



Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization

Urs G. Kormann^{1,2}  | Adam S. Hadley² | Teja Tschardt¹ | Matthew G. Betts² |
W. Douglas Robinson³ | Christoph Scherber^{1,4} 

¹Agroecology, Georg-August University Göttingen, Göttingen, Germany

²Forest Biodiversity Research Network, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

³Oak Creek Lab of Biology, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

⁴Institute of Landscape Ecology, Münster, Germany

Correspondence

Urs G. Kormann
Email: oso@hotmail.ch

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: RTG 1644; Division of Environmental Biology, Grant/Award Number: 1050954; Canadian Network for Research and Innovation in Machining Technology, Natural Sciences and Engineering Research Council of Canada

Handling Editor: Martine Maron

Abstract

1. Tropical conservation strategies traditionally focus on large tracts of pristine forests but, given rapid primary forest decline, understanding the role of secondary forest remnants for biodiversity maintenance is critical. Until now, the interactive effects of changes in forest amount, configuration and disturbance history (secondary vs. primary forest) on the conservation value of tropical landscapes have remained unknown, hampering the incorporation of these global change drivers into local and global conservation planning.
2. We disentangled effects of landscape-wide forest amount, fragment size and forest age (old growth vs. secondary forest) on abundance, α -diversity, β -diversity (biotic homogenization) and community shifts of bird communities in human-dominated landscapes of southern Costa Rica. Utilizing two complementary methods, yielding 6,900 individual detections and 223 species, we characterized bird communities in 49 forest fragments representing independent gradients in fragment size (<5 ha vs. >30 ha) and forest amount (5%–80%) in the surrounding landscape (within 1000 m).
3. Abundance and α -diversity of forest specialists and insectivores declined by half in small fragments, but only in landscapes with little old-growth forest. Conversely, secondary forest at the landscape scale showed no such compensation effect. Similarly, a null-model approach indicated significant biotic homogenization in small vs. large fragments, but only in landscapes with little old-growth forest, suggesting forest amount and configuration interactively affect β -diversity in tropical human-dominated landscapes. Finally, dramatic abundance-based community shifts relative to intact forests are largely a result of landscape-scale loss of old growth rather than changes in overall forest cover.
4. *Policy implications.* Our study provides strong evidence that retaining old growth within tropical human-modified landscapes can simultaneously curb erosion of avian forest specialist α -diversity, mitigate collapse of β -diversity (biotic homogenization) and dampen detrimental avian community shifts. However, secondary forests play, at best, a subordinate role to mitigate these processes. To maintain tropical forest biodiversity, retaining old-growth forest within landscapes should be first priority, highlighting a land-sparing approach.

KEYWORDS

community dispersion, community similarity, Costa Rica, environmental filter, fragmentation, habitat composition, habitat configuration, habitat loss, secondary forest, β -diversity

1 | INTRODUCTION

Tropical forests sustain more than 50% of all known species (Laurance, 1999), and their unabated modification by humans is likely the largest threat to biodiversity globally (Sala et al., 2000). Traditional conservation approaches often focus on large blocks of pristine forests, but it has recently been suggested that high species richness can be maintained in human-modified tropical landscapes (HMTLs) when productive land co-occurs with fragments of primary and secondary tropical forest (Laurance, Sayer, & Cassman, 2014; Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). This idea is enticing, but remains highly controversial given the large uncertainty regarding the importance of primary and secondary forest at local and landscape scales for the conservation capacity of HMTLs (Arroyo-Rodríguez et al., 2017; Barlow et al., 2016; Gibson et al., 2011; Melo et al., 2013).

Unfortunately, our understanding of how landscape-wide forest amount and successional stage mediate fragment area effects in HMTLs is currently limited (Arroyo-Rodríguez et al., 2017; Hadley & Betts, 2016; Melo et al., 2013): first, although positive local scale-effects of old-growth relative to secondary forest have been widely established for forest-dwelling organisms (α -diversity, e.g. Gibson et al., 2011), studies investigating these factors at a landscape level remain scarce (Barlow et al., 2016; Carrara et al., 2015; Hadley & Betts, 2016; Morante-Filho, Arroyo-Rodríguez, & Faria, 2016). Second, forest amount, successional stage and fragment area are often interwoven in real-world landscapes, as small fragments of secondary forest often occur in deforested landscapes. Thus, disentangling the biological relevance of these factors by either experimental design or statistical inference is logistically challenging and requires adequate sample size. Third, theories differ in their predictions on how landscape-wide forest amount may mediate fragment area effects. For example, Andrén (1994) and Rybicki and Hanski (2013) propose that below a threshold of landscape-wide habitat cover, landscape-scale connectivity is eroded and reduced fragment area will strongly reduce α -diversity (the fragmentation threshold theory, but see, Villard & Metzger 2014). Alternatively, the recently postulated “habitat amount hypothesis” (Fahrig, 2013) predicts that local species richness is determined by the landscape-wide amount of habitat, while variation in fragment size makes little difference.

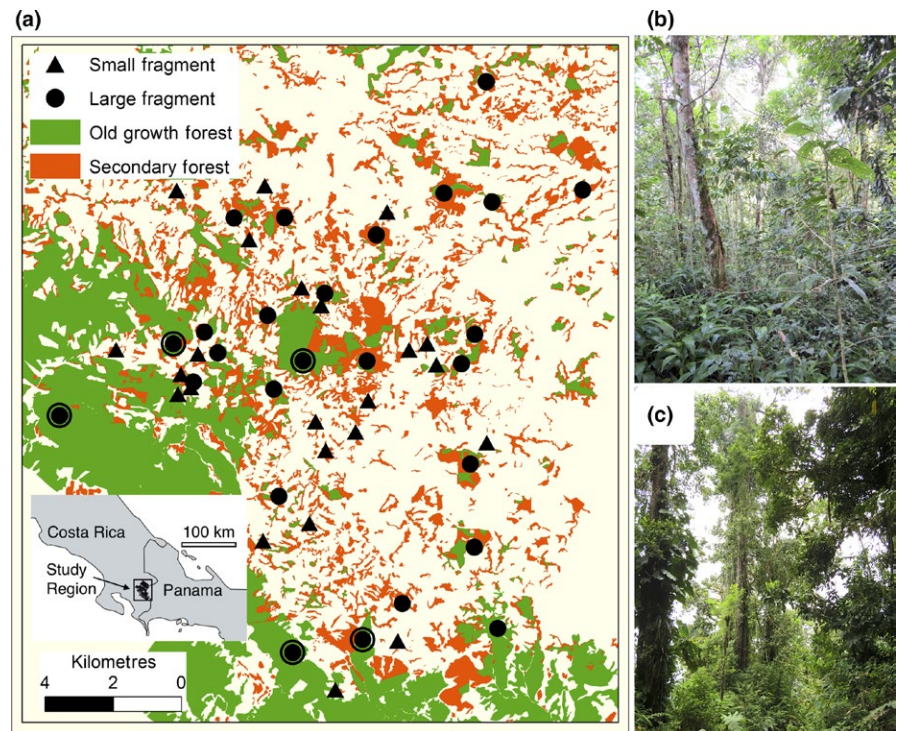
Further, most studies in HMTLs have been restricted to α -diversity so far, although complementary ecological properties like β -diversity and deterministic community-level shifts, that is, the non-random change species abundances compared to reference communities, may be as relevant for conservation planning and ecosystem functioning (Carrara et al., 2015; Karp et al., 2012; Mendenhall et al., 2014; Morante-Filho et al., 2016; Solar et al., 2015; Tscharntke et al., 2012). For example, reduced forest cover may decrease dispersal between

