




Phylogenetic and functional underdispersion in Neotropical phyllostomid bat communities

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ABSTRACT

Habitat conversion creates a mosaic of land cover types, which affect the spatial distribution, diversity, and abundance of resources. We used abundance, functional, and phylogenetic information to determine if Neotropical bat communities exhibited phylogenetic or functional overdispersion or underdispersion in response to habitat conversion. Overdispersion suggests the operation of intraclade competition, niche partitioning, limiting similarity, or character displacement, whereas underdispersion indicates the operation of interclade competition, abiotic filtering, or biotic filtering. We expected (1) biotic filtering in landscapes with extensive forest loss to result in underdispersion; (2) niche partitioning in heterogeneous landscapes with intermediate forest loss to result in overdispersion; and (3) intraclade competition during times of low resource abundance (*i.e.*, dry season) to increase, resulting in overdispersion. Most bat communities exhibited phylogenetic or functional underdispersion; none exhibited overdispersion. Expectations were not met: underdispersion did not increase with forest loss, heterogeneous landscapes did not induce overdispersion, and no evidence supported the contention that intraclade competition changed with season. Empirical responses were season-specific, likely because resource availability may affect relationships between forest cover and underdispersion and between biodiversity and underdispersion. During the dry season, only high diversity sites exhibited underdispersion (*i.e.*, functional or phylogenetic redundancy), whereas underdispersion occurred in low, intermediate, or high diversity communities during the wet season; we suggest that this difference likely arises due to changes in resource abundance. Communities with high diversity and redundancy occupied heterogeneous sites during the dry season, but communities with high redundancy were restricted to large forest reserves during the wet season.

Abstract in Spanish is available with online material.

Key words: Chiroptera; Costa Rica; functional diversity; landscape ecology; Neotropics; overdispersion; phylogenetic diversity; underdispersion.

LOCAL VARIATION IN SPECIES COMPOSITION OR BIODIVERSITY arises because of differences in the balance between mechanisms that operate at local and regional scales (Ricklefs 2004, 2008, Belmaker & Jetz 2012, Wiens 2012). Nonetheless, the relative contributions of particular mechanisms remain poorly understood. In human-modified landscapes (*i.e.*, landscapes comprising a mosaic of native vegetation and land converted for human use), mechanisms operating at local and regional scales may contribute to the structure of communities (*e.g.*, competition, environmental filters, environmental heterogeneity, landscape connectivity, dispersal limitation; Webb *et al.* 2002, Swenson *et al.* 2006, Mayfield & Levine 2010, Patrick & Stevens 2014). Intensive and extensive habitat conversion may result in homogeneous landscapes with fewer habitat types or resources, resulting in communities with relatively low taxonomic, phylogenetic, and functional biodiversity (Menge

et al. 1985, Fuhlendorf & Engle 2001). Conversely, a moderate amount of habitat conversion may increase landscape heterogeneity, increasing habitat and resource diversity and supporting communities with relatively high taxonomic, phylogenetic, and functional biodiversity (*e.g.*, Meyer *et al.* 2008, Cisneros *et al.* 2015a, Farneda *et al.* 2015). Importantly, understanding the effects of habitat loss and fragmentation on community composition is critical for designing conservation strategies that maintain biotic composition and ecosystem functioning (Cumming & Child 2009, Cardinale *et al.* 2012, Meyer *et al.* 2016).

Simultaneous consideration of abundance, evolutionary history, and ecological functions of species can provide novel insights into patterns of biodiversity in space and time (*e.g.*, Mayfield & Levine 2010, Mayfield *et al.* 2010, Kluge & Kessler 2011, Cisneros *et al.* 2014a, Dreiss *et al.* 2015). For example, deviations from expected relationships based on the random selection of species from a regional species pool provide evidence for the relative importance of ecological and evolutionary

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mechanisms that contribute to the structure of local communities (Fig. 1). If species are drawn randomly from a regional species pool, the relationship between taxonomic and phylogenetic or functional diversity should be positive (Kluge & Kessler 2011). Because species differ in evolutionary history and in functional traits, phylogenetic and functional diversity generally increase with increasing species richness. However, as more species are drawn from the pool, the likelihood of adding taxa that are phylogenetically or functionally different from those already sampled decreases (Kluge & Kessler 2011), resulting in a saturating curve (Fig. 1).

Deviations from null expectations can be classified as overdispersion or underdispersion, with each type of deviation hypothesized to arise from a different suite of assembly mechanisms. Phylogenetic overdispersion (*i.e.*, more phylogenetic diversity than expected based on a random selection of species) is

consistent with community assembly dominated by competitive exclusion of closely related species (Fig. 1A; Mayfield & Levine 2010). In contrast, phylogenetic underdispersion (*i.e.*, less phylogenetic diversity than expected based on random selection of species) is consistent with community assembly driven by environmental filtering or with interclade competition. An entire clade may have an advantage over other clades because of superior competitive abilities or because of phylogenetically-conserved adaptations to local environmental conditions (Cavender-Bares *et al.* 2009, Mayfield & Levine 2010).

