

Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments

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Abstract. Competitive interactions among species with similar ecological niches are known to regulate the assembly of biological communities. However, it is not clear whether such forms of competition can predict the collapse of communities and associated shifts in ecosystem function in the face of environmental change. Here, we use phylogenetic and functional trait data to test whether communities of two ecologically important guilds of tropical birds (frugivores and insectivores) are structured by species interactions in a fragmented Amazonian forest landscape. In both guilds, we found that forest patch size, quality, and degree of isolation influence the phylogenetic and functional trait structure of communities, with small, degraded, or isolated forest patches having an increased signature of competition (i.e., phylogenetic and functional trait overdispersion in relation to null models). These results suggest that local extinctions in the context of fragmentation are nonrandom, with a consistent bias toward more densely occupied regions of niche space. We conclude that the loss of biodiversity in fragmented landscapes is mediated by niche-based competitive interactions among species, with potentially far-reaching implications for key ecosystem processes, including seed dispersal and plant damage by phytophagous insects.

Key words: avian communities; biodiversity conservation; community disassembly; diet and morphology; ecosystem services; fragmentation; functional traits; habitat filtering; interspecific competition; limiting similarity; Mato Grosso, Brazil; tropical rain forest.

INTRODUCTION

Niche-based processes are often proposed to be dominant factors in explaining the assembly of local communities (Diamond 1975, Tilman 1982, Segre et al. 2014). For example, constraints on coexistence among competing species may regulate the sequence of invasion into a community, as well as its eventual diversity (Fargione et al. 2003, HilleRisLambers et al. 2012). However, it is less clear whether similar factors influence the opposite process of community disassembly (Rader et al. 2014); that is, the sequence and extent of local extinction resulting from habitat disturbance or fragmentation. Thus, we still lack a basic understanding of whether declines in biodiversity driven by land-use change are predictable on the basis of species interactions, particularly interspecific resource competition

(Tilman 1982, Debinski and Holt 2000, Mayfield et al. 2010).

One of the most prominent impacts of land-use change is the fragmentation of natural habitats (Fahrig 2003). However, despite decades of research on the impacts of this process, the role of species interactions remains contentious. Some studies argue that fragmentation reduces interspecific competition by generating new niche axes (Buchmann et al. 2013) or limiting the scope for monopolization, thus allowing more species to co-occur (e.g., Levin 1974, Atkinson and Shorrocks 1981). Other studies provide evidence that competition is elevated in smaller fragments (Feeley 2003, Bennett et al. 2014), which seems plausible if the overall pool of resources declines in parallel with fragment size, increasing the likelihood of resource limitation and competitive exclusion. However, these alternative hypotheses have rarely been tested directly, with most studies focusing on the extent to which local extinction is mediated by species traits rather than species interactions (e.g., Robinson et al. 1992, McKinney and Lockwood 1999, Smith and Knapp 2003, Banks-Leite et al. 2012, Senior et al. 2013).

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The focus on traits has been instrumental in identifying species attributes associated with sensitivity to habitat fragmentation, including large body mass and limited dispersal ability (Lees and Peres 2008, 2009). A trait-based approach can provide further valuable insight because functional traits (e.g., beak shape in birds, seed size in plants) have clear implications for fitness through their impact on growth, reproduction, and survival, and also provide an objective measure of an organism's role in ecosystem function (Diaz and Cabido 2001, Violle et al. 2007). However, although general patterns of susceptibility to extinction are of fundamental importance (Ewers and Didham 2006, Senior et al. 2013), they tell us little about the underlying processes structuring the collapse of ecological communities in degraded environments, or the extent to which such processes are mediated by competitive interactions among species.

Previous studies have attempted to address this question by estimating how community structure varies across environmental or disturbance gradients (e.g., Cornwell and Ackerly 2009, Katabuchi et al. 2012). However, very few empirical tests have focused on communities in habitat fragments, and all of them are apparently limited to taxonomic groups where direct competitive or territorial interactions are diffuse, such as insects (Pavoine et al. 2014, Rader et al. 2014). Moreover, even studies of community assembly focusing on disturbance gradients have either ignored functional traits (Brunbjerg et al. 2012), or have combined such traits into multivariate metrics (Mayfield et al. 2005, Dehling et al. 2014). The results have been mixed, perhaps because both methods essentially combine different functional groups of species, and pool the effects of different assembly processes with contrasting implications for community structure. In particular, some functional groups and traits may be structured by habitat filtering (when related species co-occur because they share tolerance of environmental factors, predicting that communities are underdispersed with respect to phylogenetic or trait structure), whereas others may be structured by limiting similarity (when related species cannot co-occur because they compete for similar resources, predicting that communities are overdispersed) (Webb et al. 2002, Cavender-Bares et al. 2009). It is now known that focusing on an assortment of guilds and traits can cause these opposing assembly patterns to be merged, reducing the signature of species interactions and producing an inaccurate impression of neutrality (Aiba et al. 2013, Trisos et al. 2014).

Here, we address these issues by testing for the role of interspecific competition in structuring communities of avian dietary guilds across a fragmentation gradient in a humid tropical forest landscape. We restricted our analyses to two key functional groups: frugivores and insectivores. These groups provide an essential service in maintaining ecosystem functioning, as they are critical for the top-down control of phytophagous insects (Van

Bael et al. 2008) and seed dispersal (Howe 1977, Da Silva et al. 1996), respectively. We first assessed the phylogenetic structure of frugivore and insectivore communities, assuming that evolutionary history provides a broad proxy for ecological similarity across multiple axes (Cavender-Bares et al. 2009). We then used functional traits to test for the signature of competition in specific niche axes.

