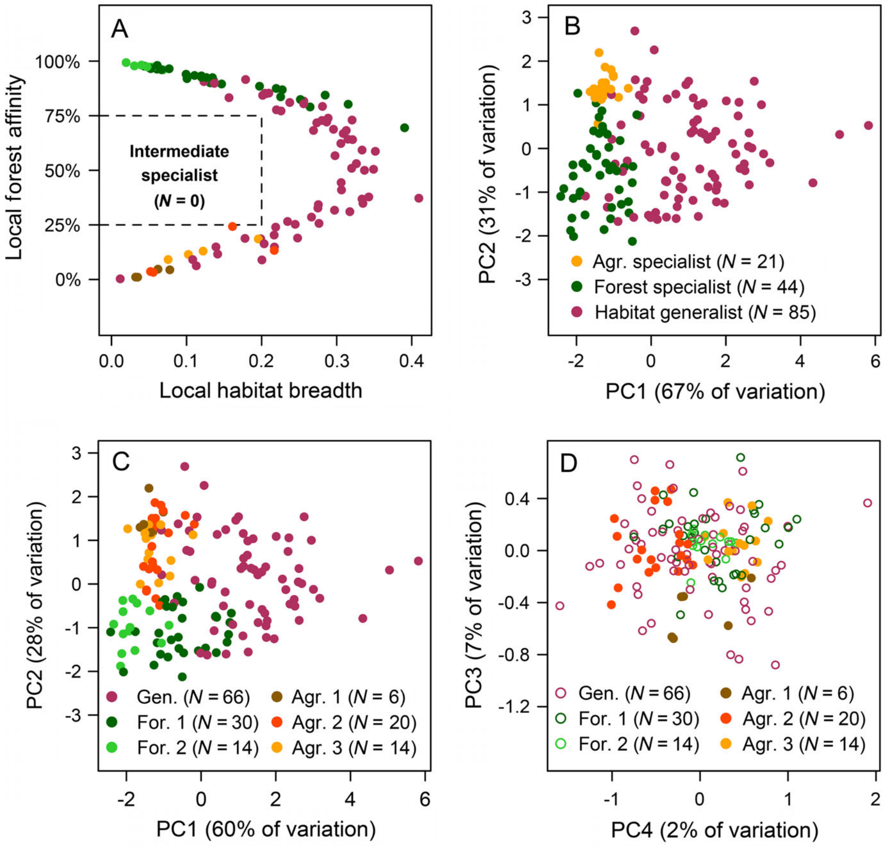

FIG. 2. Defining avian response groups to environmental gradients. Panel A demonstrates the remarkable variation species exhibit in their responses to local forest cover. Species local habitat affinities correlated with their habitat breadths (see *Methods* for definition) such that species either specialized on forest or agriculture locally or were habitat generalists. We found no evidence for intermediate specialists that maximize their abundances in local forest-edge habitats. Panel B depicts the first two principal components of a cluster analysis based on species responses to local forest cover. Mixture modeling identified three coherent groups. Habitat generalists (*N* = 21; Gen.) were common and exhibited no strong response to forest cover; forest specialists (*N* = 44; For.) were rarer and increased with local forest cover; agriculture specialists (*N* = 21; Agr.) were also rare but decreased with forest cover (Appendix S1: Fig. S8). Panels C and D depict the first two and third/fourth principal components of a second cluster analysis based on species responses to all environmental gradients. In this analysis, agriculture species were further divided into three groups, based largely on their responses to precipitation, landscape forest cover, and forest edge (Appendix S1: Fig. S9). Forest species were divided into two groups, largely according to their abundance.

more compensatory patterns (Fig. 5A, B). For example, local agricultural specialists like the Barn Swallow (*Hirundo rustica*) were disproportionately abundant at agricultural sites in agricultural landscapes (Fig. 5C) and nearly absent everywhere else. Conversely, local forest specialists like the Long-tailed Manakin (*Chiroxiphia linearis*) exhibited the steepest increases in abundance with local forest cover in forested landscapes (Fig. 5F). For generalists, the pattern was reversed as they exhibited a more compensatory pattern: greater local forest cover elicited abundance increases in agricultural landscapes and decreases in forested landscapes. Thus, birds like the Inca Dove (*Columbina inca*) thrived in areas that had some forest cover locally or in the surrounding landscape, but not both (Fig. 5D). Finally, species that could not be considered a habitat specialist or generalist (being somewhere in between; e.g., the Turquoise-browed Motmot; *Eumomota superciliosa*) exhibited no interactive dynamics.

