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## Disassembly of fragmented bat communities in Orange Walk District, Belize

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The assembly, or disassembly, of ecological communities is thought to be driven by competition, environmental filtering, and dispersal limitation. These processes leave patterns in the functional, phylogenetic, and taxonomic diversity of communities. Bat communities in the tropics tend to have many species that are niche specialists with varying dispersal propensities. We investigated the effects of fragmentation on bat communities in an isolated forest fragment and a nearby larger forest preserve in Belize. Over four field seasons (2014–2017), we captured over 1,480 individuals from 32 species using mist nets and harp traps. The community in the fragment was a nested subset of species (20) compared to the preserve (30), and species richness was relatively stable over time. Functional richness was higher in the preserve than in the fragment, and species in the preserve were more closely related phylogenetically than expected by chance. Closely related species and species with different diet guilds co-occurred at both sites more often than distant relatives and those with the same diet guild. Bat species with flexible roost use had higher abundance in the fragment than the preserve, while closely related roost-specialist species had higher abundance in the preserve. Local extirpation and decreased dispersal are the most likely mechanisms of community disassembly in this system, and variation in roosting habits results in nonrandom community composition. These results have significant implications for the effects of ongoing deforestation and habitat fragmentation in Belize and adjacent dry forest areas.

*Key words:* Chiroptera, phylogenetic community structure, harp trap

### INTRODUCTION

Ecological processes such as competition, environmental filtering, and dispersal limitation govern the assembly or disassembly of ecological communities and leave different patterns in the phylogenetic and functional diversity of communities (Cavender-Bares *et al.*, 2009). Niche theory posits that when species with similar ecological niches co-occur, limited resources may result in competitive exclusion (Hardin, 1960; Levin, 1970). If competitive exclusion is important, the diversity of traits related to niche partitioning and ecosystem functioning (i.e., functional diversity) should be high because species would have diverse niches to avoid competition (Kraft *et al.*, 2008). Under this niche hypothesis, if closely-related species share similar niches, we would expect competitive exclusion to occur. The resulting pattern in the community phylogenetics should be overdispersion — species

found to co-occur in a community would be more distantly related than expected by chance. In contrast, with character displacement, closely-related species may co-occur more frequently than expected by chance and niche traits should be divergent (Schluter and McPhail, 1992; Dayan and Simberloff, 2005). When environmental gradients filter which species can persist, species with similar adaptive traits should co-occur and there should be low functional trait diversity (Kraft *et al.*, 2008). Under this scenario, if species share similar traits due to common ancestry, we would expect phylogenetic clustering — species would be more closely related than expected by chance. If species have converged on similar functional traits independently, we would expect the same low functional diversity but with phylogenetic overdispersion (Mayfield and Levine, 2010). Finally, if dispersal limitation governs species co-occurrence in communities, then species-poor communities should be nested subsets of

species rich communities (Patterson and Atmar, 1986), and traits related to dispersal ability should predict species co-occurrence.

Against the background of natural community assembly, anthropogenic impacts are fundamentally altering community composition (Newbold *et al.*, 2015). When human disturbance causes the loss of a subset of functionally redundant species, some ecosystem functioning is typically maintained despite species loss (the insurance effect — Yachi and Loreau, 1999; Oliver *et al.*, 2015b). In general, however, species diversity declines with human disturbance, resulting in loss of functional diversity and ecosystem function (Haddad *et al.*, 2015; Newbold *et al.*, 2015; Oliver *et al.*, 2015a). This reality has repercussions for ecosystem functioning, because loss of functional diversity results in lower and more unstable biomass production (Cadotte *et al.*, 2012).

Bats are an example of a group that has important functional diversity related to ecosystem functioning. The loss of bat species that are pollinators, seed dispersers, predators on insect pests, and producers of raw organic material for fertilizer can have cascading effects on ecosystem health. Bats play key roles as pollinators and seed dispersers, for both forest plants and agricultural species (Bawa, 1990; Fujita and Tuttle, 1991; Hodgkison *et al.*, 2003). Insectivorous bats can be important for pest control and may significantly affect insect communities (Cleveland *et al.*, 2006; Williams-Guillén *et al.*, 2008; Jones *et al.*, 2009). Given the diversity and relative abundance of bats in the tropics compared to temperate zones (e.g., >300 species known from the Neotropics, <100 known from the Nearctic, Simmons, 2005; Maas *et al.*, 2015), the functional importance of bats may be higher in the tropics than in temperate zones (Patterson *et al.*, 2003).

Environmental variables influence bat community structure in multiple dimensions of diversity. Bats in general are good indicators of ecosystem health (Jones *et al.*, 2009) but their response to disturbance is species- and context-specific. In the context of small-scale deforestation in lowland Amazonian rainforests of Peru, some bat species were documented to have highest abundance in mature forest, while other species were more abundant in recently cleared or secondary vegetation (Willig *et al.*, 2007). Large-scale deforestation in French Guiana caused the loss of 48 mature-forest specialist species while simultaneously resulting in increased abundance of small-fruit eating and insectivorous bats (Brosset *et al.*, 1996). In lowland Peruvian Amazon rainforest bats, factors such as the distance

among forest patches and the proportion of edges were strong predictors of bat community diversity, while forest cover alone was not (Klingbeil and Willig, 2009). Phyllostomine bats in Mexico were shown to be more sensitive to habitat degradation than other bat clades, decreasing in relative abundance with increasing forest disturbance and fragmentation (Fenton *et al.*, 1992). Aerial insectivorous bats, especially from the families Vespertilionidae and Molossidae, have been shown to increase in abundance with human disturbance in some systems (Brosset *et al.*, 1996), while in other studies glean-ing insectivorous bats were more negatively affected by habitat disturbance than other feeding guilds (Wilson *et al.*, 1996; Klingbeil and Willig, 2009).

To date, few studies have examined the effects of human-modified landscapes on the species, phylogenetic, and functional diversity of bat communities (Cisneros *et al.*, 2015). In lowland rainforests of northeast Costa Rica, habitat heterogeneity has been shown to be positively correlated to functional, taxonomic, and phylogenetic diversity, especially in mixed habitats with large forest patches and a large proportion of land in pasture compared to other land cover types (Cisneros *et al.*, 2015). In Mexico, functional diversity of bats was positively correlated to forest cover, indicating that deforestation resulted in the loss of ecologically and economically important functional guilds such as insectivores, seed dispersers, and pollinators (García-Morales *et al.*, 2016). In Brazil, insectivorous bats were more abundant in forests undisturbed by people, while frugivorous and nectarivorous bats were more abundant in forests with light selective logging compared to undisturbed forest (Peters *et al.*, 2006). Bat community ecology clearly demonstrates the importance of ecological and anthropogenic variables on the processes of community assembly and ecosystem functioning.

The bats of Belize represent a unique and diverse assemblage in a fragmented landscape, providing an excellent system to test hypotheses of bat community ecology in relation to habitat. Seventy-one bat species are known from Belize (Fenton *et al.*, 2001). Habitat loss in Belize has accelerated in recent years, driven predominantly by agricultural expansion and cattle ranching (Wyman and Stein, 2010), but human modification of the landscape far predates modern agriculture. Thousands of years ago, Maya settlement of Belize — and modification of the landscape — was extensive (Grossberg *et al.*, 2003). Today the ancient Maya ruins in Belize sometimes provide roosting sites for cave-roosting bats,

and efforts to preserve and protect archaeological sites have incidentally resulted in the preservation of some forest patches which support significant bat communities.