Direct competition is most frequent among bird species of similar size, diet, and foraging behavior, leading to the classic view that such competition will limit co-occurrence on these axes, resulting in communities with greater dispersion in body size, beak traits, and foraging behavior than expected by chance (MacArthur 1958, Hutchinson 1959, Schoener 1965, Lack 1971). We therefore considered such axes separately, allowing us (1) to focus on traits most likely to be structured by competition, and (2) to disentangle processes applying independently to different aspects of the ecological niche. The hypothesis that competition increases in fragmented landscapes predicts that as habitat patch size decreases, dispersion in the phylogenetic and trait structure of communities will increase. Given that communities may be structured at the local scale by both limiting similarity and habitat filtering (Trisos et al. 2014), we tested for over- and under-dispersion of all phylogenetic and trait-based tests.

Our aims were to understand: (1) the importance of competition in structuring fragmented communities; (2) the effects of key properties of habitat patches (i.e., patch size, isolation, and habitat quality) on the relative importance of competition; and (3) whether these associations are influenced by foraging guild and functional traits. These goals are particularly urgent in tropical forests, where habitat fragmentation is currently proceeding most rapidly (Hansen et al. 2013), and with greatest potential impact on biodiversity and ecosystem function (Tobias et al. 2013, Edwards et al. 2014).

METHODS

Study site and community sampling

Our study focused on forest patches around Alta Floresta, Mato Grosso state, Brazil (~09°53' S; 56°28' W). Although rates of Amazonian deforestation have recently slowed, this region suffered a rapid reduction in forest cover from 91.1% to 41.7% between 1984 and 2004, a loss of 3600 km² of primary rain forest cleared primarily for cattle pasture (Michalski et al. 2008). We used data from standardized surveys carried out between June 2004 and June 2006 (Lees and Peres 2006, 2008) to compile bird community data from 30 forest patches ranging in size from 1 ha to 14 476 ha and a single "continuous" forest site (the Rio Cristalino State Park), part of an extensive area of forest reaching far to the north. Sampling intensity was standardized across sites, with the same number of point counts undertaken by the same observer, in the same season, for each forest patch regardless of size. More time was

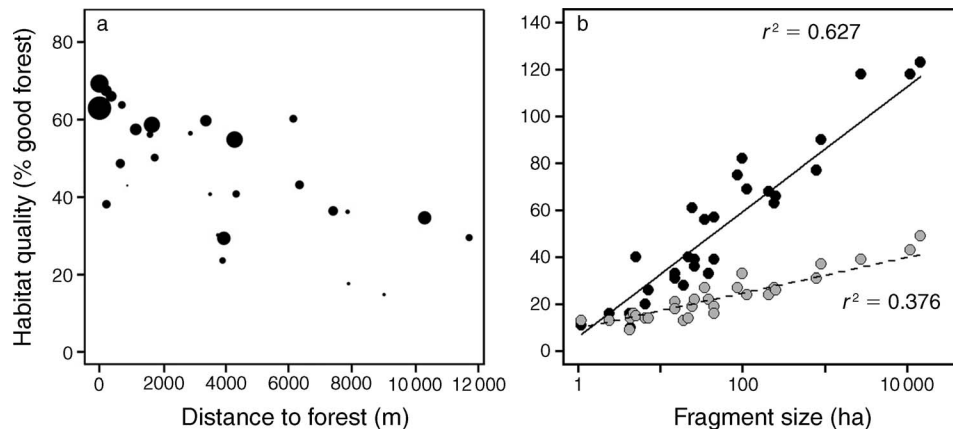


FIG. 1. Basic characteristics of study forest fragments and their bird communities. (a) Relationship between habitat quality and fragment isolation. Circles represent fragments ($n = 30$ fragments) scaled by relative size. Habitat quality is plotted as the total percentage of the fragment composed of good quality forest (i.e., tall stature, closed canopy); distance to forest is the straight-line distance from each fragment to the nearest forest > 1000 ha (distance is given as zero for fragments > 1000 ha). (b) Relationship between species richness and habitat patch size (shown on a log scale). Black circles represent the total richness of insectivore species in each forest fragment; gray circles represent the total number of frugivore species. Lines show model fit from a linear regression: solid line, insectivores; dashed line, frugivores. The r^2 values are pseudo- r^2 , calculated following McFadden (1974).

therefore spent per area of forest in larger fragments, and thus fewer rare species are likely to be overlooked in small fragments (see rarefaction curves in Lees and Peres 2006). Thus, our analyses are conservative with respect to declines in species richness or abundance with forest patch size. For further details of sampling, selection of fragments, and a map of the study area, see Lees and Peres (2006, 2008).

The total list of birds recorded in all study sites comprised 336 species (Figs. 1 and 2), representing seven major guilds: insectivores, frugivores, granivores, nectarivores, carnivores, scavengers, and omnivores (Appendix A). Guild membership was based on Sekercioglu et al. (2004), with updates from Belmaker et al. (2012) and Salisbury et al. (2012). Guilds indicate primary diet (i.e., an insectivore can be a largely insectivorous species that also consumes small amounts of nectar and berries). Species were categorized as omnivores if no primary diet was apparent. Because most community assembly models apply specifically to interactions within trophic levels (Cavender-Bares et al. 2009), we focused our analyses separately on primary consumers (frugivores; $n = 68$) and secondary consumers (insectivores; $n = 196$). We simplified trophic levels to one guild each because they dominated our study communities (Fig. 2), whereas other guilds did not provide adequate sample sizes for guild-specific analyses of community assembly (Appendix A). Restricting analyses within guilds avoids the problem that strong interactions are unlikely between trophic levels or guilds because of divergent foraging niches (Trisos et al. 2014). Moreover, separate analyses are useful because tropical insectivores and frugivores differ in the level of competitive interactions within guilds (Jankowski et al. 2012), as well as their responses to variation in fragment size, isolation, and quality

(Sekercioglu et al. 2004, Sekercioglu 2007, Lees and Peres 2008, Bregman et al. 2014).