The effect of local forest cover on species abundances was also dependent on forest edge density: for every species, the effect of local forest cover was more positive in unfragmented landscapes (Fig. 6A). Thus, for local forest affiliates like the Squirrel Cuckoo (*Piaya cayana*) abundances peaked in unfragmented landscapes with high local forest cover, and local forest cover had a muted effect in fragmented landscapes (Fig. 6D). For more generalist species that still tended to respond positively to local forest cover (like the Rufous-naped Wren; *Campylorhynchus rufinucha*), landscape fragmentation simply shifted abundances to peak at more intermediate amounts of local forest cover (Fig. 6C). On the other hand, for species that responded negatively to forest cover, like the Great-tailed Grackle (*Quiscalus*

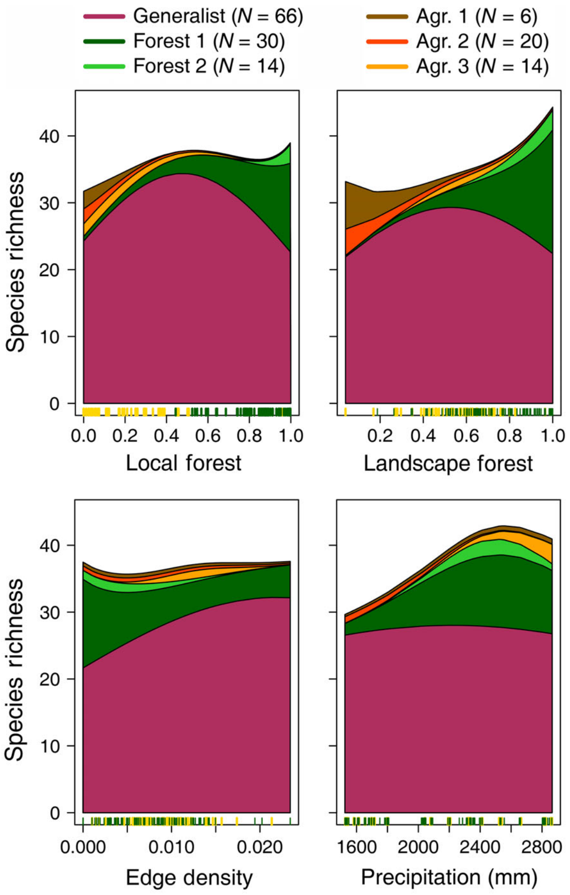

FIG. 3. Expected species richness changes along forest cover, fragmentation, and precipitation gradients, according to response group. Polygons depict the number of species likely to occur from each response group along local forest cover (50-m buffer), landscape forest cover (710-m buffer), edge density (710-m buffer), and precipitation gradients. Lines come from best-fit general linear models, explaining the number of species in each site as a quadratic function of the environmental gradient displayed (see Appendix S1: Fig. S10). Vertical lines on *x*-axis indicate the positions of individual forest (green) and agriculture (gold) sites along each environmental gradient.

mexicanus), the effect of decreasing forest cover elicited the largest increases in abundance in fragmented landscapes (Fig. 6B).

DISCUSSION

Land-cover response groups across spatial scales

Our results suggest that the common dichotomy of “forest specialists” and “habitat generalists” in tropical conservation ecology oversimplifies the diversity of ways that species respond to habitat conversion. Instead, we documented at least three response groups when considering local land-cover change alone, suggesting that species that specialize primarily on agriculture do contribute to the biodiversity of the region. Further, species’ responses to environmental gradients (namely local forest cover and regional precipitation) exhibited hump-shaped patterns, indicating that nonlinearity and some degree of specialization on particular segments of these environmental gradients is the norm. Agricultural specialists have been largely ignored in the tropics presumably because it is unclear how these species fit into pre-human biological communities. However, in other regions of the globe, these specialists are frequently the targets of conservation concern and intervention, illustrated by the long-standing interest surrounding the decline of common farmland birds in Europe (Fuller et al. 1995, Donald et al. 2006). Similarly, urban ecosystems are often described as containing “urban avoiders, adapters, and exploiters” (Blair 1996). Studies focused on agricultural landscapes in the tropics would do well to adopt such a framing, especially as “agricultural” species and generalists may play an outsized role in providing ecosystem services (or disservices; Tscharntke et al. 2012), but respond differently to changes in landscape forest clearing and fragmentation.