Functional overdispersion (*i.e.*, more functional diversity than expected based on a random selection of species) is consistent with community assembly driven by niche partitioning, limiting functional similarity, or character displacement (Fig. 1B; Kluge & Kessler 2011). In contrast, functional underdispersion (*i.e.*, less functional diversity than expected based on random selection of species) is consistent with environmental filtering. Environmental filters related to physiological tolerances, habitat affinities, or resource requirements may dominate community assembly, resulting in a less functionally diverse group of coexisting species than would be expected by chance (Cavender-Bares *et al.* 2009, Lebrija-Trejos *et al.* 2010).

In the Neotropics, bats are species rich, locally abundant, functionally diverse, and provide important ecological services (Kunz *et al.* 2011). They are the sole or primary agents of pollination and seed dispersal for many early and mid-successional plant species (Fleming & Heithaus 1981, Galindo-González *et al.* 2000), promoting secondary succession and regeneration of disturbed areas (Gorchov *et al.* 1993).

Seasonal changes in resource diversity and abundance can affect the strength of competitive interactions as resources become more limiting, with strong competitive interactions promoting increased phylogenetic or functional overdispersion (Fig. 1; Chase *et al.* 2002). Seasonal changes in resource availability affect how bats use the landscape and the composition of local communities. These responses can occur relatively quickly for bats, as their vagility allows them to track temporal fluctuations in resources within and among landscapes via short-distance movement or by increasing their home range size to meet dietary needs (Fleming & Eby 2003). As functionally similar phyllostomid bats are often members of the same clade (Wilson 1973), increased phylogenetic and functional overdispersion may be expected if competition between functionally similar species occurs. In contrast, greater resource abundance during the wet season should relax competition among functionally similar species and result in underdispersion.

We evaluated the phylogenetic and functional structure of local bat communities from the Caribbean lowlands of Costa Rica separately for dry and wet seasons. Caribbean lowlands have experienced appreciable forest loss and conversion to grazing and agricultural land uses (McClearn *et al.* 2015). We made three predictions. First, extensive forest loss should create landscape filters for forest bats. These landscape filters create barriers to unrestricted movement and change the spatial distribution and abundance of resources throughout the

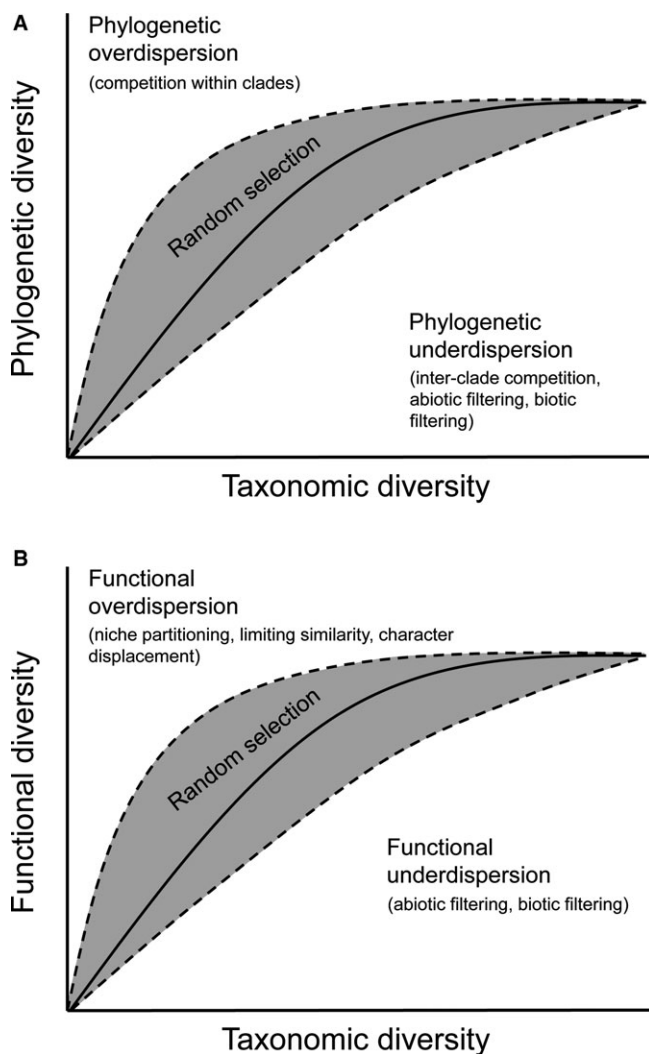


FIGURE 1. Theoretical relationships between (A) taxonomic diversity and phylogenetic diversity, and (B) taxonomic diversity and functional diversity that are consistent with particular ecological or evolutionary mechanisms or with random selection (Mayfield & Levine 2010, Kluge & Kessler 2011).

landscape, resulting in phylogenetic or functional underdispersion. Second, landscapes with intermediate levels of forest loss should harbor communities that exhibit phylogenetic or functional overdispersion due to increased habitat and resource diversity. Third, the importance of intraclade competition should increase during the dry season due to lower levels of resource abundance and diversity (e.g., Frankie *et al.* 1974, Tschapka 2004), thereby increasing the strength of competitive interactions between functionally similar species and promoting overdispersion.