For each forest fragment, landscape characteristics were extracted from satellite images by Lees and Peres (2006, 2008) using Fragstats v. 3.3 (McGarigal et al. 2002) and ArcView 3.2 (ESRI 2013). The variables selected were patch size (ha), distance to the nearest source forest patch > 1000 ha, and the proportion of closed-canopy forest within the fragment. We used 1000 ha as the threshold for source communities because tropical forest patches > 1000 ha tend to support communities with similar functional trait structure to continuous forests and may provide at least temporary refugia for most fragmentation-sensitive species (Bregman et al. 2014).

Trait sampling

To provide insight into the ecological function of species, we collected morphological data from specimens held in the Museu Paraense Emílio Goeldi, Belém, Brazil ($n = 1180$ skins), the Natural History Museum, Tring, UK ($n = 493$ skins), and the Museum of Natural Science, Louisiana State University, Baton Rouge, USA ($n = 185$ skins). We sampled multiple specimens for all 336 species recorded in our study, taking seven measurements from each specimen: bill length, width, and depth, wing length, length of primary projection, tarsus length and tail length. We then used these measurements to generate four categories of functional trait: overall body size, trophic traits, locomotory traits, and dispersal traits. Specifically, following Trisos et al. (2014), we used a two-step principal component analysis (PCA) on averaged morphological traits related to different ecological characteristics. Initially, PCAs were separately undertaken on locomotory (tail, wing, and tarsus length) and trophic (beak length, width, and

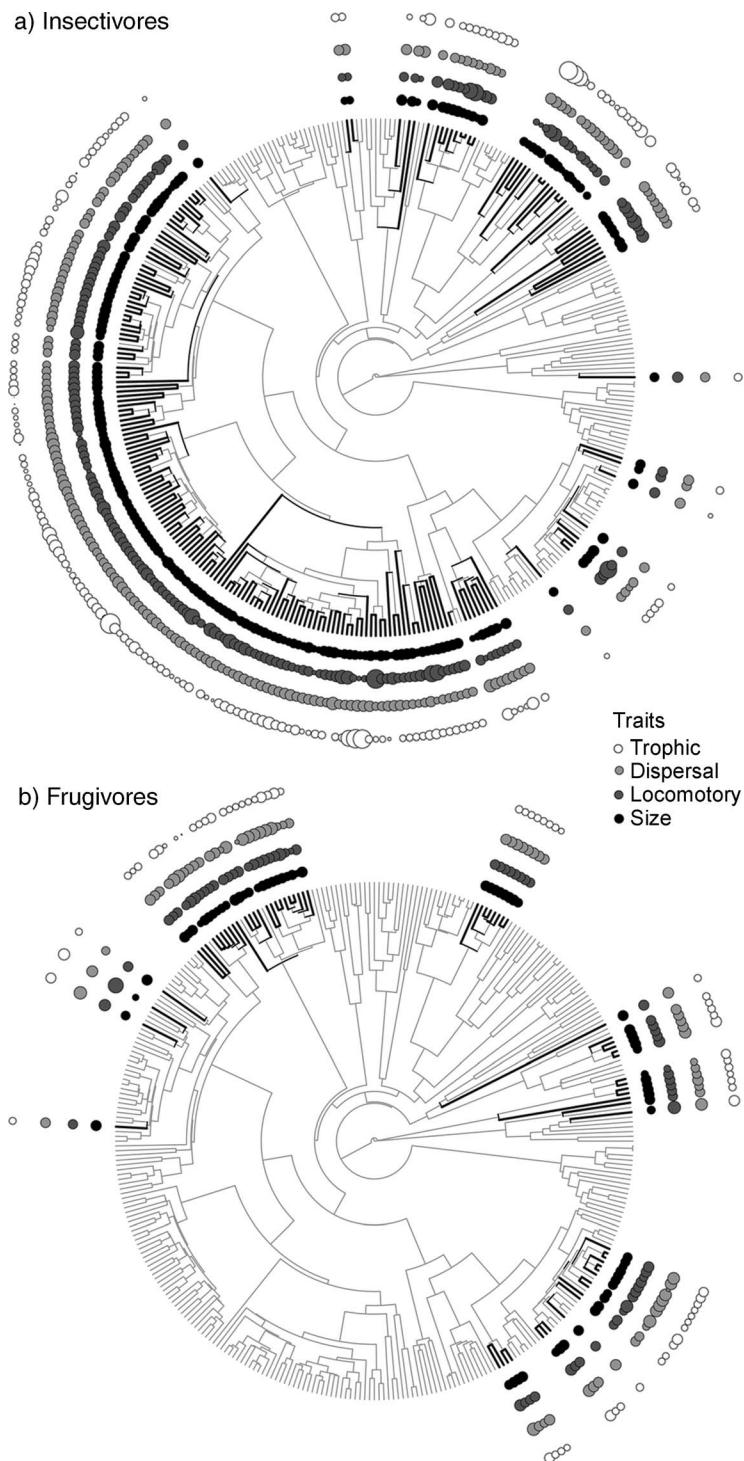


FIG. 2. Phylogenetic history and functional traits of 336 bird species surveyed in rain forest at Alta Floresta, Mato Grosso, Brazil. Each branch of the phylogram represents one species present in at least one of 31 avian communities (30 habitat patches; 1 intact forest). Black branches represent the insectivore (a; $n = 196$) and frugivore (b; $n = 68$) feeding guilds. Circles at branch tips represent functional traits, sized in relation to trait axes derived through principal component analyses (PCA). Correlates of trait axes are summarized in Appendix C: Tables C1 and C2.

depth) traits. The second components of the locomotory (short tarsus:long tail/wing) and trophic (short beak:wide/deep beak) PCAs were used as the respective trait axes. The first components of each of these PCAs were strongly related to size, so we combined them in a second PCA to form an axis of overall body size. The dispersal trait was the final axis and consisted of the log-transformed hand-wing index (Claramunt et al. 2012; also see Appendix B). We adopted this two-step approach because it accounts for correlation between traits, particularly the correlation of all traits with body size, and thus outperforms standard ordination techniques (Trisos et al. 2014). See Appendix B for further details of rationale, sampling, and measurement technique.