fragments, increase ecological drift and thus increase β -diversity “biotic differentiation hypothesis” (Arroyo-Rodríguez et al., 2013). As a non-exclusive alternative to this, reduced fragment size and landscape-wide forest amount may decrease β -diversity through species sorting when environmental heterogeneity among local fragments in a landscape is reduced (“biotic homogenization hypothesis” sensu Solar et al., 2015). This loss of disturbance-sensitive species (losers) and proliferation of few disturbance adapted species (winners), causing biotic homogenization in highly disturbed fragments (Solar et al., 2015; Tabarelli, Peres, & Melo, 2012). Overall, these knowledge gaps substantially limit our ability to inform landscape and conservation planning in tropical regions.

Here, we assessed how changes in landscape composition (landscape-wide amount of forest) and forest configuration (fragment size) interactively affect forest bird communities, disentangling, to our knowledge for the first time, the effect of old growth vs. secondary forest at local and landscape scales. We chose the fragmented Coto Brus region, where the degree of habitat destruction (70% forest loss of the original forest cover (Zahawi, Duran, & Kormann, 2015) is representative for HMTLs of many Latin American regions with moderately intensive land-use (Lindquist et al., 2012). Birds are crucial providers of key ecosystem functions, and their disappearance in tropical systems has been linked to pervasive reductions of ecosystem functions such as pollination, seed dispersal and herbivore control, and rapid evolutionary changes in mutualistic partners (Galetti et al., 2013; Hadley, Frey, Robinson, John Kress, & Betts, 2014; Karp et al., 2013; Kormann et al., 2016). Further, birds are highly sensitive to disturbance of native forest (Barlow et al., 2007; Gibson et al., 2011), with forest specialists and particularly forest-dependent insectivores being among the most vulnerable organisms to forest modification (Barlow et al., 2007; Carrara et al., 2015; Gibson et al., 2011; Morante-Filho et al., 2016; Powell, Cordeiro, & Stratford, 2015; Powell, Wolfe, et al., 2015).

We focused on responses of three complementary bird community descriptors: α -diversity and abundance at the local point-count scale, β -diversity measured as variation in species identities between fragments and directed, community-level shifts in bird abundance in fragments relative to intact reference forests. In particular, we tested the following hypotheses: under the habitat amount hypothesis, we expect no effect of fragment size on diversity beyond effects of forest area. However, under the threshold hypothesis, we expect that reduced fragment area will strongly reduce α -diversity (particularly for forest specialists) in forest poor landscapes. Further, according to the biotic homogenization hypothesis (1) reduced β -diversity among fragments and (2) avian community shifts compared to reference forest should be strongest in small fragments with little remaining forest. Also, if old-growth forest contributes more strongly than secondary forest to fragment colonization (i.e. a “mass effect”—Shmida & Wilson,

FIGURE 1 Map of the study region in Southern Costa Rica (a), and photographs of (b) old-growth forest and (c) secondary forest. Shown are small (<5 ha) and large study fragments (>30 ha) as triangles and dots, respectively, old growth (green), secondary forest (orange) and non-forest (primarily pasture; white). Reference fragments for the community shift index are surrounded by a circle. Photograph credits: Sarah Frey, Mauricio Paniaguas



1985), we expect that (3) the amount of old forest rather than total forest in the landscape will best predict bird community structure.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was performed in Southern Costa Rica, around the Las Cruces Biological Station (8°47'N, 82°57'W). The landscape was originally covered by Pacific pre-montane humid forest, but after massive deforestation 40 to 60 years ago, only app. 30% of landscape remains forested, one-third of which is secondary forest (Zahawi et al., 2015). The existing forest persists in c. 2,100 forest fragments ranging from <1 ha to >1,000 ha in size and c. 850–1,500 m a.s.l. in altitude. Non-forest land cover is largely pasture (>90%, Hadley et al., 2014).

2.2 | Study design

We used a stratified-random sampling design, which consisted of 49 forest fragments representing two uncorrelated gradients in forest amount (forest cover within 1,000 m radius) and fragment size (Figure 1, for details, see Hadley et al., 2014) stratified across elevation. We chose a 1,000 m radius to represent expected maximum daily movement distances for small- to medium-sized forest specialist birds in the region (Sekercioglu, Loarie, Oviedo Brenes, Ehrlich, & Daily, 2007; Volpe, Hadley, Robinson, & Betts, 2014). We randomly selected forest fragments from potential options within each strata using ARCGIS 10.0 (ESRI Geoinformatik GmbH, Hanover, Germany) and orthophoto-based forest cover maps (2 m resolution; Hadley et al., 2014). For fragment selection, fragments were considered to be

separate if they were at least 30 m apart, which constitutes a severe movement barrier for many neotropical forest birds (Kormann et al., 2016; Lees & Peres, 2009; Volpe et al., 2014). For the purpose of fragment selection, we a priori defined two fragment size categories (small: <5 ha, large: >30 ha) and selected fragments from both size categories that represented the variation in forest amount within a 1,000 m radius (5% to 80%). Importantly, fragments were altitudinally stratified across two elevational bands (880–1,100 a.s.l. and >1,100–1,500 a.s.l.) and interspersed across the region (Figure 1). Of the initially selected 52 fragments, 3 could not be accessed (lack of permission, steepness). Our stratified-random sampling design guaranteed that fragment size, forest amount and altitude were not strongly correlated (all Pearson's $r < .5$, see Table S1). On average, selected fragments were 80.5 m away from the next fragment (Figure S2).

2.3 | Bird surveys

In each fragment, we performed fixed radius point counts ($r = 25$ m) and stopping rule-based walkabout surveys, which we treated as separate datasets in the subsequent analysis. While point counts are well suited to assess relative bird abundance and local species richness per unit area, stopping rule-based surveys walkabouts accumulate observations until no new species have been recorded for a previously fixed time span (Herzog, Kessler, & Cahill, 2002), and are better suited to estimate species richness when bird communities contain many rare (Herzog et al., 2002; Robinson, 1999; Watson, 2010).