When we further considered species’ responses to landscape forest cover, fragmentation, and regional precipitation, we uncovered even more diversity in response groups, especially within agricultural specialists. Agricultural specialists contained distinct groups of species that maximized their abundances in wetter vs. drier regions, and in more vs. less forested landscapes. This diversity in species responses to environmental gradients occurred despite functional diversity typically declining in agricultural communities (e.g., Flynn et al. 2009; but see De Coster et al. 2015). Thus, agricultural species may embody a limited set of functional guilds and/or morphological types (e.g., shorter-lived, smaller, granivores, and/or dietary generalists; Flynn et al. 2009, Karp et al. 2011, Newbold et al. 2012), but still exhibit a surprising diversity of ecological requirements. This suggests that, for these species, “requirement niches” may not correlate with “impact niches” (Chase and Leibold 2003). Unlike agricultural specialists, forest specialists only formed two groups, based primarily on their abundances. Greater attention is needed to understand the ecology of the agricultural specialists, and why they, but not the forest specialists, form distinct response groups based on landscape and climate axes. Indeed, most research attention in the tropics has focused on forest specialists; our results underscore the remaining wealth of uncertainty regarding how and why communities form in anthropogenic habitats.

The number of unexpected response groups underscores the need for bottom-up approaches to habitat-use classification, rather than top-down approaches that dictate a finite number of preconceived species groups. Species response to forest cover need not even be fixed: some species may be forest specialists in a portion of their range but agriculture affiliates elsewhere (Frishkoff et al. 2015). Our bottom-up approach may represent a powerful way to predict biodiversity change over entire landscapes and regions. For example, using these

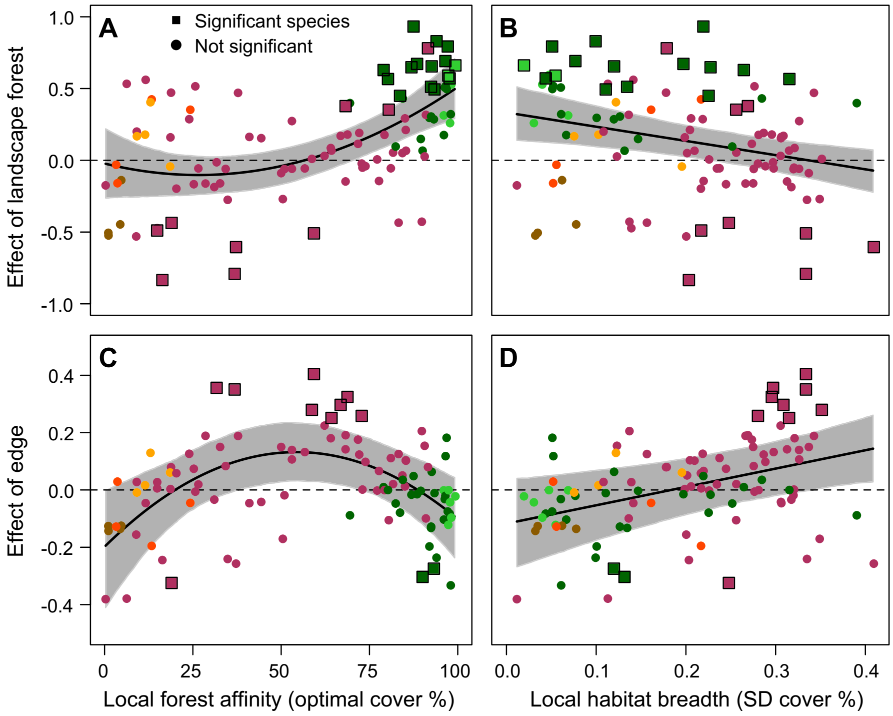

FIG. 4. Relationships between landscape forest amount, forest edge, and local habitat affinity and breadth. (A) Species' local forest affinities (see *Methods* for definition) correlated with their responses to landscape forest cover such that only strong forest-affiliated species increased with landscape forest cover. (B) In general, habitat specialists, especially forest specialists, increased with landscape forest cover more so than habitat generalists. (C) Species' exhibited a nonlinear relationship between local forest affinity and edge responses, with habitat generalists (C and D) most likely to increase in abundance in fragmented landscapes. Points depict individual species, colored according to the six response groupings in Fig. 2C, D (dark green, forest group 1; lime green, forest group 2; maroon, habitat generalist; brown, agriculture group 1; red, agriculture group 2; orange, agriculture group 3). Square points indicate a significant species-level response (90% BCI do not overlap 0). Black lines depict predicted relationships; gray shaded areas depict 95% BCI.

response groups as the basis for the countryside species-area relationship, which generalizes the species–area relationship for systems with multiple land covers (Martins and Pereira 2017).

The outcome of dynamics between response groups is roughly stable species richness in response to local forest loss up until ~50% cover followed by declining species richness with deforestation. At the landscape scale, species richness loss is near monotonic, as the diverse pool of forest specialists is not balanced by an equally diverse pool of agricultural specialists. This result contrasts with the distinctly hump-shaped species richness pattern for birds in the pacific northwest where the forest specialist pool is smaller and diversity is maximized at intermediate amounts of forest at the landscape scale (Marzluff 2005).