Phylogeny construction

To generate a phylogenetic tree, we pruned a recently published global phylogeny of ~10 000 bird species (Jetz et al. 2012) to the regional species pool (336 species). We used the *TreeAnnotator* program in the package *Beast* (Drummond et al. 2012) to derive the maximum clade credibility (MCC) tree from 1000 randomly selected trees provided by Jetz et al. (2012; trees available online).⁹ The MCC tree was estimated following a 10% burn in (i.e., the first 100 sampled trees were removed), with a posterior probability threshold of 0.5 and median node heights. The MCC tree is the best-supported tree from our sample of 1000 alternative trees. The Jetz et al. (2012) tree is based largely on molecular data, but also includes >3000 species placed on the basis of taxonomic information. This includes 58 species (17%) of our regional species pool, with an average of 11 species (9.8%) per community. Uncertainty in the phylogenetic relationships inferred from this tree affects both molecular and taxonomic placements. However, this uncertainty is far greater within clades and much reduced in community phylogenies such as ours, as these typically contain single members of particular genera and thus mainly estimate relationships between clades.

Statistical tests

Using phylogenetic and trait data sets, we generated complementary metrics capable of detecting nonrandom assembly processes at the metacommunity level (Kraft and Ackerly 2010, Aiba et al. 2013). Specifically, we extracted mean nearest taxon distance (MNTD) from a global phylogeny of birds (Jetz et al. 2012), and the variance (VAR), and the standard deviation of successive neighbor distances in biometric traits divided by the trait range (SDNDR) from data sets of biometric traits. MNTD and VAR are sensitive to both habitat filtering and competition (Webb et al. 2002, Kraft and Ackerly 2010, Aiba et al. 2013); SDNDR is sensitive to even spacing in functional traits and thus the signature of

competitive interactions (Kraft and Ackerly 2010). We generated MNTD using the *picante* R package; and VAR and SDNDR using code provided by Trisos et al. (2014).

Observed metrics for each community were compared to a null expectation calculated by drawing 999 random communities from the total species pool using a standard independent swap algorithm (Gotelli and Graves 1996). Species richness was constrained for each patch, with species weighted by their overall occurrence frequency (the proportion of patches in which they occurred). To construct the total species pool, we included all species identified in the study patches plus the adjacent tract of continuous forest (Lees and Peres 2006), assuming that this was a reasonable reflection of the pre-fragmentation species pool.

If niche traits are conserved on a phylogeny and competitive interactions are dominant in shaping community structure, then co-occurring species should be less related (in phylogenetic or functional trait space) than by chance. To test for phylogenetic signal of our trait axes, we calculated Blomberg's *K* (Blomberg et al. 2003) and compared observed values to a null model predicting a random distribution of traits across the tips of our phylogeny. We detected significant phylogenetic signal in all trait axes in both insectivores and frugivores (Appendix C: Table C3). Values of *K* ranged from 0.47 to 1.38, suggesting intermediate to high phylogenetic conservatism. The majority of traits exhibited intermediate conservatism ($K < 1$), indicating that they are more conserved than a random association of traits and phylogeny, but less conserved than a model of trait association under a model of Brownian motion. Niche traits therefore appear to be nonrandomly distributed across the tips of the phylogeny, allowing us to test for competition in both phylogenetic structure and functional trait structure. Given that contrasting assembly processes can act on different ecological niche axes, we conducted these tests separately on each category of functional trait.

To summarize, we addressed the two main aims of our study using a three-stage approach (Aim 2 was explored in Analyses 2a and 2b):

Analysis 1.—To test for the dominant community assembly process operating at landscape levels, we compared the observed values for MNTD, VAR, and SDNDR against our null expectation. Specifically, we used two-tailed Wilcoxon analyses to test whether the observed values were above or below the null expectation. One-tailed tests are sometimes used for SDNDR (e.g., Kraft and Ackerly 2010), but we elected to use more conservative two-tailed tests throughout to minimize Type I error. In this analysis, all patches were grouped together irrespective of patch and landscape attributes.

Analysis 2a.—To test whether communities are assembled differently in forest patches of varying size, quality, and isolation, we performed general linear

⁹ <http://www.birdtree.org>

TABLE 1. Community structure (MNTD, mean nearest taxon distance; SDNDR, standard deviation of successive neighbor distances in biometric traits divided by the trait range; and VAR, variance) in assemblages of avian insectivores and frugivores surviving in tropical forest fragments ($n = 30$ forest plots for each guild).