Each fragment was visited once for surveys between May and June 2011 (40 fragments) and in early June 2012 (9 fragments), when most resident species reproduce (Stiles & Skutch, 1989). We randomized the visitation order. In small fragments, we performed three

point counts and six in large fragments, which lasted 12 min. each. Walkabouts lasted 80 ± 20 min ($M \pm SE$ are given throughout) in small fragments and 155 ± 33 min in large fragments. All surveys were conducted by the same, experienced observer (Jeisson Figueroa). A detailed survey protocol is provided in "Survey methods" (S3). Birds were classified as forest insectivores, if their main diets were insects (Stiles & Skutch, 1989) and if two of three sources indicated that their habitat was largely restricted to forest (Table S4; sources considered: Hughes, Daily, & Ehrlich, 2002; Stiles & Skutch, 1989; W. Douglas Robinson, pers. comm.)

2.4 | Forest parameters

For every point count, we determined elevation and the distance to the nearest fragment edge, using "distance on ground" in Google Earth and a digital elevation model (NASA Shuttle Radar Topography Mission). Also, the observer directly assigned one of three alternative forest classes to each point count in the field: old-growth (characterized by no visible logging and a high abundance of large trees DBH >50 cm), selectively logged (recent signs of tree stubs, felled trees) and regenerating secondary forest. We verified old-growth forest designation using a published forest age classification based on historical aerial images (Zahawi et al., 2015); areas were considered to be old growth, if they already occurred as forests on the oldest aerial image available when settlement first occurred (1947). We found no mismatches with field classification. Similarly, secondary forest point counts were always younger than 24 years, based on aerial imagery. For every point count, we also calculated the amount of old-growth forest and the total amount of forest (all forest categories combined) within a 100-m, 500-m and 1,000-m radius buffer, using GIS.

2.5 | Statistical analyses

2.5.1 | α -Diversity and raw detections

All analyses were performed in R version 3.3.0. (R Core Team, 2016). To assess the response of the entire bird community, forest specialists and forest insectivores to local and landscape factors, we investigated α -diversity and the number of total counts (raw detections) of these three groups at the point-count scale. Statistical community-level analyses exist that explicitly adjust for imperfect detection, but a recent review highlighted their high uncertainty rate and limited value for hyperdiverse systems (Banks-Leite et al., 2014). Indeed, detectability-adjusted estimates of species richness showed very high uncertainty, although their analysis yielded qualitatively similar results as using raw numbers (Chao's estimator, Figure S5 and Table S7). Instead, we minimized bias through study design by (1) having a consistent observer for all surveys, (2) including time of day in the analysis and (3) excluding point counts with high acoustic interference from cicadas.

First, we fitted a full linear mixed-effects model to the α -diversities (raw species richness) and total counts at the point count level for each of these groups (lme, package nlme, version 3.1-113, Pinheiro, Bates, DebRoy, & Sarkar, 2014; following Gras et al., 2016). This model

included local forest type (FORTYP), fragment area in ha (AREA, continuous variable), proportion of old-growth forest (OLDFOR), proportion of total forest amount (ALLFOR), edge distance (DIST), altitude (ALT), daytime (TIME) as explanatory variables. To test whether patch size effects are mediated by landscape-scale forest amount, we included interactions between AREA and OLDFOR, AREA and ALLFOR. As an initial exploratory analysis revealed potential nonlinear effects of AREA, DIST and OLDFOR (function gamboost, package mboost, version 2.3-0, Hothorn, Buehlmann, Kneib, Schmid, & Hofner, 2012), we log₁₀-transformed AREA and DIST and included a quadratic term for OLDFOR in further analysis. Continuous explanatory variables were centred and standardized to improve the interpretability of regression coefficients. We included fragment ID as random intercept, variance functions to account for heteroscedasticity (Table S6) and a linear spatial correlation structure to account for spatial dependency of nearby fragments (corLin(form = ~X + Y)). Models were checked with VIFs and diagnostic plots for residual normality, heteroscedasticity and leverage.

Second, the models were simplified by retaining those predictors that contributed to the model, as indicated by an AICc-based multimodel inference framework ("MuMIn", Bartoń, 2013). Variables and their interactions were considered important, if their corresponding 95% confidence intervals excluded 0. Third, the model including these variables and interactions was refitted using restricted maximum likelihood. Significant differences of forest types were assessed using pairwise post hoc comparisons on the final model (Tukey's test function glht, package multcomp, version 1.3-6, Hothorn, Bretz, Westfall, & Heiberger, 2008). We report statistical significance from the final model using ANOVA type II (see Table 1). Model residuals for α -diversity and total counts did not show any spatial or altitudinal pattern (Figure S11).

As ALLFOR and OLDFOR were correlated (Pearson's $r = .69$), we additionally ran the model selection procedure with all variables but without ALLFOR, or without OLDFOR, respectively. However, this showed that the results were robust against the simultaneous inclusion of both factors (Table S9). Last, to assess the scale of the forest amount effect, we repeated these analyses at with ALLFOR and OLDFOR measured at $r = 100$ m and $r = 500$ m. However, this did not improve model fit (Table S10).

2.5.2 | β -diversity

To assess whether biotic homogenization was strongest among small fragments surrounded by little old-growth forest (homogenization hypothesis), we assessed beta-diversity as a function of old-growth forest amount and fragments size. We first categorized the fragments into four groups based on their size (large vs. small) and the landscape proportion of old growth-forest (high vs. low). We used the median proportion of old growth-forest (25.6%) as the cut-off between connected and isolated fragments (25.6%) to ensure similar fragment numbers per group.