The Lamanai Archaeological Reserve in Orange Walk District is one such site that preserves substantial forest supporting a healthy bat community. Archaeological excavations began in 1974, and the protected forest and Maya sites make the Lamanai Reserve one of the Maya sites most visited by tourists (Grossberg *et al.*, 2003). A published inventory of the bat fauna accomplished using a combination of mist nets, harp trap, acoustic sensors, and targeted searches showed that at least 30 species of bats were found in the area (Fenton *et al.*, 2001). Bats in this system fill many trophic guilds and use a variety of roost types, which may allow closely related species to diverge in niche traits and allow them to co-occur. There are small forest fragments in the agricultural landscape adjacent to the Lamanai Reserve that have remained despite rapid deforestation, due in part to the presence of unexcavated Maya ruins. This system allowed us to compare the bat fauna in the larger preserve forest at Lamanai to that of a nearby forest fragment that was once part of continuous forest. Using capture data from four years of field surveys, we sought to assess how many bat species currently occur in the area around Indian Church, Belize, how the diversity and abundance differ between a forest fragment and the forest preserve, how species diversity has changed over time, how trait and phylogenetic similarity among bat species predict species co-occurrence, and how ecological traits predict bat abundance.

Specifically, we tested the following predictions. We predicted that species richness and diversity are lower in the forest fragment than the preserve, with species in the fragment being a nested subset of those in the preserve. Further, we predicted that there is greater phylogenetic and functional diversity in the preserve than the fragment. In addition, we tested the hypothesis that co-occurring species are more closely related and similar in their traits, indicating environmental selection on those similar traits. To do so, we tested alternative predictions that there is a positive relationship between co-occurrence, phylogenetic and functional distance, indicating niche partitioning and evolutionary divergence, or that co-occurrence would be negatively related to trait or phylogenetic distance. Finally, we hypothesized that species traits would be related to the relative abundance of the corresponding niche in the fragment compared to the preserve forest. We

predicted that larger species and animalivorous species would have lower abundance in the fragment because of lower resource abundance and because they are averse to disturbance. We further predicted species that exploit more roost types would have higher abundance while roost specialists will have lower abundance in the fragment because of its smaller area.

## MATERIALS AND METHODS

### *Study Sites*

We sampled in the riverine preserve forest of Lamanai Archaeological Reserve and the adjacent forests near the Lamanai Outpost Lodge (17.75117N–88.65446W, hereafter, the preserve forest), and the forest fragment of the Ka'kabish Archaeological Project (17.8147N–88.73052W, hereafter, the fragment) during four field trips of 1–2 weeks at the end of April and beginning of May in 2014–2017 (Fig. 1). The preserve forest at Lamanai is about 450-ha of semi-deciduous tropical forest at varying stages of regrowth from past land clearance for agriculture and human settlement. Settlement in the Lamanai area dates to 300 B.C. or earlier and probably reached its height during the Classic Maya period when a large city was constructed at the site (Pendergast, 1981). Parts of the area were later cleared for a Colonial-period sugar mill, church, and village. The Maya site, sugar mill, and church have been partially excavated, some structures have been reconstructed (e.g., large temples), and the area is now protected as an Archaeological Reserve which is open to the public. This protected area, which is administered by the Belize Institute of Archaeology, forms most of the preserve forest that we sampled. The mill and original Indian Church village site are now overgrown, and the modern town of Indian Church stands adjacent to the southwestern portion of the preserve forest. The northern part of the Archaeological Reserve is primarily closed-canopy forest (15–20-m), with more disturbance as one moves south. The preserve forest is adjacent to a wide lagoon section of the New River. The presence of this large body of water, and the many streams that originate in the forest and tropical savannah and empty into the lagoon, create habitat for bats specialized on over-water foraging, including *Noctilio* and *Rhynchonycteris*. However, because these habitats were not available for systematic sampling at the forest fragment we restrict our analyses here to only those species caught in the forest. To the south, the Lamanai Archaeological Reserve borders on the land of Lamanai Outpost Lodge, which preserves secondary forest that is essentially continuous with that of the Archaeological Reserve. Gaps, clearings, and roads occur patchily throughout most of the preserve and adjacent forest to the south, and while none of the area can be considered primary forest, it provides essentially continuous habitat for bats.

The forest fragment Ka'kabish consists of about 45-ha of closed canopy semi-deciduous tropical forest overlying another Maya city (Haines, 2011). Unlike Lamanai, the Maya city at Ka'kabish has not been fully excavated nor reconstructed, and it is not open to the public. Looters at the site have dug several trenches into the temples that have created cave-like roosts for bats. The Ka'kabish fragment was part of a continuous stretch of forest connected to the preserve forest before the year 2000,