Metric and trait	Insectivores				Frugivores			
	SES mean (SE)	No. plots < expected	V	P	SES mean (SE)	No. plots < expected	V	P
MNTD								
Phylogeny	0.100 (0.982)	14	176	0.253	−0.050 (0.982)	13	270	0.452
SDNDR								
Locomotory	−0.220 (0.946)	24	426	<0.001†	−0.248 (0.646)	28	457	<0.001†
Trophic	−0.206 (0.821)	22	409	<0.001†	−0.127 (1.296)	25	404	<0.001†
Dispersal	0.252 (0.916)	11	174	0.886	−0.153 (1.024)	19	329	0.024†
Overall	−0.513 (0.942)	22	419	<0.001†	−0.336 (0.841)	28	451	<0.001†
VAR								
Locomotory	−0.025 (0.853)	21	349	0.015	−0.044 (0.663)	15	263	0.543
Trophic	−0.034 (0.892)	19	335	0.035	0.757 (0.934)	0	0	<0.001†
Dispersal	−0.051 (0.833)	26	393	<0.001	−0.109 (1.007)	16	222	0.839
Overall	0.272 (0.765)	5	28	<0.001†	−0.029 (0.769)	6	71	<0.001†

Notes: All P values < 0.05 are set boldface. The dagger symbol indicates that observed values differ significantly from the null model in the direction providing evidence for competitive interactions (MNTD and VAR are predicted to be greater than expected; SDNDR is predicted to be lower than expected). The mean standardized effect size (SES) is provided along with its standard error (SE). Statistics (V and P values) are from two-tailed Wilcoxon signed-rank tests.

models (GLMs) with standardized estimates of phylogenetic and trait metrics as response variables. We then generated average estimates for our explanatory variables (see Appendix B). Using these model-averaging techniques decreases the likelihood that important explanatory variables are left out of our final model, but may lead to overparametrization if too many variables are included and sample sizes are small (Grueber et al. 2011). Therefore, we only generated estimates from the most strongly supported models, defining this as <2 second-order Akaike information criterion (AIC_c) away from the best model (Burnham et al. 2002).

Analysis 2b.—Although the GLM technique used in Analysis 2a allows us to test whether standardized metrics were associated with patch characteristics (i.e., size, isolation, and quality), it gives no evidence of whether the metrics are significantly structured. For example, a standardized metric may exhibit a significant decline as fragment size increases, but if the values are not significantly different from our null expectation, then there is no evidence that the process being examined is important in driving community assembly. We therefore arbitrarily split our community sample into the top 50% and bottom 50% for each of the habitat properties (size, quality, and isolation) and ran two-tailed Wilcoxon analyses for MNTD, VAR, and SDNDR. This allowed comparison between small (<50%) and large (>50%) patches, low quality (<50%) and high quality (>50%) patches, and least isolated (<50%) and most isolated (>50%) patches.

Validating assumptions

Apparent correlations among predictors entered in multivariate models (e.g., patch size and quality; Fig. 1) may violate the assumption of independence in GLMs.

Thus, we tested for multicollinearity by estimating the variance inflation factor (VIF) for each predictor using the *usdm* package. In addition, because our community data may be spatially autocorrelated, we tested for independence of all trait data by implementing a Mantel test in the *ade4* package, to compare observed values to null values based on 999 replicate Monte Carlo draws. All statistical tests were carried out in R (R Core Team 2014).

RESULTS

Landscape-wide assembly processes

When we ran analyses across the study landscape as a whole, observed values for the phylogenetic metric, MNTD, were not significantly different from our null expectation for either frugivores or insectivores (Analysis 1; Table 1). This suggests that, when all communities are pooled and forest patch characteristics ignored, there is neither phylogenetic over- nor underdispersion; species are neither more nor less phylogenetically related than expected by chance. In contrast, when we focused on functional traits, we found evidence for competition in frugivores and both habitat filtering and competition in insectivores (Analysis 1). Specifically, there was a signature of competition in all traits in frugivores and all but dispersal traits in insectivores, with observed SDNDR values being significantly lower than expected under our null model (Table 1). Evidence for habitat filtering in insectivores consisted of lower than expected variance in beak shape, locomotory, and dispersal traits.

Influence of habitat properties on community assembly processes

Overall effect of patch size.—Patch size was an important predictor of community structure in phylogenetic and functional metrics, for both insectivores and

TABLE 2. Schematic summary of results from model averaging; circles show explanatory variables retained in the final model output within 2 AIC_c of the best model (solid circles, significant predictors; open circles, nonsignificant predictors).

Guild, metric, and trait	Environmental variables				Model estimates for variables with significant relationships and interactions
	FS	D	GF	INT	
Insectivores, MNTD					
Phylogeny	•				FS, -0.580
Insectivores, SDNDR					
Locomotory	○	○	○		
Trophic	○	○		○	
Dispersal	○		○		
Overall	•		○		FS, 0.884
Insectivores, VAR					
Locomotory	○	○	○		
Trophic	•	○			FS, -0.852
Dispersal	○	○		○	
Overall	•				FS, -0.297
Frugivores, MNTD					
Phylogeny	•	○	○	•	FS, 1.111; FS × GF, -2.013
Frugivores, SDNDR					
Locomotory	○	○			
Trophic	•	○	○	•	FS, 1.212; D × FS, -2.455; FS × GF, -2.729
Dispersal	○	•	○	•	D, -1.752; D × FS, 2.364
Overall		○	○		
Frugivores, VAR					
Locomotory			○		
Trophic	•		○		FS, -1.032
Dispersal	○		○		
Overall	○	○	○		

Notes: Variables are FS, fragment size; D, distance to forest > 1000 ha; GF, proportion of the fragment classified as good forest; INT, the interaction term, i.e., notable interactions between variables retained in the final model (see Appendix C: Table C4 for final model). Estimates are provided for significant relationships and interactions, where $P < 0.05$ is the critical level.

frugivores (Analysis 2a; Table 2). Patch size was retained in all models within 2 AIC_c values of the best model (see Appendix C: Table C4), suggesting that it has a strong influence on community assembly processes in focal guilds. Although this evidence implies that patch size alters the relative dominance of competition and habitat filtering, it is not specific regarding the relationship between patch size and these community assembly processes.