Local forest cover determines bird abundances

Biodiversity studies in human-dominated landscapes also often focus on remaining natural habitats; for example, assessing shifts in assemblages among forest patches of varying sizes (e.g., Kormann et al. 2018). Thus, little variation often exists among sites at the local scale, and agricultural species are only detected if they venture into forests. In other studies, communities are compared between natural and human-modified habitats, largely ignoring habitat variation at larger spatial scales. Our study design ensured that forest cover varied independently across spatial scales (Appendix S1: Fig. S1), allowing us to detect the community's scale of response. We found that the amount of forest at local scales (50 m) most strongly dictated species abundances, with 70% of species exhibiting a significant shift in abundance across the local forest gradient. This was unexpected, as we hypothesized that highly mobile species like birds would primarily respond to habitat conversion at larger spatial scales (Gonthier et al. 2014). However, it aligns with studies of on-farm practices and landscape heterogeneity that find both local and landscape level composition simultaneously structuring species' abundances (Batáry et al. 2011, Quinn et al. 2014).

Interactions between species responses to habitat amount at multiple scales

Nevertheless, species tended to increase in abundance at sites with more forest in the landscape, with 16% of species exhibiting a significant response. Even more

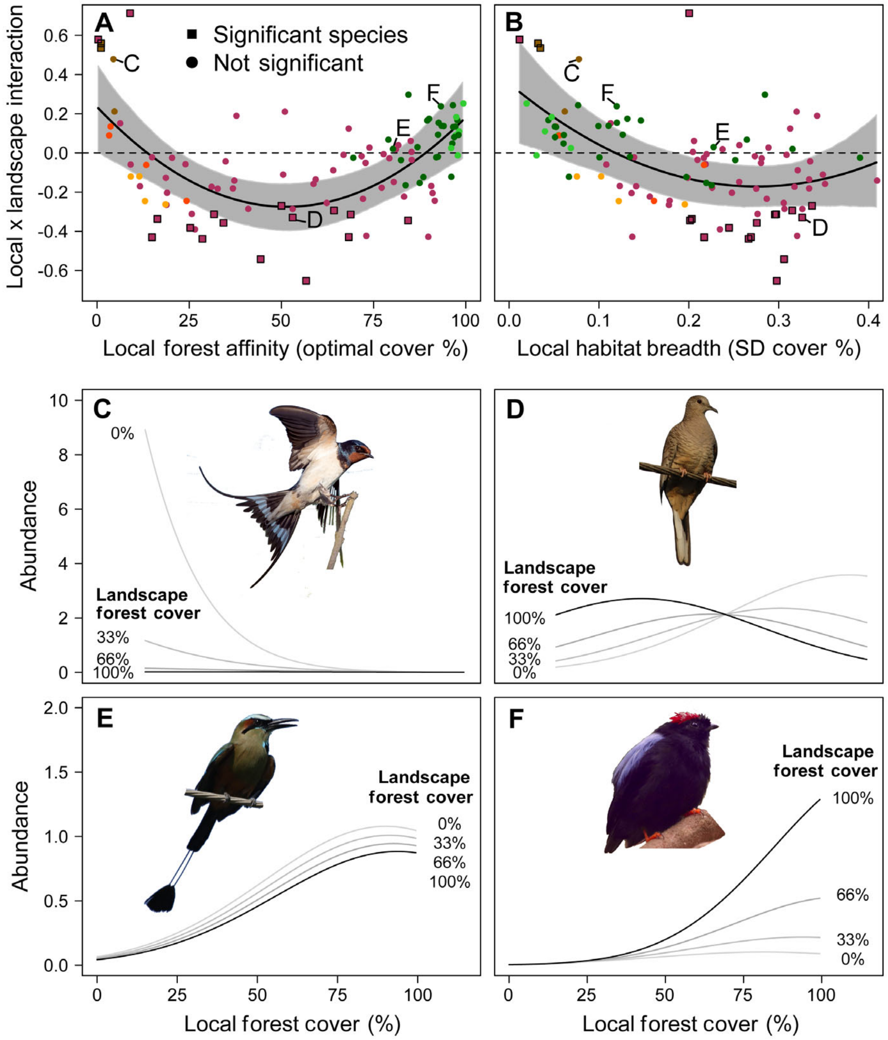

FIG. 5. Compensatory and synergistic responses among bird species to local and landscape forest cover. Habitat specialists, both of forest and agriculture, were likely to exhibit synergistic responses to local and landscape-level forest cover (panel A, B). For example, Barn Swallow (*Hirundo Rustico*; panel C), an agriculture specialist, was abundant only in agriculture in deforested landscapes. On the other hand, forested specialists like the Long-tailed Manakin (*Chiroxiphia linearis*; panel F) were disproportionately abundant at forest sites in forested landscapes. Unlike habitat specialists, habitat generalists like the Inca Dove (*Columbina inca*; panel D), tended to exhibit compensatory responses to local and landscape forest cover, peaking in abundance at forested sites in deforested landscapes or deforested sites in forested landscapes. Species with more intermediate habitat breadths exhibited no local/landscape interaction; for example, the Turquoise-browed Motmot's (*Eumomota superciliosa*) consistently increased with local forest cover in all landscapes. In panels A and B, points represent species, colored according to their response grouping (Fig. 2C, D). Square points indicate a significant species-level response (90% BCI do not overlap 0). Black lines depict predicted relationships; gray shaded regions represented 95% BCI. Letters correspond to focal species graphed in panels C–F. In panels C–F, lines represent predicted changes in abundance along local forest cover gradients; darker lines represent landscapes with increasing forest cover.

critically, we observed two distinct ways by which forest cover and configuration interacted across scales, driving complex patterns in species abundances.

First, at a species level, we found that species responses to local and landscape-level forest cover were often coupled. That is, species that strongly increased with local forest cover tended to also increase in more forested landscapes, reaffirming the importance of large forest blocks for forest specialist birds (Gibson et al. 2011, Betts et al. 2017, Pfeifer et al. 2017). In contrast, habitat generalists often preferred less forested landscapes. These generalist species likely use agricultural habitats at broad scales to gather resources and complete their lifecycles, but still depend on small patches of trees at local scales. Indeed, radio-tracking studies in Costa Rica indicated that habitat generalist birds often nest and forage within agricultural plots, but also intensively use fine-scale forest patches (Sekercioglu et al. 2007, Mendenhall et al. 2011). Surprisingly, though we predicted that they would prefer landscapes with less forest