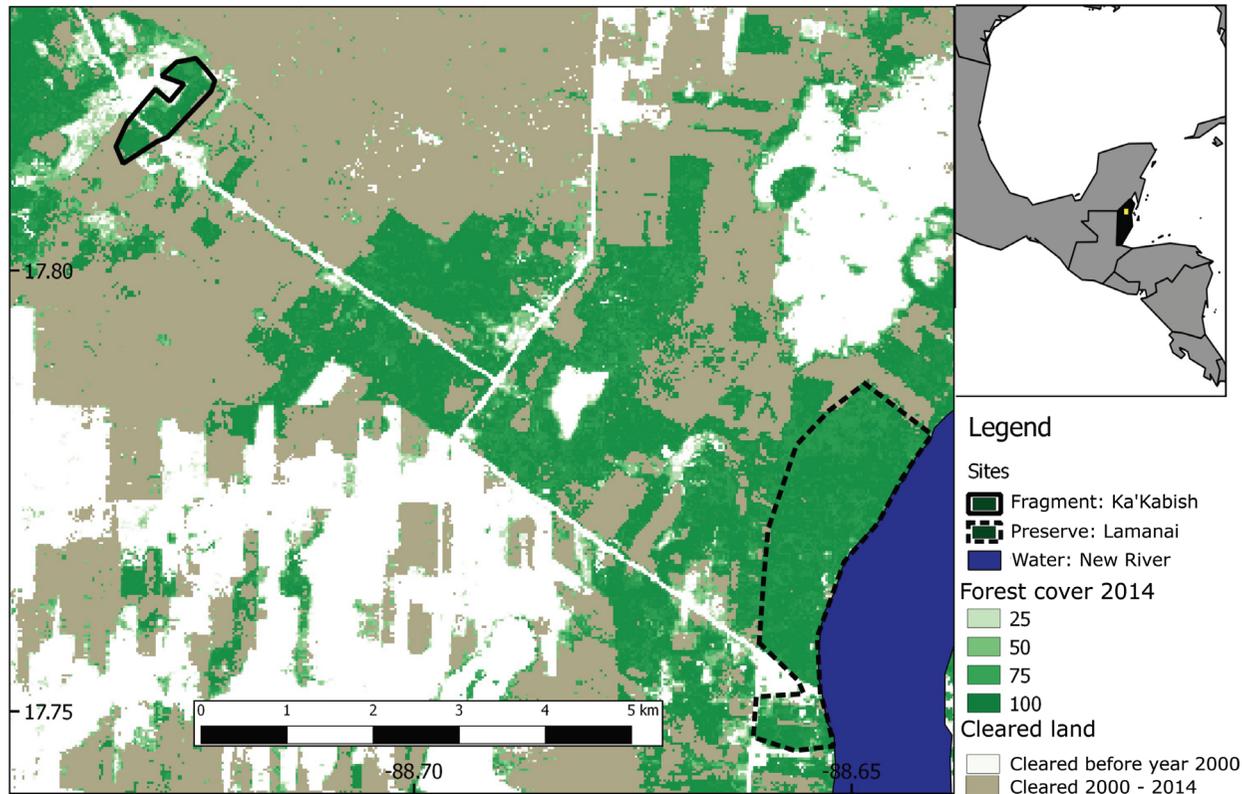


FIG. 1. Map of the study area. The forest cover (green) represents pixels with > 50% canopy cover per pixel in the year 2014, with nonforest before the year 2000 in white. Pixels that were deforested between 2000 and 2014 (grey) were based on a change of pixel value from >50% forest cover to 0. Landcover data from Hansen *et al.* (2013). The preserve forest site (dotted line) includes both the Lamanai Archaeological Preserve (boundaries approximated) and the forested properties of the Lamanai Outpost Lodge. The forest fragment site (solid line) was sampled in the southern portion of the forest. The inset map shows Belize in black, with the sampled region within the Orange Walk district shown in yellow

but is now embedded in a matrix of agricultural land for crops and cattle pasture (Fig. 1). Ka'kabish is located approximately 10km from the preserve forest at Lamanai, though there are small patches of forest in the intervening landscape matrix that could be used as 'stepping stones' as well patches of forest west of the fragment site. Also unlike Lamanai, Ka'kabish has no near-by bodies of water to provide over-water specialist bats with necessary habitat, which is one factor potentially limiting the diversity of bats at this site.

### Capture Methods

With the help of a multi-institutional team of bat researchers, we used mist nets and harp traps to sample the bat fauna at the preserve and the fragment. Mist nets were deployed at ground level (nets 6–12 m long  $\times$  2 m high, 43 net nights) and using a triple-high net arrangement (12 m long  $\times$  6 m high, 17 net nights). The high net array was supported with telescoping poles and pulley rigs (see specifications for high net rig at BatNets.com). Nets were set across and along trails, gaps in vegetation, and under the high forest canopy in plazas in the Maya ruins. We also deployed Austbat harp traps (www.faanat-eck.com, 33 trap nights) across trails and in front of looter's tunnels. Mist nets were attended continuously once set and opened, and harp traps were checked regularly to guard against predators. We placed captured bats in individual cloth holding bags

and returned to a central location where they were sexed and identified. After identification, most individuals were released at or near their site of capture; no preserve bats were released at the fragment, nor vice versa. We did not mark captured bats so some recaptures were possible. All research was conducted in accordance with accepted standards for humane capture and handling of bats published by the American Society of Mammalogists (Sikes *et al.*, 2016) and approved Institutional Animal Care and Use Committee protocols (AMNH IACUC 20170403, Brown University IACUC 1205016 and 1504000134, University of Georgia IACUC AUP A2009-10003-0 and A2014 04-016-Y3-A5) and Belize Forestry Department Scientific Research and Collecting Permits (CD/60/3/14 (17), CD/60/3/ 15 (20), WL/1/1/16 (26), and WL/2/7/17 (21)).

### Phylogeny

The phylogeny used here was taken from Shi and Rabosky (2015), which combined multiple mitochondrial and nuclear loci and time calibrated the tree using fossil dates.

### Traits

We collected data on the following traits of bat species: body mass (as reported in Reid, 2009); roost type (open areas,

tree hollows, crevices, caves) and number of roost categories used (1,2,3) based on Fenton *et al.* (2001), diet type (omnivore, animalivore, herbivore) and foraging style (aerial forager, gleaner) following Fenton *et al.* (2001) and Reid (2009), and wing aspect ratio (Norberg and Rayner, 1987) (Supplementary Table S1). Body mass is strongly correlated with resource requirements, life history, and dispersal ability in mammals, and in bats it is additionally constrained by flight and echolocation (Arita and Fenton, 1997). Roost type and number of roost categories used by a species may be linked to local patterns of distribution and site fidelity, and flexibility in roost requirements may affect the success of species in modified habitats (Kunz, 1982); roost availability appears to be a factor limiting the ability of some species to colonize and subsist in particular areas (Voss *et al.*, 2016). Wing aspect ratio is related to flight capabilities in cluttered versus open environments, and is linked to foraging style (Norberg and Rayner, 1987). Diet is linked to the trophic level of the species, as well as their resource requirements (Patterson *et al.*, 2003). We note that grouping all animalivores together may obscure subtle differences among them and we also analyzed the data defining the diet niche more finely and as a composite of diet and foraging style to distinguish between aerial insectivores and gleaners (Supplementary Table S1); results were qualitatively the same. Trait dissimilarities among species were calculated as the Gower dissimilarity among all traits, as well as the Gower distance among species for each trait separately.

### Measures of Diversity

We quantified the following measures of diversity: species richness, rarefied species richness, estimated species richness (Chao's estimator and the Abundance-based Coverage Estimator, ACE — Colwell *et al.*, 2012), species diversity and species associations or co-occurrence (Shannon index and Jaccard index, respectively, Magurran, 2013), and phylogenetic and functional diversity (Villéger *et al.*, 2008; Pearse *et al.*, 2015).

### Statistical Tests

To test each of the hypotheses, we used a variety of statistical analyses. To test for a difference in species diversity between fragment and preserve forest, we compared observed values of species richness, rarefied species richness, and Shannon's diversity index to the 95% distribution of diversity indices derived from bootstrapped data. The original matrix of individual bats caught per site was bootstrapped using the 'sample' function in R, randomizing both rows and columns. This bootstrapped distribution represents the null hypothesis that individual bats of all species could have been captured at either site. Diversity metrics were calculated using the 'specnum', 'rarefy', 'estimateR', and 'diversity' functions in the 'vegan' package for R (Oksanen *et al.*, 2014). To test if the fragment community was a nested subset of the preserve community, we calculate the 'temperature' of the species X site matrix, a measure of disorder in the matrix, where a completely nested matrix has a temperature of 0° and a completely random matrix has a temperature of 100° (Atmar and Patterson, 1993). We calculated temperature and compared the observed value to 1000 simulated matrices based on the 'RANDNEST' null model (Jonsson, 2001), which maintains species frequencies but randomizes the sites. This null was chosen over others because it was found to be the most powerful and appropriate for this question (Jonsson, 2001). Tests were

implemented in the 'vegan' package for R, using the 'oecosimu' and 'nestedtemp' functions, specifying the 'c0' null model.

To test the hypothesis that trait and phylogenetic similarity among bats predicts community composition, we used Mantel tests of Jaccard index of species association predicted by phylogenetic/functional distance. Pairwise Jaccard species associations were calculated using the 'sp.assoc' function in the 'spaa' package (Zhang *et al.*, 2013) for R. Phylogenetic distance was calculated using the 'cophenetic' function in the R package 'ape' (Paradis *et al.*, 2004). Functional distances were calculated for all traits combined and for each trait separately using the Gower dissimilarity metric, chosen because it can handle both categorical and quantitative data, using the 'daisy' function the R package 'cluster' (Maechler *et al.*, 2015). Mantel tests were performed using the 'mantel' function the R package 'ecodist' (Goslee and Urban, 2007).