Effect of patch size on competition.—In insectivore communities, both phylogenetic and functional trait data provided evidence that the signature of competition was stronger in small forest patches (Analysis 2a; Fig. 3). Specifically, MNTD was positive in small patches (average SES MNTD = 0.662, $P = 0.022$), suggesting that species were less evolutionarily related than expected by chance, whereas MNTD was negative in larger patches (average SES MNTD = -0.461, $P = 0.018$). These results are consistent with a phylogenetic signature of competition in smaller patches and of habitat filtering in larger patches. The evidence from functional traits differed slightly in that we detected competition across all forest patch sizes: standardized SDNDR values for overall body size, beak shape, and

locomotory traits were generally more negative than expected (Appendix C: Table C5). However, linear regression (Analysis 2a) revealed that standardized SDNDR of overall body size increased with patch size (Fig. 3, Table 2; Appendix C: Table C4), again suggesting that competition increased as patch size decreased.

In frugivore communities, we found slightly different patterns of community assembly in relation to habitat patches. Focusing on phylogenetic structure, MNTD was positively correlated with habitat patch size, and significantly underdispersed in small patches (Fig. 3; Appendix C: Table C5), suggesting that competition was absent from all patches, large and small, whereas habitat filtering was most prevalent in small patches. However, functional traits (Analysis 2a) suggested that competition played a role in structuring frugivore communities in all patch sizes. Specifically, in all habitat patches, SDNDR was lower than expected on all trait axes, whereas the variance in overall size and beak shape was greater than expected in smaller habitat patches (Appendix C: Table C6). The linear regression (Analysis 2a) revealed that SDNDR of one functional trait, beak shape, decreased with patch size (Appendix C: Table

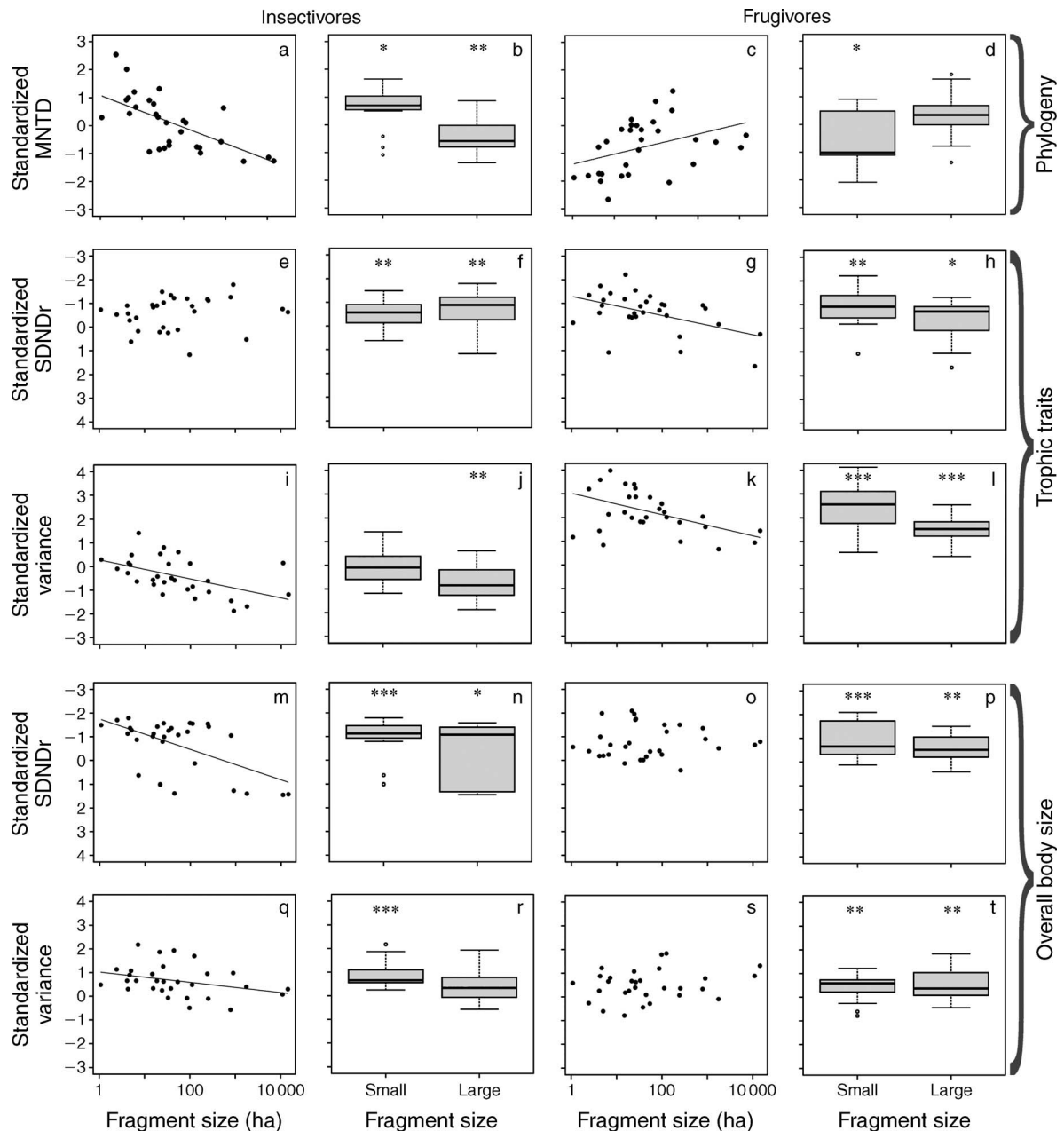


FIG. 3. The structure of avian communities ($n = 30$) in relation to the size of forest fragments (small fragments, 1–26 ha; large fragments, 33–14476 ha; see *Methods*). Structure was calculated from phylogenies (a–d) and from functional traits (e–t), including trophic traits (beak shape; e–l) and overall body size (m–t). Regression lines for significant relationships show the fit of a model with fragment size (shown on a log scale) as the sole predictor of structure. Note that plots for standardized SDNDR are reversed to facilitate interpretation (increased values indicate increased support for competition). Components of the Tukey boxplots are median, upper and lower quartiles, and whiskers including points within 1.5 interquartile range (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Final model outputs are included in Appendix C; results from dispersal traits and locomotory traits were nonsignificant (given in Fig. C2).