We then tested whether or not groups differed in β -diversity, that is, the degree of variation in species identities among fragments, using multivariate tests of group dispersion in species space (Anderson,

TABLE 1 Model summary for the best linear mixed-effects models predicting total counts and α -diversity per point count, for all birds, forest birds and insectivorous forest birds, respectively. Significant variables are indicated in bold. Comparisons of forest types are based on Tukey's post hoc tests

	Total counts			α -Diversity		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
All species						
Intercept	12.81	0.35	.00	11.00	0.33	.00
Daytime	-0.71	0.32	.03	-0.71	0.26	.01
Forest species						
Intercept	4.46	0.48	.00	3.77	0.35	.00
Forest type						
Old growth—sel. logged	1.16	0.57	.10	0.83	0.42	.11
Secondary—sel. logged	-0.98	0.56	.18	-0.64	0.41	.27
Secondary—old growth	-2.15	0.45	.00	-1.47	0.35	.00
Edge distance	0.76	0.21	.00	0.65	0.17	.00
Old-growth forest %	—	—	—	0.20	0.15	.20
Daytime	-0.60	0.20	.00	-0.48	0.15	.00
Old-growth forest % × area	—	—	—	-0.34	0.13	.01
Forest insectivores						
Intercept	3.51	0.37	.00	2.72	0.28	.00
Forest type						
Old growth—sel. logged	0.33	0.44	.73	0.29	0.33	.64
Secondary—sel. logged	-0.85	0.40	.09	-0.55	0.30	.16
Secondary—old growth	-1.17	0.34	.00	-0.85	0.26	.00
Area	0.37	0.22	.10	0.25	0.16	.13
Edge distance	0.53	0.18	.00	0.44	0.13	.00
Old growth %	0.30	0.20	.14	0.22	0.13	.10
Altitude	0.30	0.16	.07	—	—	—
Daytime	-0.44	0.15	.00	-0.33	0.11	.00
Old growth % × area	-0.36	0.15	.02	-0.31	0.11	.01

Ellingsen, & McArdle, 2006; but see Anderson et al., 2011). This method allows to statistically assess the degree of biotic homogenization among treatments with different sample sizes, where large treatment-wise dispersion indicates a large variation in species identities among fragments and thus a low species overlap between fragments (high β -diversity), and small values indicate small variation in species identities and thus community homogenization (function `betadisper`, package `vegan`, Oksanen et al., 2013). We used a probabilistic, null-model-based measure of multivariate dispersion (Raup–Crick dissimilarities), which controls for differences in α -diversity among sites, and can be interpreted as the probability that two fragments share less species than expected for randomly drawn samples of their joint species pool, given their existing differences in richness (Anderson et al., 2011). This index of β -diversity is independent of differences in α -diversity between groups and has been suggested to be superior to classical measures of β -diversity for samples showing little species overlap (Anderson et al., 2011).

We pooled the first three point counts per fragment to achieve equal sampling intensity, but analyses based on the walkabout dataset yielded qualitatively the same results (Figure S12a). We accounted

for the slightly unequal number of fragments per group by adjusting the groupwise mean distance to the group median with a $\sqrt{n/(n-1)}$ correction (n = number of sites per group, Stier, Geange, Hanson, & Bolker, 2013). Significance among groups was calculated with permutation tests (9,999 permutations implemented in function `betadisper`).

2.5.3 | Community shift

To test for interactive effects of fragment size, old growth and secondary forest amount on deterministic changes in bird community abundances (biotic homogenization hypothesis), we used a community shift index (Mendenhall et al., 2014). This index ranges from 0 to 1 and describes how the abundances within an avian forest fragment community collectively shift compared to five intact reference forests in the study region (Figure 2). Small CSI values indicate an intact bird community similar to the pristine reference forests, whereas values close to 1 indicate a strongly altered community. Reference forests were assumed to harbour a largely undisturbed bird community and

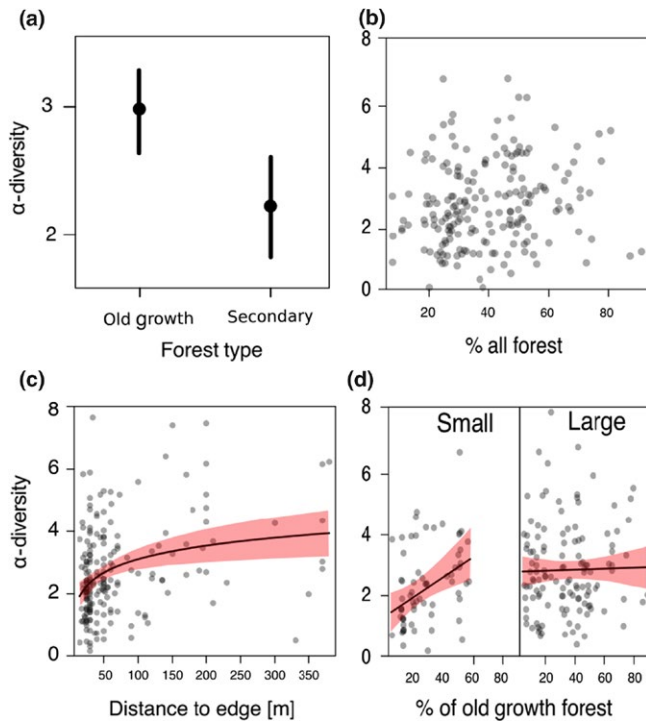


FIGURE 2 Effects of (a) forest type within the point count, (b) the percentage of all forest within 1,000 m (c) distance to the nearest forest edge and (d) fragment size and percentage of old-growth forest within 1,000 m radius on α -diversity of avian forest insectivores per point count. Note that the entire forest bird community and raw counts responded similarly. Lines and solid dots are predictions, whiskers and red bands depict the 95% confidence intervals, and grey dots are partial residuals. In (d), small and large refer to predictions for fragments of 2.5 and 100 ha size, respectively. Effects in (a), (c) and (d) are significant at $\alpha = 0.05$

were evenly spread in the study region, with three reference forest in the upper and two in the lower altitudinal band. We acknowledge that even these reference fragments are relatively small when compared to the original tracts of contiguous forest that existed in this system and may represent a shifted baseline. Thus, our results should be considered conservative estimates because effect sizes might be even larger compared to true past baselines.

The community shift index (CSI) was defined as

$$CSI_i = \frac{1}{k} * \sum_{j=1}^k D_{ij}$$

where CSI_i is the community shift index for fragment i out of n fragments, k is the number of reference forests, and D_{ij} is the observed dissimilarity between fragment i and reference forest j . In particular, we used Chao's dissimilarity index, an abundance-based index taking into account imperfect detection (Chao, Chazdon, & Shen, 2005; Oksanen et al., 2013).

Following the above equation, we first calculated the mean dissimilarity of every forest fragment to five large and (near-) pristine reference forests, using the walkabout dataset (indicated by dotted blue circles in Figure 2). Using the aggregated point count dataset did yield

similar results (Figure S12b). Finally, we standardized mean dissimilarity per fragment by dividing through its maximum value.

Using a glm, we then tested whether patch size effects on CSI were mediated by landscape-scale forest amount. The CSI was the response variable, fragment area (AREA), proportion of old-growth forest (OLDFOR), proportion of all forest (ALLFOR) and altitude (ALT), $AREA \times OLDFOR$ and $AREA \times ALLFOR$ the predictors. Predictor values were averaged across the corresponding point counts. We also included the total abundance of birds per fragment as predictor (Mendenhall et al., 2014), as Chao dissimilarity, and thus, the CSI is influenced by abundance. Model residuals did not show any spatial autocorrelation (Figure S11). Model selection was accomplished as for plot-based analyses, but by mandatorily retaining abundance in all models.