To test the hypothesis that phylogenetic and functional diversity is different between the fragment and preserve forest, we compared observed values of mean nearest taxon distance, MNTD (Webb, 2000) to expectations based on 1000 randomization of the species on the phylogeny, maintaining the species richness at each site. MNTD and the random distributions were calculated using the 'pez.dispersion' function the R package 'pez' (Pearse *et al.*, 2015). We compared observed values of functional richness (Fric), functional divergence (Fdiv) and functional evenness (Feve) (Villéger *et al.*, 2008). These metrics are based on multivariate projections of the trait data in principle coordinates, and measuring aspects of the size of the 'trait space' and the distance among species in that space. Fric is the volume of functional trait space encompassed by species in the community. Fdiv is the divergence in the distribution of abundance in trait space. Feve is the regularity of the distribution of abundance in trait space. Functional diversity metrics were calculated using the 'dbFD' function in the R package 'FD' (Laliberté *et al.*, 2014), using the 'Cailliez' correction to deal with negative eigenvalues in principle coordinate axes.

To test the hypothesis that traits predict the difference in abundance between the preserve and fragment forests, we calculated the difference in abundance at the fragment from the preserve forest as the dependent variable, with the traits as independent variables. We tested the relationships among variables using regression analyses, controlling for phylogenetic distance using a Pagel's lambda transformation on the residual error ('gls' function in the R package 'nlme' — Pinheiro *et al.*, 2011, fitted with maximum likelihood, specifying the correlation structure as 'corPagel' from the 'ape' package).

## RESULTS

### Species Diversity

Bats were captured during 83 net/trap nights: 72 nights in the preserve forest, and 11 nights in the fragment. In total, we captured 1,483 individual bats: 1,168 in the preserve forest, and 315 in the fragment. We captured 32 species over four years of sampling at the two localities. Two species (*Natalus mexicanus* and *Chrotopterus auritus*) had not been captured in a previous faunal inventory of the study sites. Species richness was higher in 2016 and 2017

(28 and 30 species, respectively) than 2014 and 2015 (25 and 20 species, respectively) probably due to greater sampling effort in 2016–2017.

The lowest sampling effort was in 2014, when we captured 244 individuals representing 25 species (three net/trap nights at the fragment, eight nights at the preserve). Rarefying species richness across years based on our 2014 results, we would have expected 20 species in 2015, 24 in 2016 and 27 in 2017. The number of species captured in the preserve forest versus the fragment has remained relatively stable across years (Table 1).

Species richness in the preserve forest (30 species) was higher than in the fragment (20 species, Table 2). The species richness at the preserve forest was within the range expected from the bootstrapped community data, while the richness at the fragment was less than expected from the bootstrapped data (Table 2). The results were the same for rarefied species richness when we accounted for differences in sampling effort between the two sites. Shannon diversity was higher in the preserve forest than in the fragment, and slightly higher (2.824) than expected from the bootstrapped data (2.818), illustrating that the community at the preserve forest is more diverse and abundances are more evenly distributed across species than at the fragment (Table 2).

Testing for nestedness in the fragment community compared to the preserve forest community, we found the temperature of the matrix was  $10.8^\circ$ , significantly lower than the expected temperature

TABLE 1. Observed and rarefied species richness in two study sites during each year of sampling

Year	Fragment		Preserve forest	
	Observed	Rarefied	Observed	Rarefied
2014	15	9.5	22	22.0
2015	6	6.0	20	19.3
2016	13	8.6	27	21.4
2017	17	10.5	27	21.9

based on the null model ( $20.3\text{--}35.6^\circ$ ,  $P = 0.005$ ). These results illustrate that the bat community in the fragment is a nested subset of the community at the forest preserve.

### Species Associations

Species associations were negatively related to phylogenetic distance, and the 95% confidence intervals of the Mantel correlation coefficient did not include 0, but the relationship was not statistically significant (Mantel  $r = -0.11$ , 95% CI =  $-0.04\text{--} -0.19$ , one-tailed  $P = 0.15$ ); species that co-occurred more frequently were more closely related than species that co-occurred less frequently. Species associations were positively correlated with diet dissimilarity but were not correlated with other trait distances (Table 3). The correlation between species associations and diet dissimilarity suggests that species with dissimilar diets co-occurred more frequently than species with similar diets.

TABLE 2. Comparisons of diversity metrics between the forest fragment and the preserve forest. Numbers in parentheses for species richness, rarefied species richness, and Shannon diversity indicate the null distributions (2.5th and 97.5th percentiles) of diversity metrics indicating the diversity expected if species had equal chance of occurring in both sites, based on 1000 random samples with replacement of the bat individual X site matrix. Numbers in parentheses for Chao's and ACE estimators are the 95% confidence intervals based on the SE of the estimator. Phylogenetic diversity was measured as the mean nearest taxon distance between pairs of species in the community; negative values indicate species are more closely related than expected by chance, numbers in square brackets are the  $P$ -values of phylogenetic diversity compared to null expectation based on randomizing the community matrix while preserving the species richness in each site. Functional richness was measured as the volume of the convex hull of 'functional space' in principle coordinates axes, functional evenness was the regularity of the distribution of species' abundance in the functional space, and functional divergence was measured as the divergence in the distribution of abundance in this space

Diversity metric	Fragment	Preserve forest
Species richness	20 (23–29)	30 (28–32)
Rarefied species richness	20 (23–29)	25.32 (25.04–27.67)
Shannon diversity	2.07 (2.62–2.83)	2.82 (2.71–2.82)
Chao's estimator richness	20 (19.76–20.24)	33 (24.85–41.15)
ACE estimator richness	20.32 (16.47–24.18)	32.95 (27.54–38.35)
Phylogenetic diversity	-0.70 [0.25]	-2.03 [0.02]
Phylogenetic diversity — Phyllostomidae only	-0.82 [0.21]	-1.06 [0.12]
Functional richness	$7.21^{e-24}$	$1.30^{e-18}$
Functional evenness	0.63	0.43
Functional divergence	0.94	0.94

TABLE 3. Results of Mantel tests for relationship among species association index and phylogenetic/functional distances. For each row, the dependent matrix was the Jaccard species association index and the predictor matrix is given

Predictor matrix	Mantel $r$	Low CI	High CI	$P$ -level
Phylogenetic distance	-0.11	-0.04	-0.19	0.15
Trait distance	0.03	-0.02	0.07	0.36
Mass distance	0.09	-0.01	0.16	0.26
Roost distance	0.04	-0.01	0.08	0.34
Diet distance	0.12	0.06	0.16	0.05

### Phylogenetic and Functional Diversity

The community at the preserve forest was significantly phylogenetically clustered (Table 2,  $P = 0.02$ ) — species were more closely related than expected by chance. In contrast, the community at the fragment was not different from null expectation ( $P = 0.18$ ). However, when we analyzed phyllostomid bats only, neither community was significantly different than the null expectation (Table 2).

Functional richness was higher at the preserve forest than the fragment, while functional evenness (the evenness in abundance of species with different functional traits) was lower at the preserve forest than the fragment. Functional divergence among species was similar between the two sites (Table 2).