C4), whereas variance of beak shape increased with patch size, suggesting that the relative role of competition increased as patch size decreased.

We note that the linear relationship between the trophic trait and patch size was mediated by the interaction between patch size, isolation, and the

proportion of the patch covered in closed-canopy forest (Table 2; Appendix C: Table C4). Specifically, evidence of competition increased as patch size declined, unless forest quality was high or isolation low. Furthermore, for the dispersal trait, we also found a significant decline in standardized SDNDR with increasing isolation, except

in larger patches (Table 2; Appendix C: Table C4). In other words, the signal of competition was strongest in isolated habitat patches, unless the size of the patch was large.

Evidence for habitat filtering.—For insectivores, the evidence for habitat filtering was strongest in larger habitat patches, where MNTD and standardized variance for beak shape were lower than expected (Fig. 3b, j; Appendix C: Table C5). In smaller fragments, we found no evidence for habitat filtering, with the only significant result for variance being in overall body size where the standardized value was greater than expected, i.e., opposite to the prediction of filtering (Fig. 3; Appendix C: Table C5). For frugivores, this general pattern was reversed, with MNTD being significantly lower than expected in small, but not large, fragments (Fig. 3; Appendix C: Table C6). However, there was no evidence for habitat filtering in any functional trait because the standardized variance of communities was not significantly lower than that expected by chance in either small or large patches (Fig. 3, Table 2; Appendix C: Table C6).

Validating assumptions.—Maximum VIF across continuous predictor variables entered into our GLMs was 2.3 (Appendix C: Table C11). All variables were therefore <4 VIF, consistent with statistical independence and confirming that our model assumptions were unlikely to be violated by multicollinearity. In addition, we found no evidence of spatial autocorrelation across the landscape for any response variable (Appendix C: Table C12).

DISCUSSION

Our results indicate that the structure of bird communities in tropical rain forest is strongly influenced by fragment size, in broad agreement with previous studies concluding that habitat disturbance alters assembly processes (Grime 1979, Chesson and Huntly 1997, Violle et al. 2010). The most consistent pattern detected was that of significant overdispersion of functional trait structure in communities surviving in smaller habitat patches, with this signature reduced or absent in larger habitat patches. This pattern of overdispersion held true in both insectivorous and frugivorous birds, but varied in relation to patch characteristics, particularly habitat quality and degree of isolation. In addition, we found that the phylogenetic structure of insectivore communities was overdispersed in smaller habitat fragments. These findings are consistent with the hypothesis that extinctions associated with fragmentation are biased toward species co-occurring with closely related lineages, or located in denser regions of trait space.

Species interactions are theoretically strongest among lineages with shared recent ancestry and similar ecological niches (Darwin 1859, Diamond 1975), and thus a pattern of overdispersion in trait or phylogenetic data is generally interpreted as evidence of limiting similarity

mediated by interspecific competition (Cavender-Bares et al. 2009). There may be problems with this interpretation when current-day communities are compared against null communities randomly generated from regional species pools, because in this case a pattern of overdispersion may simply reflect the dominant geographical mode of speciation (allopatric speciation) rather than species interactions per se (Warren et al. 2014). Our analyses circumvent this problem because they are essentially comparing the structure of fragmented communities against the species pool occurring at the same location pre-fragmentation. Thus, shifts in structure are likely to reflect local processes playing out over the decades since fragmentation, rather than regional processes operating at biogeographic scales.

Another challenge is posed by spatial scale. Numerous studies testing for the pattern of overdispersion in animal or plant communities have concluded that the importance of competition varies with spatial resolution, typically increasing at smaller spatial scales when habitat is not fragmented (Weiher and Keddy 1995, Wiens 2011). This scale dependency of competition is expected because related species coexisting at small scales (e.g., 1 ha) are more likely to interact directly than those coexisting within larger grain sizes (e.g., 100 km²) (Cavender-Bares et al. 2006, Swenson et al. 2007). Our study corroborates this finding by revealing increased evidence for competition in communities with decreasing patch size across a smaller span of scales (90% of forest patches < 1000 ha). Given that bird species are relatively mobile, they are more likely to interact directly within habitat patches at these smaller scales, and thus our finding of decreasing trait dispersion with increasing patch size is not likely to be explained simply because species richness builds up through the accumulation of noninteracting competitors.

We found that patch size was the most important driver of community disassembly processes in this fragmented landscape, being retained in all models and a significant predictor in all but one model. Declines in species richness with forest fragment size are ubiquitous (Blake and Karr 1987, dos Anjos 2004), in accordance with classical species–area relationships (MacArthur and Wilson 1967, Banks-Leite et al. 2012). In theory, this process of defaunation can play out without any regulation by competitive interactions among related species. Species may simply be lost from smaller fragments because of area constraints, most commonly when the minimum area requirements for viable populations are not met (Lees and Peres 2008). Small habitat patches also suffer environmental changes, including the detrimental and synergistic impacts of increased sunlight, wind, desiccation, fire, and selective logging (Kattan et al. 1994, Laurance et al. 1998), eventually leading to local extinctions when the environment becomes unsuitable for any particular species (Laurance et al. 2011). Finally, changes in patch and

landscape structure may also drive extinction through interactions across trophic levels, for example, through disrupted codependencies (e.g., mutualisms) or mesopredator release (Crooks and Soule 1999).