3 | RESULTS

We sampled 6,906 individuals representing 223 different bird species. The 209 point counts yielded 2,520 bird individuals, 189 species including 31 singletons (cumulative time = 2,508 min). A total of 977 individuals from 76 species were forest specialists (14 singletons), including 45 forest insectivore bird species (645 individuals, 8 singletons). The 49 walkabouts totalled 5,825 min and yielded 4,386 individuals of 216 species (26 singletons), with 1,622 individuals and 83 species being forest specialists (10 singletons). About 82% (182) of the species were detected with both methods (Table S4 and Figure S5a).

3.1 | α -Diversity and raw detections

Overall, α -diversity and raw counts for the entire bird community were unaffected by landscape composition and configuration (Table 1). In contrast, forest specialists and forest insectivores showed three distinct patterns: first, landscape-wide old-growth forest and fragment size significantly interacted; forest specialists and forest insectivores α -diversity decreased by c. 40% in small fragments compared to large fragments, but only within old-growth poor landscapes (Figure 2, Table 1). Contrastingly, small fragments in old-growth rich landscapes retained α -diversity comparable to large fragments (Figure 2, Table 1). This pattern was mirrored by forest insectivore raw detections: c. 40% fewer forest insectivores were seen during point counts in small, isolated fragments compared to small connected or large fragments (Figure S8). Importantly, the total forest cover was not retained in any analysis. Second, old-growth forest harboured 24% more forest insectivore species at the plot level than secondary forests (richness: 2.96 ± 0.16 vs. 2.21 ± 0.20 , $p = .016$; Figure 2, Table 1). Third, forest insectivore α -diversity decreased substantially in proximity to edges ($p < .001$ in both cases, Figure 2, Table 1). For example, 1.92 ± 0.16 species were found on average per plot at 25 m edge distance, while this increased to 3.00 ± 0.27 species at 200 m edge distance (Figure 2).

Importantly, we found no significant effect of the total forest cover on abundance and richness at the plot level; variable importance of ALLFOR never exceeded 0.5 in any model. Models including OLDFOR always

considerably outperformed the corresponding model with ALLFOR ($\Delta\text{AICc} > 2$ for in all comparisons and for all responses, Table S9).

3.2 | β -Diversity

The four landscape groups differed significantly in β -diversity (ANOVA: $df = 3,45$; $F = 6.74$; $p < .001$). Generally, large connected fragments showed the highest β -diversity, followed by large isolated, small connected and finally small isolated fragments. Importantly, β -diversity in small isolated fragments was significantly reduced by 86%, 83% and 83% compared to large connected, large isolated and small connected fragments, respectively (Figure 3a, Table 2), indicating biotic homogenization. In contrast, pairwise differences in β -diversity among the other three fragment categories were not statistically significant (Table 2).

3.3 | Community shift

The only important variable influencing community shift was the proportion of old-growth forest (variable weight = 1). The CSI decreased significantly with increasing proportion of old-growth forest (ANOVA: $\chi^2 = 36.21$, $df = 1$, $p < .001$), indicating that bird communities were highly similar to pristine forest at high proportions of old-growth forest, irrespective of fragment size (Figure 3b).

4 | DISCUSSION

We found three key results; first, there were significantly fewer species and individuals of forest specialists and forest insectivores in

small fragments, but this only occurred at low amounts of old-growth forest within the landscape. Thus, there were not only locally more forest species and insectivores in old-growth forest (c. 32% increase in α -diversity), but this effect was amplified at the landscape level. Importantly, secondary forest did not have any capacity to mediate these negative effects of small fragment size in our study landscape.

Second, high amounts of old-growth forest also curbed biotic homogenization; β -diversity for the entire bird community collapsed by 85% in small fragments, but again, only at low amounts of old-growth forest in the landscape. Third, the community shift index suggests that changes in the amount of old-growth forest in the landscape, but not of secondary forest or reduced fragment size, caused abundance-based community shifts and thus predictable avian community reassembly. Thus, species composition was restructured substantially when old-growth forest cover declined, even within large fragments. Overall, this shows that retaining old growth within HMTLs is crucial for limiting loss of forest specialist α -diversity, community homogenization and avian community shifts. Finally, we demonstrate that landscape composition and fragment size synergistically shape the trajectory of biotic communities in HMTLs.

The three complementary lines of evidence we provide (α -diversity, β -diversity, community shifts) constitute, to our knowledge, some of the first empirical evidence for the importance of not simply retaining forest habitat, but prioritizing old-growth forest conservation within tropical landscapes. High landscape-scale proportions of old growth, but not of secondary forests, provided a “subsidy-effect” which extended to the landscape level to mitigate negative fragmentation effects in nearby small fragments. These benefits persist even 50 years after large-scale deforestation occurred. Despite the fact that

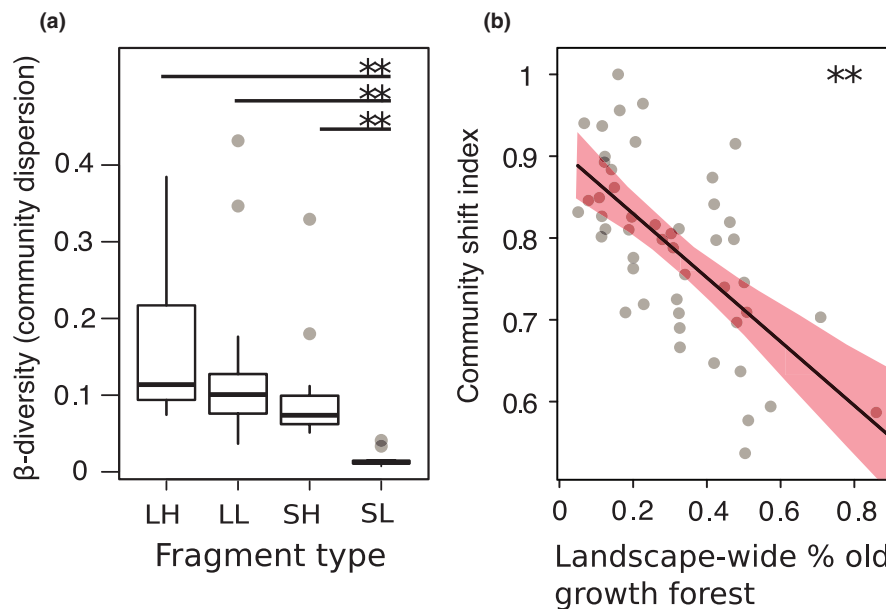


FIGURE 3 β -Diversity and community shift of the entire bird community in forest fragments. (a) Boxplots of β -diversity measured as community dispersion based on Raup–Crick distances. Fragments groups: large with high amount of old-growth forest (LH), large with low amount of old-growth forest (LL), small with high amount of old-growth forest (SH) and small with low amount of old-growth forest (SL). (b) Avian community shift in forest fragments compared to pristine forest as a function of the percentage of old forest within 1,000 m. Shown are predictions (black solid line), the 95% confidence interval (red) and partial residuals (grey dots) for the best model. High values represent a strong community shift and low values high similarity to pristine forest. ** indicates significance at $\alpha = 0.01$ [Colour figure can be viewed at wileyonlinelibrary.com]

successional pathways and species communities of secondary forest fragments can be highly variable depending on forces operating at multiple spatio-temporal scales (Arroyo-Rodríguez et al., 2017), secondary forests were generally of inferior conservation value than old-growth forest in our study.