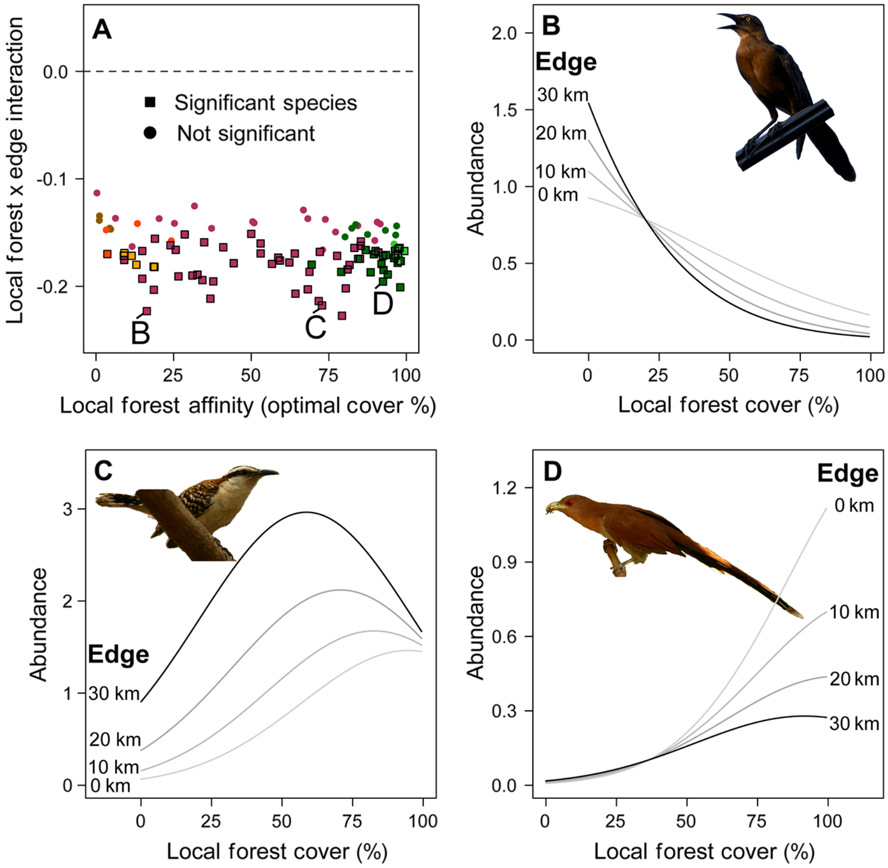

FIG. 6. Interactive effects of local forest amount and landscape forest edge on species abundances. (A) Effects of local forest cover were less positive for all species in more fragmented landscapes. Thus, agricultural affiliates like (B) the Great-tailed Grackle (*Quiscalus mexicanus*) peaked in agricultural sites in fragmented landscapes, and forest affiliates like (D) the Squirrel Cuckoo (*Piaya cayana*) peaked in forested sites in unfragmented landscapes. In increasingly fragmented landscapes, species with more intermediate forest affinities, like (C) the Rufous-naped Wren (*Campylorhynchus rufinucha*), reached peaked abundances at sites with lower local forest cover. In panel A, points represent species, colored by response group (Fig. 2C, D). Square points indicate species for which 90% BCI do not overlap 0. Letters correspond to focal species graphed in panels B–D. In panels B–D, lines represent predicted changes in abundance along local forest cover gradients; darker lines represent landscapes with a higher total edge length (increasingly fragmented).

cover, local agriculture specialists were not affected by landscape-level forest amount. This suggests that the most strongly agricultural-affiliated species may restrict their movements to small spatial scales within agriculture, and are more spatially self-contained than generalists. Radio-tracking data on agricultural birds are needed to test this hypothesis.

Second, within species, we observed significant interactive effects of local and landscape forest cover on population abundances. Specifically, habitat generalists often exhibited strong compensatory dynamics, either increasing with local forest cover in agricultural landscapes or decreasing with local forest cover in forested landscapes. This finding generally supports the intermediate landscape-complexity hypothesis (Tscharntke et al. 2005, 2012). For specialists, however, we observed more synergistic effects: local forest specialists were disproportionately abundant in forested landscapes and local agricultural specialists tended to be more abundant in agricultural landscapes.

Abundance response to fragmentation

Landscape configuration (i.e., edge density) had relatively modest effects relative to composition (i.e., forest amount). Habitat generalists often benefitted from fragmentation, most specialists had no response, and a few forest specialists declined in fragmented landscapes. The role of fragmentation and configuration on animal populations has been contentious. Paralleling our results, many studies report landscape composition to be a larger determinant of species abundances than configuration (e.g., Fahrig 2003, Carrara et