### Traits Predicting Abundance

Body mass and number of roost categories used by a species were significant predictors of the difference in abundance between the preserve forest and the fragment (Fig. 2 and Table 4). The results show that larger-bodied species and those that use three or more roost types have higher abundance in the fragment than in the preserve forest.

### Differences in Capture Rates between Nets and Traps

More species were captured using mist nets at ground level (species richness = 29, rarefied species richness = 21.39, sampling effort = 150 individuals as for high nets) than harp traps (species richness = 24, rarefied richness = 19.28) or triple high mist nets (species richness = 13) in total and accounting for differences in sampling effort (Supplementary Fig. S1). There were differences in capture rates between mist nets and harp traps among taxa. The mormoopid species *Pteronotus davyi* and *P. mesoamericanus* and the vespertilionid species

*Rhogeessa aeneus*, *Myotis elegans*, and *M. keaysi* had higher capture rates in harp traps than in mist nets, while phyllostomids had higher capture rates in mist nets (Supplementary Fig. S2 and Supplementary Table S2).

### DISCUSSION

Our data indicate that the bat community in the preserve forest at Lamanai Archaeological Reserve is more diverse than the bat community in a nearby forest fragment. Species richness was relatively stable over the four years of the study at both localities. While functional trait richness was higher at the preserve forest than the fragment, other measures of functional diversity were similar between sites. Bats in the preserve were more closely related phylogenetically than at the fragment. At our study sites, closely related bat species and those that use different roost types and have different diets tend to co-occur more frequently than distantly related species that use the same roosts and have the same diets. These results demonstrate that competition for resources, especially food and roosts, is a driving mechanism of community assembly in our study site. Roosts have also been found to be a limiting factor for bat ecology in Amazonian communities (Voss *et al.*, 2016). We found that bat species that

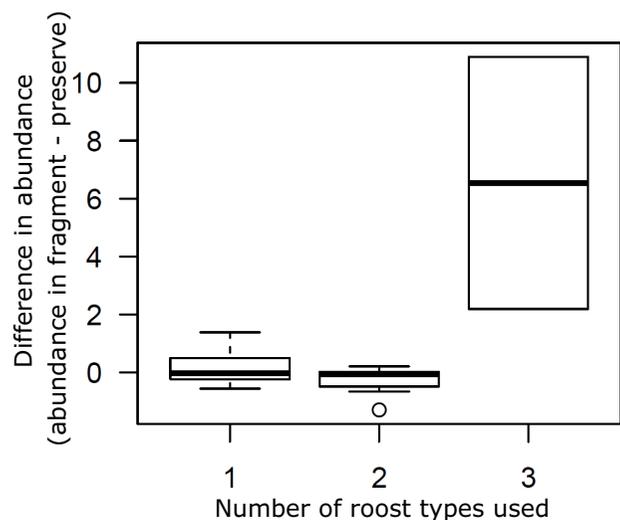


FIG. 2. Boxplots comparing the difference in abundance between the fragment and the preserve for bats that use one, two, or three roost types. Bats with higher capture rates in the fragment than the preserve have positive values, while species with lower capture rates in the fragment are negative. The black bar represents the median, the box encloses the first and third quartiles, the whiskers represent 1.5 times the quartiles, and the open point represents a value beyond 1.5 times the lower quartile

TABLE 4. Results of phylogenetic regressions testing if traits predict the difference in abundance between the preserve forest and the fragment. Correlation coefficients are given with *P*-values

Trait	Correlation coefficient	<i>P</i> -level
Number of roost categories used	1 = 0.12	0.86
	2 = -0.25	<0.001
	3 = 4.04	<0.001
Body mass	0.02	<0.001
Diet	Animalivore = 0.21	0.82
	Herbivore = -1.3	0.28
	Omnivore = -1.38	0.24
Roost type	Caves = 0.27	0.85
	Crevices = -0.62	0.80
	Foliage = 0.52	0.67
	Hollows = 0.27	0.82
	Open = -0.65	0.83
Aspect ratio	0.04	0.93

used more roost types had higher abundance in the fragment, signifying that flexibility in roost use may aid in species colonization and/or persistence in the fragment. Alternatively, if the bats in the fragments are not permanent residents, then those species with flexible roost use are better able to temporarily exploit the fragment.

We compared our bat species inventory to a previous survey conducted at the site (that of Fenton *et al.*, 2001), and record two new species for the area not captured previously, *Natalus mexicanus* and *Chrotopterus auritus*. Both were captured at the fragment in a looter's tunnel within partially excavated Maya ruins. We also note a third species was captured in this study but not in previous inventories, *Eumops nanus*, which was captured in the distinct, open, tropical savannah habitat east of the preserve forest and lagoon and thus not included in our analyses. Six species captured in the previous inventory were not captured during our study (*Centurio senex*, *Lasiurus ega*, *Lamproncycteris brachyotis*, *Tonatia brasiliense*, *Saccopteryx leptura*, *Platyrrhinus helleri* — Fenton *et al.*, 2001), although some of these were captured in small numbers prior to 2010 by EC and between 2010 and 2013 by NBS when data collection was not focused on community sampling (Supplementary Table S3). At least one other species, *Vampyrum spectrum*, was captured at the preserve in March 2015 by another research group (K. Sears, personal communication) but was not captured during our study.

The differences in species lists between this study and the previous inventory may partially be due to suspected migratory behaviors of some bats (e.g., *Centurio*) that may simply not be present in

the area during our regular late April/early May sampling periods. Bat species richness at the two sites was consistent across years, controlling for sampling effort, illustrating that the communities may be at a stable equilibrium. We acknowledge the caveat that our sampling may be biased because mist nets tend to capture only a subset of bat species in the community (Francis, 1989; Meyer *et al.*, 2011) and mist nets set at ground level are biased towards sampling phyllostomids (Cisneros *et al.*, 2015). Because of these known biases, we also employed harp traps during each of the sampling nights, which captured several vespertilionid and mormoopid species that were not captured in mist nets. Therefore, although all measures of species richness based on sampling are incomplete (O'Hara, 2005), our estimates include species frequently missed using a single capture method.

Bat diversity was higher in the preserve forest than the fragment, and the community at the fragment was a nested subset of the community at the preserve forest. These results are in line with numerous studies that have documented the decline in species richness with forest fragmentation (e.g., Laurance *et al.*, 2002; Bregman *et al.*, 2014). Like other faunal assemblages, the smaller area available in fragments may lead to smaller effective population sizes and thus higher local extinction probabilities, as well as lower habitat heterogeneity for niche partitioning (MacArthur and Wilson, 1967; Fahrig, 2013). Habitat heterogeneity can help explain some of the differences that we observed in species richness; among other things, the fragment is missing two species present at the preserve forest that are over-water specialist species (*Noctilio leporinus* and *Rhynchonycteris naso*), illustrating how the availability of diverse habitats at the preserve is one factor that may lead to higher species richness at that site.