Although previous work has revealed shifts in community composition, α - and β -diversity in tropical countrysides around the world (e.g. Barlow et al., 2007; Carrara et al., 2015; Mendenhall et al., 2014; Morante-Filho, et al., 2016; Morante-Filho, Faria, Mariano-Neto, & Rhodes, 2015), we separate the relative contributions of landscape composition and fragment size to show that they can synergistically affect ecological changes in tropical countrysides.

We suggest two explanations for this old-growth rescue effect: first, optimal foraging theory (MacArthur & Pianka, 1966) predicts that if moving between fragments is associated with elevated risk (e.g. predation) or if small isolated fragments exhibit prey paucity, spatial proximity of old growth may enable individuals to include nearby small fragments in their foraging territory (landscape supplementation, Dunning, Danielson, Pulliam, & Ecology, 1992); small isolated fragments, on the other hand, may be too “costly” to visit. This idea is supported by the finding that small fragments were increasingly used by forest specialist birds when they were physically linked to nearby large forests by wooded corridors (Kormann et al., 2016). Alternatively, nearby old-growth forest may substantially contribute to the landscape-wide pool of colonizers, thereby reducing local extinctions and increasing recolonization of vacant fragments (“landscape species pool hypothesis” Tschardt et al., 2012). Indeed, in our study region, decreased fragment size has been associated with elevated community turnover and increased adult mortality for birds in our study area (Borgella & Gavin, 2005; Ruiz-Gutiérrez, Gavin, & Dhont, 2008). Taken together, this suggests that large tracts of old-growth forest are likely net exporters of many forest specialist species, while small fragments are not. Further, under this hypothesis, the fact that we found no capacity of secondary forest to provide a rescue effect from fragmentation is not surprising, given that secondary forests harboured 40% less forest specialists than old-growth forest.

Fragment size and landscape composition did not alter α -diversity of the entire bird community (compensatory dynamics sensu Supp & Ernest, 2014). Thus, if we had focused on overall α -diversity only, we would wrongly have concluded that HML bird communities do not experience edge effects and are insensitive to altered fragment size and landscape composition. However, the 50% collapse in forest birds in small, isolated fragments underpins that overall α -diversity is a poor

descriptor of anthropogenic effects on communities. In line with the “fragmentation threshold hypothesis” (Andr n, 1994) and empirical work (Betts, Forbes, & Diamond, 2007; Betts, Forbes, Diamond, & Taylor, 2006), we thus report that negative fragmentation effects on habitat specialists are enhanced at low levels of habitat amount and that modification of native habitat may not primarily decrease species richness or overall abundance, but rather induce community shifts towards generalist “winner” species (e.g. Tabarelli et al., 2012).

Our data strongly support the “homogenization hypothesis”, as we found strong evidence that the reduction of fragment size and total cover of old-growth forest lead to reduced β -diversity. To our knowledge, our study is among the first to demonstrate interactive effects of forest amount and configuration on β -diversity. In accordance with the “landscape species pool hypothesis” (Tschardt et al., 2012), these results support the idea that avian communities in small, connected fragments are subsidized more often and by a broader diversity of immigrants from nearby old-growth forest, whereas small isolated fragments only recruit individuals from a restricted landscape-wide species pool. In contrast, our data do not support the “biotic differentiation hypothesis” (Arroyo-Rodr guez et al., 2013). Rather, over the long-term (50 years post-fragmentation) small isolated fragments appear to harbour a small, depauperate subset of generalists.

Further, our results also shed new light on the “dominance of β -diversity hypothesis” (sensu Tschardt et al., 2012), which states that although α -diversity may decrease when fragment size decreases, communities will diverge between fragments, and the resulting increase in β -diversity may even compensate for negative impacts of reduced alpha diversity on gamma diversity (Morante-Filho, et al., 2016; Morante-Filho, et al., 2015; Solar et al., 2015; Tschardt et al., 2012). Our results suggest that this compensation effect can be moderated by landscape composition (i.e. availability of old-growth forest in the landscape).

Paralleling the landscape effects, we found that α -diversity of the entire bird community for edge and interior plots was surprisingly similar, whereas forest specialist dropped by 33% from 25 to 200 m edge proximity (and -40.5% for forest insectivores). This suggests that forest species were largely substituted by more generalist species in edge proximity, a pattern that has for example been observed in trees (Laurance et al., 2006), arthropods (Ewers & Didham, 2008) and birds in Brazil (Banks-Leite, Ewers, & Metzger, 2010). About 60% of forest in the study region and 20% of the remaining global forest cover are less than 100 m away from the next forest edge (Haddad et al., 2015; Zahawi et al., 2015). Edge effects similar to the ones observed here could therefore cause tremendous changes in community

TABLE 2 Effect of fragment type on β -diversity, measured as community dispersion based on Raup–Crick distances. Shown are permutational p -values (9,999 permutations) for pairwise comparisons between small isolated, small connected, large isolated and large connected fragments. Isolated and connected refer to fragments with <25% and >25% old forest at the landscape scale, respectively. Small fragments were <5 ha, large fragments >35 ha. Significant values are indicated in bold

	Large isolated	Small connected	Small isolated
Large connected	0.533	0.116	<0.001
Large isolated		0.447	<0.001
Small connected			<0.001

composition, trophic interactions and potentially ecosystem functions in the Coto Brus area and tropical regions globally.

Until now, combined effects of changes in forest composition, disturbance and configuration on the conservation value of HMTLs remained unclear, which critically restricts conservation planning. We show that future policy interventions such as REDD+ will have to (1) go beyond simply the maintenance of forest cover to prioritize old-growth forest conservation and (2) take into account landscape configuration. Although small forest remnants, which are among the most abundant tropical landscape elements, can harbour bird species found in pristine forests—this only occurs given a high proportion of proximal old-growth forest. Changes in α -diversity, β -diversity and resulting community shifts at low old-growth amounts extend previous calls on the importance of old-growth forest for biodiversity conservation within HMTL (Gibson et al., 2011; Laurance et al., 2012; Powell, Cordeiro, et al., 2015; Powell, Wolfe, et al., 2015). Although regenerating forest in biologically depauperate landscapes can substantially bolster conservation value of these sites, our data caution against potentially misleading expectations that moderately modified HMTLs with abundant secondary forest may represent a panacea for the conservation of tropical biodiversity. Instead, conservation efforts in HMTL should focus on safeguarding large tracts of old-growth forest and insure that potential disturbance thresholds are not crossed.