al. 2015). In large-scale ecological experiments, however, habitat configuration has strongly influenced species diversity and ecological functions (Haddad et al. 2015, 2016), due to both dispersal limitation preventing recolonizations and edge effects changing the local environment of fragmented sites (Laurance et al. 2010). In our study, more species benefited from fragmentation than suffered from it, suggesting that the increasing density of edge habitat and minimized distance between open and closed habitat resource pools may outstrip the negative consequences of edge effects and dispersal limitation. However, we found that fragmentation primarily benefitted habitat generalists and some agricultural specialists. Additionally, fragmentation interacted with local forest amount, such that fragmentation benefited species in agriculture and depressed populations in forests. These results affirm both prior experimental studies (Laurance et al. 2010) and syntheses (Pfeifer et al. 2017), which have found that vulnerable forest birds often decline with fragmentation. However, because greater edge amount corresponds with greater habitat heterogeneity, these findings also support the idea that habitat heterogeneity in agriculture is key to species preservation (Benton et al. 2003). Heterogeneity of agriculture types and other land covers may also sustain populations in anthropogenic landscapes, beyond a simple agriculture vs. forest dichotomy (e.g., Quinn et al. 2014).

Conservation implications

Like many studies, our results suggest that conserving forest specialists requires increasing forest cover and decreasing fragmentation, at both local and landscape scales. Encouragingly, however, we found that most species responded strongly to local forest cover, suggesting that highly localized restoration initiatives could be effective at recruiting forest birds. Where to target such initiatives, however, will strongly depend on project goals. If the intention is to preserve forest birds, then siting restoration plots in unfragmented, forested landscapes may be most advantageous (Reid et al. 2014, 2015). Yet if the goal is to promote habitat generalists that frequent agricultural areas and provide ecosystem services (e.g., Karp et al. 2013, Maas et al. 2016), then adding forest cover to deforested landscapes may be best. Overall, our work highlights the need to keep contiguous forest as intact as possible, while simultaneously fostering corridors and mixed habitat in agricultural landscapes to support generalists. This finding adds to a growing body of evidence suggesting mixed strategies may be most capable of maximizing conservation outcomes at landscape scales (Socolar et al. 2016, Elsen et al. 2018).