The preserve forest and the fragment were once part of a contiguous forest that was only sparsely fragmented until the mid-2000s, when large scale land-clearance for agriculture and pasture severed the connections between them (Fig. 1). The distance between the preserve forest and the fragment may be traversable by vagile species (e.g., *Artibeus lituratus* has been observed to disperse >100-km and is potentially migratory — Arnone *et al.*, 2016), however the distance is greater than that travelled nightly by most of the bats in this system. For example, several studies of *Sturnira*, *Glossophaga*, and *Carollia* species reported that these bats rarely travelled more than 2–3 km (Bernard and Fenton, 2003; Loayza and Loiselle, 2008; Aguiar *et al.*, 2014;

Cortés-Delgado and Sosa, 2014), and a study of *Carollia perspicillata* and *A. lituratus* found maximum travel distances of ca 0.96 and 2 km, respectively, with averages being about half the maximum (Trevelin *et al.*, 2013). *Desmodus rotundus* usually ranges 2–3 km in Brazil (Trajano, 1996), and rarely traveled more than one km between roosts in Argentina, with only 1–3% of > 2,000 recaptured individuals changing roosts greater than one km apart, usually juvenile males dispersing from their natal roosts (Delpietro *et al.*, 2017). Further, some of the bats in our system have strong preference for mature forest and avoid anthropogenic landscapes, and have high roost site fidelity, returning to the same roosts in mature forest every day (e.g., *Dermanura watsonii* — Ripperger *et al.*, 2015; *A. lituratus*, *C. perspicillata* — Trevelin *et al.*, 2013). Lastly, in a multi-year mark-recapture study at the preserve forest and the fragment, no *D. rotundus* species captured at the preserve were ever recaptured at the fragment, nor vice versa (D. Becker, personal communication).

Phylogenetic diversity was lower in the preserve forest because closely related species co-occurred more frequently than expected if species were randomly drawn from across the bat phylogenetic tree, while at the fragment, phylogenetic diversity was not different from random expectation. This result can be taken as evidence that the bat community in the preserve forest is more fully ‘packed’ with species than the fragment because closely related species should only co-occur when they can partition niche space and avoid competition (Stevens *et al.*, 2012). In contrast, the random pattern of phylogenetic relatedness among species in the fragment community support the role of neutral processes in community assembly whereby the successful colonization of a habitat patch is a stochastic process (*sensu* Hubbell, 2001). Counter to this hypothesis, though, the effect of roost-type diversity on increased species abundance in the fragment illustrates that species with flexible roost use were differentially able to exploit the fragment forest.

Functional richness was higher at the preserve forest than the fragment, but other measures of functional diversity were comparable between sites. When close relatives co-occur, the hypothesized process is usually environmental selection for adaptive traits shared by close relatives (Cavender-Bares *et al.*, 2009; Mayfield and Levine, 2010). Close relatives may diverge in niche traits to avoid competition, however, in which case close relatives with disparate traits can co-occur (MacArthur and Levins,

1964; Mayfield and Levine, 2010). Species co-occurrence was positively related to dissimilarity in diet, and there was a positive relationship between species co-occurrence and roost type dissimilarity (though not statistically significant). These patterns illustrate that species which exploit different diet niches and roosts occur together more often than those that have the same diet and use the same roost types. In our system it appears that closely-related bat species with divergent dietary guilds and roost preferences co-occur more frequently than distantly related species with similar diets and roost types, supporting ecological divergence in diet guild and roost preference as a driving force in bat community assembly.

Species co-occurrence patterns in our study were partially explained by phylogenetic distance; closely related species tended to co-occur more frequently than distantly related species. Further, species that used different roost types were more likely to co-occur than species that used the same roost types. The phylogenetic pattern may reflect the dominance of phyllostomid bats in samples collected using mist nets and harp traps. The Family Phyllostomidae is a unique and ecologically diverse bat radiation that has diversified faster and more broadly into different ecological niches than other bat clades (Rojas *et al.*, 2011; Dumont *et al.*, 2014; Shi and Rabosky, 2015). When analyzing phyllostomid bats alone, there was no difference in the phylogenetic diversity of bats from the null expectation. We found that, despite our samples being dominated by closely related species, divergence in roost preferences may allow these close relatives to partition niches and co-occur.

Research has shown that bats may be considered bioindicators because of their important ecological functions and varying sensitivities to anthropogenic activities (Jones *et al.*, 2009). Many animalivorous bats are sensitive to deforestation (e.g., Wilson *et al.*, 1996), partly due to the availability of roosts (Voss *et al.*, 2016), and they are vulnerable to chemical pollutants because of the biomagnification effects at higher trophic levels (Jones *et al.*, 2009; Becker *et al.*, 2017a, 2017b). Phyllostomine bats (primarily gleaning animalivores) are generally thought to decline in abundance with increasing deforestation, while frugivorous species that specialize on pioneer plant species tend to increase in abundance in disturbed forest (Fenton *et al.*, 1992; Brosset *et al.*, 1996). In this study, we did not find an effect of diet type on the difference in abundance between the preserve forest and fragment

sites. This is most likely because frugivorous species had ample access to pioneer plant species at forest edges, as well as mature canopy trees. Instead, the number of roost types used by bats was a significant predictor of the difference in abundance between the preserve forest and the fragment; bats that used more roost types had higher abundance in the fragment. This likely illustrates that bat species with more flexible roost selection have a greater chance to colonize and dominate in the fragment than species that are more specialized in roost preferences. These results are in line with a recent study that found the availability of roosts was a limiting factor for bat community composition in Amazonia (Voss *et al.*, 2016), illustrating that roost guilds are as important for bat ecology as trophic guilds.

In summary, we found significant differences in bat community composition between a preserve forest and a forest fragment in Belize. Closely related bat species tended to co-occur in the forest preserve and had greater functional diversity than the random species assemblage of the fragment. Future research should investigate the potential for individual movement into the agricultural matrix and determine if any species is able to use the small patches of fragmented forest to facilitate dispersal. Bats provide important services in this system, consuming pest insects and pollinating trees and probably cultivated plants as well. They also facilitate forest regeneration by dispersing tree seeds. Conserving the bat communities in the study region is an important application of these results because the landscape is quickly being converted to agriculture and lacking protected status, many fragments may be deforested in the near future.

#### SUPPLEMENTARY INFORMATION

Contents: Table S1. Trait data used in analyses of functional diversity and trait-mediated differences in abundance between the fragment and preserve forests; Table S2. Number of captures and capture rates in the fragment and preserve forest between 2014 and 2017; Table S3. Bat presence in the fragment and preserve forests between 2010 and 2013 with capture technique. Supplementary Information is available exclusively on BioOne.