ACKNOWLEDGEMENTS

We thank Jeisson Figueroa for fieldwork, Guillermo Duran, Diego Zarrate-Charry and Zak Zahawi for GIS support and all landowners for access to their properties. Victor Arroyo-Rodríguez, Jos Barlow, Danny Karp and Jim Zook and two anonymous reviewers provided very valuable input during initial discussions or commented on earlier versions of the manuscript. This research was funded by the DFG Research Training Group 1644 Scaling Problems in Statistics (U.G.K.), NSF-DEB-1050954 (M.G.B., W.D.R., A.S.H.) and NSERC-PDF (A.S.H.).

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; U.G.K. collected the data; U.G.K. and C.S. analysed the data; U.G.K., A.S.H., M.G.B. and C.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.0t9d3> (Kormann et al., 2018).

ORCID

Urs G. Kormann  <http://orcid.org/0000-0001-9875-4836>

Christopher Scherber  <http://orcid.org/0000-0001-7924-8911>

REFERENCES

- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., ... Swenson, N. G. (2011). Navigating the multiple meanings of beta-diversity: A roadmap for the practicing ecologist. *Ecology Letters*, *14*, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*, 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat – A review. *Oikos*, *71*, 355–366. <https://doi.org/10.2307/3545823>
- Arroyo-Rodríguez, V., Melo, F. P., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., ... Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, *92*, 326–340. <https://doi.org/10.1111/brv.12231>
- Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F. P., Santos, B. A., Tabarelli, M., & Chazdon, R. (2013). Plant β -diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. *Journal of Ecology*, *101*, 1449–1458. <https://doi.org/10.1111/1365-2745.12153>
- Banks-Leite, C., Ewers, R. M., & Metzger, J. P. (2010). Edge effects as the principal cause of area effects on birds in fragmented secondary forest. *Oikos*, *119*, 918–926. <https://doi.org/10.1111/j.1600-0706.2009.18061.x>
- Banks-Leite, C., Pardini, R., Boscolo, D., Cassano, C. R., Puettker, T., Barros, C. S., & Barlow, J. (2014). Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. *Journal of Applied Ecology*, *51*, 849–859. <https://doi.org/10.1111/1365-2664.12272>
- Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., ... Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 18555–18560. <https://doi.org/10.1073/pnas.0703333104>
- Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R., ... Braga, R. F. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, *535*, 144–147. <https://doi.org/10.1038/nature18326>
- Bartoń, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. Vienna, Austria: The Comprehensive R Archive Network (CRAN).
- Betts, M. G., Forbes, G. J., & Diamond, A. W. (2007). Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology*, *21*, 1046–1058. <https://doi.org/10.1111/j.1523-1739.2007.00723.x>
- Betts, M. G., Forbes, G. J., Diamond, A. W., & Taylor, P. D. (2006). Independent effects of fragmentation on forest songbirds: An organism-based approach. *Ecological Applications*, *16*, 1076–1089. [https://doi.org/10.1890/1051-0761\(2006\)016\[1076:IEOFOF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1076:IEOFOF]2.0.CO;2)
- Borgella, R., & Gavin, T. A. (2005). Avian community dynamics in a fragmented tropical landscape. *Ecological Applications*, *15*, 1062–1073. <https://doi.org/10.1890/04-0352>
- Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J. H., Schondube, J. E., de Freitas, S. M., & Fahrig, L. (2015). Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biological Conservation*, *184*, 117–126. <https://doi.org/10.1016/j.biocon.2015.01.014>
- Chao, A., Chazdon, R. L., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*, 148–159.
- Dunning, J. B., Danielson, B. J., Pulliam, H. R., & Ecology, I. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*, 169–175. <https://doi.org/10.2307/3544901>