Conclusions

Integrating the local and landscape effects of habitat conversion across species has long posed a challenge for community ecology. Our results suggest that this challenge can be made manageable by allowing community properties to emerge from individual species responses to the environment. We propose a series of hypotheses from our results. First, we posit that, for most species, local conditions control animal populations, while broader landscape scale patterns play a more supporting role. This hypothesis may be especially true for animals that actively select their habitats and avoid habitats in which their fitness is minimized. In contrast, landscape-scale variables may be more important for species with complex life cycles in which one phase is particularly specialized (e.g., requiring non-impacted primary forest for nesting) but other stages are generalized (e.g., capacity to feed and acquire resources across land-cover types). Second, we suggest that the “intermediate landscape-complexity hypothesis” is most appropriate for habitat generalists and least applicable to specialists. Finally, counterintuitive as it may be, we propose that a sizeable proportion of species in tropical human-dominated landscapes specialize on anthropogenic habitats, rather than conforming as “habitat generalists.” What controls the relative size of this anthropogenic specialist community remains an open question. Ultimately, our results indicate that while responses to habitat conversion are scale-dependent, context-dependent, species-specific, and nonlinear, analyzing species-level responses to independent environmental gradients represents a viable method for understanding whole community shifts in the Anthropocene.

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Literature Cited

Barlow, J., et al. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535:144–147.

Batáry, P., A. Báldi, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. Proceedings of the Royal Society B 278:1894–1902.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology & Evolution 18:182–188.

Betts, M. G., L. Fahrig, A. S. Hadley, K. E. Halstead, J. Bowman, W. D. Robinson, J. A. Wiens, and D. B. Lindenmayer. 2014. A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. Ecography 37:517–527.

Betts, M. G., C. Wolf, W. J. Ripple, B. Phalan, K. A. Millers, A. Duarte, S. H. M. Butchart, and T. Levi. 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. Nature 547:441–444.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Boesing, A. A. L., E. Nichols, and J. P. Metzger. 2018. Land use type, forest cover, and forest edges modulate avian cross-habitat spillover. Journal of Applied Ecology 55:1252–1264.

Carrara, E., V. Arroyo-Rodriguez, J. H. Vega-Rivera, J. E. Schondube, S. M. de Freitas, and L. Fahrig. 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.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11:1–13.

De Coster, G., C. Banks-Leite, and J. P. Metzger. 2015. Atlantic forest bird communities provide different but not fewer functions after habitat loss. Proceedings of the Royal Society B 282:20142844.

Donald, P. F., F. J. Sanderson, I. J. Burfield, and F. P. J. van Bommel. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems and Environment 116:189–196.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. Basic and Applied Ecology 4:129–138.

Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589–606.

Elsen, P. R., K. Ramesh, and D. S. Wilcove. 2018. Conserving Himalayan birds in highly seasonal forested and agricultural landscapes. Conservation Biology 32:1313–1324.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40:1649–1663.

Fischer, J., J. Stott, and B. S. Law. 2010. The disproportionate value of scattered trees. Biological Conservation 143:1564–1567.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22–33.

Frishkoff, L. O., E. A. Hadly, and G. C. Daily. 2015. Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. Global Change Biology 21:3901–3916.

Frishkoff, L. O., D. S. Karp, J. R. Flanders, J. Zook, E. A. Hadly, G. C. Daily, and L. K. M'Gonigle. 2016. Climate change and habitat conversion favour the same species. Ecology Letters 19:1081–1090.

Frishkoff, L. O., D. L. Mahler, and M.-J. Fortin. 2017. Integrating over uncertainty in spatial scale of response within multispecies occupancy models yields more accurate assessments of community composition. bioRxiv 1–29. https://doi.org/10.1101/143669

Fuller, R. J., R. D. Gregory, D. W. Gibbons, J. H. Marchant, J. D. Wilson, S. R. Baillie, and N. Carter. 1995. Population declines and range contractions among lowland farmland birds in Britain. Conservation Biology 9:1425–1441.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Gibson, L., et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:1–19.

Gonthier, D. J., et al. 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proceedings of the Royal Society B 281:1–8.

Haddad, N. M., et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1–9.

Haddad, N. M., A. Gonzalez, L. A. Brudvig, M. A. Burt, D. J. Levey, and E. I. Damschen. 2016. Experimental evidence does not support the habitat amount hypothesis. Ecography 125:336–342.

Jackson, H. B., and L. Fahrig. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63.

Karp, D. S., G. Ziv, J. Zook, P. R. Ehrlich, and G. C. Daily. 2011. Resilience and stability in bird guilds across tropical countryside. Proceedings of the National Academy of Sciences USA 108:21134–21139.

Karp, D. S., C. D. Mendenhall, R. F. Sandi, N. Chaumont, P. R. Ehrlich, and G. C. Daily. 2013. Forest bolsters bird abundance, pest control, and coffee yield. Ecology Letters 16:1339–1347.