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#### LITERATURE CITED

- AGUIAR, L., E. BERNARD, and R. B. MACHADO. 2014. Habitat use and movements of *Glossophaga soricina* and *Lonchophylla dekeyseri* (Chiroptera: Phyllostomidae) in a Neotropical savannah. *Zoologia (Curitiba)*, 31: 223–229.
- ARITA, H. T., and M. B. FENTON. 1997. Flight and echolocation in the ecology and evolution of bats. *Trends in Ecology & Evolution*, 12: 53–58.
- ARNONE, I. S., E. TRAJANO, A. PULCHÉRIO-LEITE, and F. D. C. PASSOS. 2016. Long-distance movement by a great fruit-eating bat, *Artibeus lituratus* (Olfers, 1818, in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica*, 16: 1–6.
- ATMAR, W., and B. D. PATTERSON. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96: 373–382.
- BAWA, K. S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics*, 21: 399–422.
- BECKER, D. J., M. M. CHUMCHAL, H. G. BRODERS, J. M. KORTSIAN, E. L. CLARE, T. R. RAINWATER, S. G. PLATT, N. B. SIMMONS, and M. B. FENTON. 2017a. Mercury bioaccumulation in bats reflects dietary connectivity to aquatic food webs. *Environmental Pollution*, 233: 1076–1085.
- BECKER, D. J., M. M. CHUMCHAL, A. B. BENTZ, S. G. PLATT, G. Á. CZIRJÁK, T. R. RAINWATER, S. ALTIZER, and D. G. STREICKER. 2017b. Predictors and immunological correlates of sublethal mercury exposure in vampire bats. *Royal Society Open Science*, 4: 170073.
- BERNARD, E., and M. B. FENTON. 2003. Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. *Biotropica*, 35: 262–277.
- BREGMAN, T. P., C. H. SEKERCIOGLU, and J. A. TOBIAS. 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biological Conservation*, 169: 372–383.
- BROSSET, A., P. CHARLES-DOMINIQUE, A. COCKLE, J.-F. COSSON, and D. MASSON. 1996. Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology*, 74: 1974–1982.
- CADOTTE, M. W., R. DINNAGE, and D. TILMAN. 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93 (Supplement): S223–S233.
- CAVENDER-BARES, J. K. H. KOZAK, P. V. A. FINE, and S. W. KEMBEL. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12: 693–715.
- CISNEROS, L. M., M. E. FAGAN, and M. R. WILLIG. 2015. Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, 21: 523–533.
- CLEVELAND, C. J., M. BETKE, P. FEDERICO, J. D. FRANK, T. G. HALLAM, J. HORN, J. D. LÓPEZ, G. F. MCCracken, R. A.

- MEDELLÍN, and A. MORENO-VALDEZ. 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment*, 4: 238–243.
- COLWELL, R. K., A. CHAO, N. J. GOTELLI, S.-Y. LIN, C. X. MAO, R. L. CHAZDON, and J. T. LONGINO. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, 5: 3–21.
- CORTÉS-DELGADO, N., and V. J. SOSA. 2014. Do bats roost and forage in shade coffee plantations? A perspective from the frugivorous bat *Sturnira hondurensis*. *Biotropica*, 46: 624–632.
- DAYAN, T., and D. SIMBERLOFF. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters*, 8: 875–894.
- DELPIETRO, H., R. RUSSO, G. CARTER, R. LORD, and G. DELPIETRO. 2017. Reproductive seasonality, sex ratio and philopatry in Argentina's common vampire bats. *Royal Society Open Science*, 4: 160959.
- DUMONT, E. R., K. SAMADEVAM, I. GROSSE, O. M. WARSJ, B. BAIRD, and L. M. DAVALOS. 2014. Selection for mechanical advantage underlies multiple cranial optima in new world leaf-nosed bats. *Evolution*, 68: 1436–1449.
- FAHRIG, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40: 1649–1663.
- FENTON, M. B., L. ACHARYA, D. AUDET, M. HICKEY, C. MERRIMAN, M. OBRIST, D. SYME, and B. ADKINS. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica*, 24: 440–446.
- FENTON, M., E. BERNARD, S. BOUCHARD, L. HOLLIS, D. JOHNSTON, C. LAUSEN, J. RATCLIFFE, D. RISKIN, J. TAYLOR, and J. ZIGOURIS. 2001. The bat fauna of Lamanai, Belize: roosts and trophic roles. *Journal of Tropical Ecology*, 17: 511–524.
- FRANCIS, C. M. 1989. A comparison of mist nets and two designs of harp traps for capturing bats. *Journal of Mammalogy*, 70: 865–870.
- FUJITA, M. S., and M. D. TUTTLE. 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology*, 5: 455–463.
- GARCÍA-MORALES, R., C. E. MORENO, E. I. BADANO, I. ZURIA, J. GALINDO-GONZÁLEZ, A. E. ROJAS-MARTÍNEZ, and E. S. ÁVILA-GÓMEZ. 2016. Deforestation impacts on bat functional diversity in tropical landscapes. *PLoS ONE*, 11: e0166765.
- GOSLEE, S. C., and D. L. URBAN. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22: 1–19.
- GROSSBERG, R., A. TREVES, and L. NAUGHTON-TREVES. 2003. The incidental ecotourist: measuring visitor impacts on endangered howler monkeys at a Belizean archaeological site. *Environmental Conservation*, 30: 40–51.
- HADDAD, N. M., L. A. BRUDVIG, J. CLOBERT, K. F. DAVIES, A. GONZALEZ, R. D. HOLT, T. E. LOVEJOY, J. O. SEXTON, M. P. AUSTIN, and C. D. COLLINS. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1: e1500052.
- HAINES, H. 2011. How the other-half lived: continuing discussions of the enigma that is Ka'Kabish, Belize. *Research Reports in Belizean Archaeology*, 8: 137–150.
- HANSEN, M. C., P. V. POTAPOV, R. MOORE, M. HANCHER, S. TURUBANOVA, A. TYUKAVINA, D. THAU, S. STEHMAN, S. GOETZ, and T. LOVELAND. 2013. High-resolution global maps of 21st-century forest cover change. *Science*, 342: 850–853.
- HARDIN, G. 1960. The competitive exclusion principle. *Science*, 131: 1292–1297.
- HODGKISON, R., S. T. BALDING, A. ZUBAID, and T. H. KUNZ. 2003. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. *Biotropica*, 35: 491–502.
- HUBBELL, S. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ, 392 pp.
- JONES, G., D. S. JACOBS, T. H. KUNZ, M. R. WILLIG, and P. A. RACEY. 2009. Carpe noctem: the importance of bats as bio-indicators. *Endangered Species Research*, 8: 93–115.
- JONSSON, B. G. 2001. A null model for randomization tests of nestedness in species assemblages. *Oecologia*, 127: 309–313.
- KLINGBEIL, B. T., and M. R. WILLIG. 2009. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. *Journal of Applied Ecology*, 46: 203–213.
- KRAFT, N. J., R. VALENCIA, and D. D. ACKERLY. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322: 580–582.
- KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–56, *in* Ecology of bats (T. H. KUNZ, ed.). Plenum Publishing Corporation, New York, xiv + 425 pp.
- LALIBERTÉ, E., P. LEGENDRE, and B. SHIPLEY. 2014. Package 'FD': measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Available at <https://cran.r-project.org/web/packages/FD/FD.pdf>.
- LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. VASCONCELOS, R. K. DIDHAM, P. C. STOFFER, C. STOFFER, R. O. BIERREGAARD, S. G. LAURANCE, and E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, 16: 605–618.
- LEVIN, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, 104: 413–423.
- LOAYZA, A. P., and B. A. LOISELLE. 2008. Preliminary information on the home range and movement patterns of *Sturnira lilium* (Phyllostomidae) in a naturally fragmented landscape in Bolivia. *Biotropica*, 40: 630–635.
- MAAS, B., D. S. KARP, S. BUMRINGSRI, K. DARRAS, D. GONTHIER, J. C. C. HUANG, C. A. LINDELL, J. J. MAINE, L. MESTRE, and N. L. MICHEL. 2015. Bird and bat predation services in tropical forests and agroforestry landscapes. *Biological Reviews*, 91: 1–21.
- MACARTHUR, R., and R. LEVINS. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the USA*, 51: 1207–1210.
- MACARTHUR, R. H., and E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, 203 pp.
- MAECHLER, M., P. ROUSSEEUW, A. STRUYF, M. HUBERT, K. HORNIK, M. STUDER, and P. ROUDIER. 2015. Package 'cluster': cluster analysis extended Rousseeuw et al. Available at <https://cran.r-project.org/web/packages/cluster/cluster.pdf>.
- MAGURRAN, A. E. 2013. Measuring biological diversity. Blackwell Science Ltd., Malden, MA, 264 pp.
- MAYFIELD, M. M., and J. M. LEVINE. 2010. Opposing effects of

- competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13: 1085–1093.
- MEYER, C. F., L. AGUIAR, L. F. AGUIRRE, J. BAUMGARTEN, F. M. CLARKE, J. F. COSSON, S. E. VILLEGAS, J. FAHR, D. FARIA, and N. FUREY. 2011. Accounting for detectability improves estimates of species richness in tropical bat surveys. *Journal of Applied Ecology*, 48: 777–787.
- NEWBOLD, T., L. N. HUDSON, S. L. HILL, S. CONTU, I. LYSSENKO, R. A. SENIOR, L. BÖRGER, D. J. BENNETT, A. CHOIMES, and B. COLLEN. 2015. Global effects of land use on local terrestrial biodiversity. *Nature*, 520: 45–50.
- NORBERG, U. M., and J. M. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London*, 316B: 335–427.
- O'HARA, R. 2005. Species richness estimators: how many species can dance on the head of a pin? *Journal of Animal Ecology*, 74: 375–386.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. STEVENS, and H. WAGNER. 2014. Vegan: community ecology package. R package version 2.2-0. Available at <http://CRAN.Rproject.org/package=vegan>
- OLIVER, T. H., M. S. HEARD, N. J. ISAAC, D. B. ROY, D. PROCTER, F. EIGENBROD, R. FRECKLETON, A. HECTOR, C. D. L. ORME, and O. L. PETCHEY. 2015a. Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, 30: 673–684.
- OLIVER, T. H., N. J. ISAAC, T. A. AUGUST, B. A. WOODCOCK, D. B. ROY, and J. M. BULLOCK. 2015b. Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, 6: 10122.
- PARADIS, E., J. CLAUDE, and K. STRIMMER. 2004. APE: analysis of phylogenetics and evolution in R language. *Bioinformatics*, 20: 289–290.
- PATTERSON, B. D., and W. ATMAR. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28: 65–82.
- PATTERSON, B. D., M. R. WILLIG, and R. D. STEVENS. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pp. 536–579, *in* *Bat ecology* (T. H. KUNZ and B. FENTON, eds.). University of Chicago Press, Chicago, 745 pp.
- PEARSE, W., M. W. CADOTTE, J. CAVENDER BARES, A. R. IVES, C. J. TUCKER, S. C. WALKER, and M. R. HELMUS. 2015. Pez: phylogenetics for the environmental sciences. *Bioinformatics*, 31: 2888–2890.
- PENDERGAST, D. M. 1981. Lamanai, Belize: Summary of excavation results, 1974–1980. *Journal of Field Archaeology*, 8: 29–53.
- PETERS, S. L., J. R. MALCOLM, and B. L. ZIMMERMAN. 2006. Effects of selective logging on bat communities in the southeastern Amazon. *Conservation Biology*, 20: 1410–1421.
- PINHEIRO, J., D. BATES, S. DEBROY, and D. SARKAR. 2011. nlme: linear and nonlinear mixed effects models. R package version 3.1-97. [<https://cran.r-project.org/web/packages/nlme/nlme.pdf>].
- R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org/>.
- REID, F. 2009. A field guide to the mammals of Central America and Southeast Mexico. Oxford University Press, Oxford, UK, 301 pp.
- RIPPERGER, S. P., E. K. KALKO, B. RODRÍGUEZ-HERRERA, F. MAYER, and M. TSCHAPKA. 2015. Frugivorous bats maintain functional habitat connectivity in agricultural landscapes but rely strongly on natural forest fragments. *PLoS ONE*, 10: e0120535.
- ROJAS, D., A. VALE, V. FERRERO, and L. NAVARRO. 2011. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. *Molecular Ecology*, 20: 2217–2228.
- SCHLUTER, D., and J. D. MCPHAIL. 1992. Ecological character Displacement and speciation in sticklebacks. *American Naturalist*, 140: 85–108.
- SHI, J. J., and D. L. RABOSKY. 2015. Speciation dynamics during the global radiation of extant bats. *Evolution*, 69: 1528–1545.
- SIKES, R., W. L. GANNON, AND THE ANIMAL CARE USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97: 663–688.
- SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529, *in* *Mammal species of the World: a taxonomic and geographic reference*, 3rd edition (D. E. WILSON and D. M. REEDER, eds.). Johns Hopkins University Press, 2142 pp.
- STEVENS, R. D., M. M. GAVILANEZ, J. S. TELLO, and D. A. RAY. 2012. Phylogenetic structure illuminates the mechanistic role of environmental heterogeneity in community organization. *Journal of Animal Ecology*, 81: 455–462.
- TRAJANO, E. 1996. Movements of cave bats in southeastern Brazil, with emphasis on the population ecology of the common vampire bat, *Desmodus rotundus* (Chiroptera). *Biotropica*, 28: 121–129.
- TREVELIN, L. C., M. SILVEIRA, M. PORT-CARVALHO, D. H. HOMEM, and A. P. CRUZ-NETO. 2013. Use of space by frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil. *Forest Ecology and Management*, 291: 136–143.
- VILLÉGER, S., N. W. MASON, and D. MOUILLOT. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89: 2290–2301.
- VOSS, R. S., D. W. FLECK, R. E. STRAUSS, P. M. VELAZCO, and N. B. SIMMONS. 2016. Roosting ecology of Amazonian bats: evidence for guild structure in hyperdiverse mammalian communities. *American Museum Novitates*, 3870: 1–43.
- WEBB, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, 156: 145–155.
- WILLIAMS-GUILLÉN, K., I. PERFECTO, and J. VANDERMEER. 2008. Bats limit insects in a neotropical agroforestry system. *Science*, 320: 70–70.
- WILLIG, M. R., S. J. PRESLEY, C. P. BLOCH, C. L. HICE, S. P. YANOVIK, M. M. DÍAZ, L. A. CHAUCA, V. PACHECO, and S. C. WEAVER. 2007. Phyllostomid bats of lowland Amazonia: effects of habitat alteration on abundance. *Biotropica*, 39: 737–746.
- WILSON, D., C. ASCORRA, S. SOLARI, and D. WILSON. 1996. Bats as indicators of habitat disturbance. Pp. 613–626, *in* *Manu: the biodiversity of southeastern Peru* (D. E. WILSON and A. SANDOVAL, eds.). Smithsonian Books, Washington, D.C., 679 pp.

- WYMAN, M. S., and T. V. STEIN. 2010. Modeling social and land-use/land-cover change data to assess drivers of smallholder deforestation in Belize. *Applied Geography*, 30: 329–342.
- YACHI, S., and M. LOREAU. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the USA*, 96: 1463–1468.
- ZHANG, J., Q. DING, and J. HUANG,.2013. Package ‘spaa’: species association analysis. R package version 0.2.1. Available at <https://cran.r-project.org/web/packages/spaa/spaa.pdf>.

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