- Ewers, R. M., & Didham, R. K. (2008). Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 5426–5429. <https://doi.org/10.1073/pnas.0800460105>
- Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663. <https://doi.org/10.1111/jbi.12130>
- Galetti, M., Guevara, R., Cortes, M. C., Fadini, R., Von Matter, S., Leite, A. B., ... Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, 340, 1086–1091. <https://doi.org/10.1126/science.1233774>
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., ... Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381. <https://doi.org/10.1038/nature10425>
- Gras, P., Tscharrntke, T., Maas, B., Tjoa, A., Hafsa, A., & Clough, Y. (2016). How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry. *Journal of Applied Ecology*, 53(3), 953–963. <https://doi.org/10.1111/1365-2664.12625>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, 1–9.
- Hadley, A. S., & Betts, M. G. (2016). Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports*, 1, 55–66. <https://doi.org/10.1007/s40823-016-0007-8>
- Hadley, A. S., Frey, S. J. K., Robinson, W. D., John Kress, W., & Betts, M. G. (2014). Tropical forest fragmentation limits pollination of a keystone understory herb. *Ecology*, 95, 2202–2212. <https://doi.org/10.1890/13-0929.1>
- Herzog, S. K., Kessler, M., & Cahill, T. M. (2002). Estimating species richness of tropical bird communities from rapid assessment data. *The Auk*, 119, 749–769. [https://doi.org/10.1642/0004-8038\(2002\)119\[0749:ESROTB\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2002)119[0749:ESROTB]2.0.CO;2)
- Hothorn, T., Bretz, F., Westfall, P., & Heiberger, R. M.. (2008). Multcomp: Simultaneous Inference in General Parametric Models—R Package Version 1.0–0. Vienna, Austria: R Foundation for Statistical Computing.
- Hothorn, T., Buehlmann, P., Kneib, T., Schmid, M., & Hofner, B. (2012). mboost: Model-based boosting. R package version, 2-1.
- Hughes, J. B., Daily, G. C., & Ehrlich, P. R. (2002). Conservation of tropical forest birds in countryside habitats. *Ecology Letters*, 5, 121–129. <https://doi.org/10.1046/j.1461-0248.2002.00294.x>
- Karp, D. S., Mendenhall, C. D., Sandí, R. F., Chaumont, N., Ehrlich, P. R., Hadly, E. A., & Daily, G. C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters*, 16, 1339–1347. <https://doi.org/10.1111/ele.12173>
- Karp, D. S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R., & Daily, G. C. (2012). Intensive agriculture erodes beta-diversity at large scales. *Ecology Letters*, 15, 963–970. <https://doi.org/10.1111/j.1461-0248.2012.01815.x>
- Kormann, U., Hadley, A. S., Tscharrntke, T., Betts, M. G., Robinson, W. D., & Scherber, C. (2018). Data from: Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.0t9d3>
- Kormann, U., Scherber, C., Tscharrntke, T., Klein, N., Larbig, M., Valente, J. J., ... Betts, M. G. (2016). Corridors restore animal-mediated pollination in fragmented tropical forest landscapes Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. *Proceedings of the Royal Society B*, 283, 20152347.
- Laurance, W. F. (1999). Reflections on the tropical deforestation crisis. *Biological Conservation*, 91, 109–117. [https://doi.org/10.1016/S0006-3207\(99\)00088-9](https://doi.org/10.1016/S0006-3207(99)00088-9)
- Laurance, W. F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C. J., Sloan, S. P., ... Zamzani, F. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489, 290–294. <https://doi.org/10.1038/nature11318>
- Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., ... D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 19010–19014. <https://doi.org/10.1073/pnas.0609048103>
- Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution*, 29, 107–116. <https://doi.org/10.1016/j.tree.2013.12.001>
- Lees, A. C., & Peres, C. A. (2009). Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos*, 118, 280–290. <https://doi.org/10.1111/j.1600-0706.2008.16842.x>
- Lindquist, E. J., D'Annunzio, R., Gerrand, A., MacDicken, K., Achard, F., Beuchle, R., ... San-Miguel-Ayanz, J. (2012). *Global forest land-use change 1990–2005*. Rome, Italy: FAO.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment author. *The American Naturalist*, 100, 603–609. <https://doi.org/10.1086/282454>
- Melo, F. P. L., Arroyo-Rodriguez, V., Fahrig, L., Martinez-Ramos, M., & Tabarelli, M. (2013). On the hope for biodiversity – Friendly tropical landscapes. *Trends in Ecology & Evolution*, 1649, 1–7.
- Mendenhall, C. D., Karp, D. S., Meyer, C. F. J., Hadly, E. A., & Daily, G. C. (2014). Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, 509, 213–217. <https://doi.org/10.1038/nature13139>
- Morante-Filho, J. C., Arroyo-Rodriguez, V., & Faria, D. (2016). Patterns and predictors of β -diversity in the fragmented Brazilian Atlantic forest: A multiscale analysis of forest specialist and generalist birds. *Journal of Animal Ecology*, 85, 240–250.
- Morante-Filho, J. C., Faria, D., Mariano-Neto, E., & Rhodes, J. (2015). Birds in anthropogenic landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic forest. *PLoS ONE*, 10, 1–18.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ... Wagner, H. (2013). Package 'vegan'. *Community ecology package, version, 2*.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D., & R Core Team. (2014). nlme: Linear and nonlinear mixed effects models. R package version 3.1-117.
- Powell, L. L., Cordeiro, N. J., & Stratford, J. A. (2015). Ecology and conservation of avian insectivores of the rainforest understory: A pan-tropical perspective. *Biological Conservation*, 188, 1–10. <https://doi.org/10.1016/j.biocon.2015.03.025>
- Powell, L. L., Wolfe, J. D., Johnson, E. I., Hines, J. E., Nichols, J. D., & Stouffer, P. C. (2015). Heterogeneous movement of insectivorous Amazonian birds through primary and secondary forest: A case study using multistate models with radiotelemetry data. *Biological Conservation*, 188, 100–108. <https://doi.org/10.1016/j.biocon.2015.01.028>
- R Core Team. (2016). *R: A language and environment for statistical computing, version 3.3.0*. Vienna, Austria: R Foundation for Statistical Computing.
- Robinson, W. D. (1999). Long-term changes in the Avifauna of Barro Colorado Island, Panama, a tropical forest isolate. *Conservation Biology*, 13, 85–97. <https://doi.org/10.1046/j.1523-1739.1999.97492.x>
- Ruiz-Gutiérrez, V., Gavin, T. A., & Dhont, A. A. (2008). Habitat fragmentation lowers survival of a tropical forest bird. *Ecological Applications*, 8, 838–846. <https://doi.org/10.1890/07-1090.1>
- Rybicki, J., & Hanski, I. (2013). Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters*, 16, 27–38. <https://doi.org/10.1111/ele.12065>
- Sala, O. E., Iii, F. S. C., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., & Walker, M. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Sekercioglu, C. H., Loarie, S. R., Oviedo Brenes, F., Ehrlich, P. R., & Daily, G. C. (2007). Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology*, 21, 482–494. <https://doi.org/10.1111/j.1523-1739.2007.00655.x>

- Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity biological determinants of species diversity. *Journal of Biogeography*, 12, 1–20. <https://doi.org/10.2307/2845026>
- Solar, C. R. R., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., ... Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, 18, 1108–1118. <https://doi.org/10.1111/ele.12494>
- Stier, A. C., Geange, S. W., Hanson, K. M., & Bolker, B. M. (2013). Predator density and timing of arrival affect reef fish community assembly. *Ecology*, 94, 1057–1068. <https://doi.org/10.1890/11-1983.1>
- Stiles, F. G., & Skutch, A. F. (1989). *Guide to the birds of Costa Rica*. Costa Rica: Comistock.
- Supp, S. R., & Ernest, S. K. (2014). Species-level and community-level responses to disturbance: A cross-community analysis. *Ecology*, 95, 1717–1723. <https://doi.org/10.1890/13-2250.1>
- Tabarelli, M., Peres, C. A., & Melo, F. P. (2012). The 'few winners and many losers' paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*, 155, 136–140. <https://doi.org/10.1016/j.biocon.2012.06.020>
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batary, P., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes – Eight hypotheses. *Biological Reviews*, 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Villard, M. A., & Metzger, J. P. (2014). Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, 51, 309–318. <https://doi.org/10.1111/1365-2664.12190>
- Volpe, N. L., Hadley, A. S., Robinson, W. D., & Betts, M. G. (2014). Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecological Applications*, 24, 2122–2131. <https://doi.org/10.1890/13-2168.1>
- Watson, D. M. (2010). Optimizing inventories of diverse sites: Insights from Barro Colorado island birds. *Methods in Ecology and Evolution*, 1, 280–291.
- Zahawi, R. A., Duran, G., & Kormann, U. (2015). Sixty-seven years of land-use change in southern Costa Rica. *PLoS ONE*, 10, e0143554. <https://doi.org/10.1371/journal.pone.0143554>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Kormann UG, Hadley AS, Tscharntke T, Betts MG, Robinson WD, Scherber C. Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. *J Appl Ecol*. 2018;00:1–11. <https://doi.org/10.1111/1365-2664.13084>