Karp, D. S., L. O. Frishkoff, A. Echeverri, J. Zook, P. Juárez, and K. M. A. Chan. 2018. Agriculture erases climate-driven β-diversity in Neotropical bird communities. Global Change Biology 24:338–349.

Kéry, M., and M. Schaub. 2011. Bayesian population analysis using WinBUGS: A hierarchical perspective. Academic Press London, UK:1–554.

Kormann, U., C. Scherber, T. Tscharntke, N. Klein, M. Larbig, J. J. Valente, A. S. Hadley, and M. G. Betts. 2016. Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. Proceedings of the Royal Society B 283:20152347.

Kormann, U. G., A. S. Hadley, T. Tscharntke, M. G. Betts, W. D. Robinson, and C. Scherber. 2018. Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. Journal of Applied Ecology 55:1288–1298.

Laurance, W. F., et al. 2010. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation 144:56–67.

Lindell, C. A., W. H. Chomentowski, and J. I. M. R. Zook. 2004. Characteristics of bird species using forest and agricultural land covers in southern Costa Rica. Biodiversity and Conservation 13:2419–2441.

Maas, B., et al. 2016. Bird and bat predation services in tropical forests and agroforestry landscapes. Biological Reviews 91:1081–1101.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Martins, I. S., and H. M. Pereira. 2017. Improving extinction projections across scales and habitats using the countryside species-area relationship. Scientific Reports 7:12899.

Marzluff, J. M. 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems 8:157–177.

Melo, F. P. L., V. Arroyo-Rodriguez, L. Fahrig, M. Martinez-Ramos, and M. Tabarelli. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends in Ecology & Evolution 28:462–468.

Mendenhall, C. D., C. H. Sekercioglu, F. O. Brenes, P. R. Ehrlich, and G. C. Daily. 2011. Predictive model for sustaining biodiversity in tropical countryside. Proceedings of the National Academy of Sciences USA 108:16313–16316.

Mendenhall, C. D., G. C. Daily, and P. R. Ehrlich. 2012. Improving estimates of biodiversity loss. Biological Conservation 151:32–34.

Mendenhall, C. D., D. S. Karp, C. F. J. Meyer, E. A. Hadly, and G. C. Daily. 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509:213–217.

Mendenhall, C. D., A. Shields-Estrada, A. J. Krishnaswami, and G. C. Daily. 2016. Quantifying and sustaining biodiversity in tropical agricultural landscapes. Proceedings of the National Academy of Sciences USA 113:14544–14551.

Newbold, T., J. P. W. Scharlemann, S. H. M. Butchart, C. H. Sekercioğlu, R. Alkemade, H. L. Booth, and D. W. Purves. 2012. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B 280:20122131.

Newbold, T., et al. 2016. Global patterns of terrestrial assemblage turnover within and among land uses. Ecography 39:1151–1163.

Nowakowski, A. J., L. O. Frishkoff, M. E. Thompson, T. M. Smith, and B. D. Todd. 2018. Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. Proceedings of the National Academy of Sciences USA 115:E3454–E3462.

Perfecto, I., J. H. Vandermeer, and A. Wright. 2009. Nature's Matrix: Linking agriculture, conservation, and food sovereignty. Cromwell Press Group, London, UK.

Plummer, M.. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20–22. in K. Hornik, F. leisch, and A. Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing. Technische Universitaet Wien, Vienna, Austria.

Pfeifer, M., et al. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551:187–191.

Quinn, J. E., R. J. Johnson, and J. R. Brandle. 2014. Identifying opportunities for conservation embedded in cropland anthromes. Landscape Ecology 29:1811–1819.

Reid, J. L., C. D. Mendenhall, J. A. Rosales, R. A. Zahawi, and K. D. Holl. 2014. Landscape context mediates avian habitat choice in tropical forest restoration. PLoS ONE 9: e90573.

Reid, J. L., C. D. Mendenhall, R. A. Zahawi, and K. D. Holl. 2015. Scale-dependent effects of forest restoration on Neotropical fruit bats. Restoration Ecology 23:681–689.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. Academic Press, London, UK.

Scrucca, L., M. Fop, T. B. Murphy, and A. E. Raftery. 2016. mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. R Journal 8:205–233.

Sekercioglu, C. H., S. R. Loarie, F. Oviedo Brenes, P. R. Ehrlich, and G. C. Daily. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology 21:482–494.

Socolar, J. B., J. J. Gilroy, W. E. Kunin, and D. P. Edwards. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31:67–80.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. Ecology Letters 8:857–874.

Tscharntke, T., et al. 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biological Reviews 87:661–685.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1910/full

Data Availability

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.fg8kq66