Under a simple model of species–area relationships, this process of community disassembly is assumed to be neutral, with species dropping out randomly through extinction as patch size declines (MacArthur and Wilson 1967). Alternatively, habitat changes associated with fragmentation seem likely to drive community disassembly through habitat filtering in smaller patches, leading to the loss of related species with particular attributes, thus producing a signature of clustering in phylogenetic and functional traits (Ockinger et al. 2010). Our results suggest that neither of these processes predominates because fragmented communities are structured by the opposite pattern of increasing dispersion in phylogenetic and functional traits with decreasing habitat patch size. Importantly, we also detect increasing dispersion of functional traits with lower habitat quality and greater isolation of fragments from other major forest patches. These patterns are not expected under a purely neutral model governed by area constraints or habitat filtering, and instead are consistent with disassembly driven by species interactions within trophic levels. If, after fragmentation, communities become overdispersed with respect to traits, this must suggest that the original community had a less dispersed structure (i.e., species must have occupied more clustered positions on average, near to other species). Here, this effect operates over an ecological, rather than an evolutionary, time frame, implying that species remaining in smaller habitat patches outcompeted those lost during or after disturbance.

There are two major routes by which competition may intensify with decreasing patch size and habitat quality. First, reduced availability of resources could increase competition between pairs of species with similar ecological niches, causing one of them to drop out from the community. Second, changes in environmental conditions may increase mortality rates and reduce population size in some species, increasing their susceptibility to the negative impacts of competitive interactions (Turner 1996, Chesson and Huntly 1997). The impact of such interactions may be reduced in less disturbed habitat fragments, i.e., those with a larger area of intact forest, if these offer an abundance of resources and a broader range of microhabitats. In all cases, nonrandom patterns in local extinctions driven by species interactions are likely to be masked when species recolonize from adjacent source populations, potentially explaining why overdispersion of communities is accentuated with increasing isolation of habitat patches, because in these cases immigration from source populations is theoretically reduced.

An alternative possibility is that overdispersion arises because of a shift from specialist to generalist bird species as habitat patch size declines (Bregman et al.

2014). Communities in intact forests are dominated by forest specialists, which are thought to occupy narrower niches, potentially making communities more tightly packed. In contrast, bird communities in small or highly disturbed forest patches tend to contain a larger proportion of generalists, with wider niches, potentially leading to greater spacing between species. Although it is difficult to rule out this possibility, there is no *a priori* reason why broader niches should have centroids that are more highly dispersed, because they could simply be more overlapping with similar centroids, leading to greater clustering. Our results are therefore consistent with the view that extinctions driven by the reduction in size, habitat quality, and connectedness of rain forest fragments are nonrandom, and mediated by niche-based interactions among related species.

It is worth emphasizing that the direction of relationships detected in this study are contrary to the prediction that lower species richness will relax competition for resources and thus reduce the signature of interspecific competition in disturbed habitats (Grime 1979, Huston 1979, Buchmann et al. 2013). Likewise, they are not consistent with the idea that habitat disturbance destabilizes community structure through environmental stochasticity and penetration of matrix conditions into habitat patches (Ewers and Didham 2006), leading to greater variation or randomness in structure compared with intact tracts of forest (Didham et al. 1998). Instead, our results suggest that rain forest disturbance and fragmentation are associated with predictable shifts in community structure as a result of elevated competition, with implications varying across clades, guilds, and traits depending on factors such as diet and dispersal ability (see Appendix B).

Given that many of the traits assessed here are representative of a species' role or "function" in the ecosystem (Violle et al. 2007), our results provide an insight into how key ecosystem processes are affected by fragmentation. It has long been proposed that habitat fragmentation will affect ecosystem function (e.g., Klein 1989, Laurance et al. 2011, Bregman et al. 2014), largely because function is likely to shift and decline with losses of biodiversity (Loreau et al. 2001). However, our findings add an extra dimension to this idea by revealing that local extinction associated with the fragmentation, disturbance, and isolation of tropical forests leads to functionally important groups becoming progressively overdispersed. Such overdispersion may be interpreted as maximizing the resilience and diversity of functionality because it suggests a relatively broad spread, or complementarity, of functional traits. However, ecosystem processes could be disrupted by the "thinning out" of species, with niches clustered around important optima. In the case of insectivorous birds, this may result in reduced predation of certain classes of herbivorous insects in smaller fragments, leading to increased leaf damage, and thus reduced photosynthesis and plant growth (Van Bael et al. 2003, Mooney et al.

2010, Tobias et al. 2013). In frugivorous birds, it could lead to reduced dispersal of seeds in particular size classes, with important implications for the long-term demographics and recruitment of trees and shrubs in fragmented landscapes (Terborgh et al. 2008, Sethi and Howe 2009, Galetti et al. 2013). Similar effects could occur broadly across numerous guilds of vertebrates and insects, although further studies are required to learn whether the deterministic disassembly process identified here is detrimental to ecosystem function.

The effects of forest fragmentation have been studied intensively over recent decades, with most previous analyses focusing on species richness or species traits, and ignoring interactions among species. The main exceptions are studies dealing with food webs and other interactions between different trophic levels (e.g., Galetti et al. 2013, Martinson and Fagan 2014). Our results suggest that interactions among species within the same trophic level can play an important, yet overlooked, role in regulating the effects of fragmentation on biodiversity and ecosystem function. This finding provides empirical support for theoretical models suggesting that species interactions mediate community disassembly in disturbed or fragmented environments (Chesson and Huntly 1997, Buchmann et al. 2013, Lasky and Keitt 2013). The fact that responses to a decline in patch size appear to depend on interactions among species suggests that the likelihood of local extinction is governed not only by intrinsic traits, environmental variables, or matrix conditions, but also by the identity of species co-occurring in the same habitat patch. This adds a new perspective to recent debates about whether the responses of multiple species to fragmentation are interdependent (Didham et al. 2012). Further studies should investigate the functional implications of community structure in fragments, in particular the extent to which overdispersion of functional traits influences ecosystem function.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-1731.1.sm>