MATERIALS AND METHODS

STUDY SYSTEM.—Phyllostomids are species rich, comprise many subfamilies, and represent many broadly defined foraging guilds (*i.e.*, frugivores, nectarivores, carnivores, insectivores, sanguinivores, and omnivores), reflecting appreciable variation in abundance, phylogenetic, and functional attributes. In the Caribbean lowlands of Costa Rica, bats were sampled at 15 forest sites in a human-modified landscape in Sarapiquí, Costa Rica (Fig. S1; Cisneros *et al.* 2015a,b). This region has experienced considerable forest loss, with ~25% of original forest cover remaining (McClearn *et al.* 2015). Sites were embedded within landscapes that represent a gradient of forest loss and fragmentation. The region consisted of fragments of wet tropical forest in various successional stages, agricultural plantations (e.g., banana, pineapple), cattle pastures, and recently logged areas. Percent forest cover was quantified at each of three spatial scales (circles of 1 km, 3 km, or 5 km radii) for each site using a land cover map from 2011 (Fagan *et al.* 2013). Percent forest cover varied from 10 to 100% at 1 km, from 10 to 88% at 3 km, and from 22 to 71% at 5 km. For ease of exposition, we refer to sites with <50%, 50 to 75%, and >75% forest cover at the 1 km scale as landscapes with extensive forest loss, intermediate forest loss, and low forest loss, respectively. Five sites belong to each of these three categories.

The climate is warm with appreciable rainfall throughout the year (4374 mm/month annual rainfall). Distinct wetter (435 mm/month from May to December) and drier (224 mm/month from January to April) seasons affect resource diversity and abundance (Organization for Tropical Studies 2012). Bats were surveyed in 2010 using ground-level mist nets for four nights at each site during each season. Analyses were restricted to phyllostomids to minimize species-specific capture biases (Kalko 1998). Additional details of sampling methods are available elsewhere (Cisneros *et al.* 2015a,b). The protocol for animal use of this research followed ASM guidelines (Sikes & Gannon 2011) and was approved by the IACUC at the University of Connecticut (IACUC number: A09-014). We used previously archived data (Cisneros *et al.* 2014b, 2015a) for all analyses.

PHYLOGENETIC AND FUNCTIONAL DATA.—Phylogenetic diversity was based on branch lengths from a rooted species-level supertree for bats (Jones *et al.* 2005). A supertree with branch lengths is required to calculate phylogenetic diversity using the same

approach as that used for abundance and functional diversity, making values for dimensions comparable and in the same units (*i.e.*, effective number of species).

Functional traits must be selected with care to ensure that they measure functional aspects of interest and to ensure that results are interpretable and ecologically meaningful (Petchey & Gaston 2006). Functional diversity was estimated based on 11 categorical and 10 continuous attributes of bats (Cisneros *et al.* 2015b, Appendix S1). Categorical traits were binary (*i.e.*, a species did or did not exhibit a trait) and represented three functional components: diet (fruit, nectar, invertebrates, vertebrates, blood), foraging location (canopy, subcanopy, understory), and foraging strategy (gleaning, hovering, pounce). Continuous characteristics reflected three functional components, including body size (mass, forearm length), masticatory mode (greatest length of skull, condylobasal length, maxillary tooth row length, breadth across upper molars, post-orbital constriction, breadth of braincase), and aerodynamics (wing aspect ratio, wing loading). Functional attributes were obtained from the literature and restricted to records from Central America when possible (Cisneros *et al.* 2015a,b). Missing continuous data were estimated using linear regression, with mass as the independent variable and trait values of other species from the same subfamily as the dependent variable. Missing categorical data were replaced by values from congeners. Only 4.1% of species traits were estimated or replaced. These approaches for missing data are conservative and likely result in an underestimation of functional diversity. This should have little effect evaluation of functional dispersion as effects will apply equally to functional diversity values based on empirical and randomly generated communities; however, it is possible that missing data could result in a more conservative test of dispersion.

For each season, we created a pairwise dissimilarity matrix based on all 21 functional attributes using Gower's distances from the R package "cluster" (Maechler *et al.* 2012). Functional attributes were weighted to ensure that each functional component contributed equally to Gower's distances. To characterize functional variation among species for each season, we used the first dimension from non-metric multidimensional scaling (NMDS) based the pairwise dissimilarity matrices for the 30 taxa recorded during the dry season or the 33 taxa recorded during the wet season using the R package "ecodist" (Goslee & Urban 2007). That dimension accounted for 65% of the total variation within each season.

AN INTEGRATED FRAMEWORK FOR BIODIVERSITY MEASUREMENT.—In its original formulation, Hill numbers (Hill 1973) represent the effective number of species in a community (*i.e.*, the number of equally abundant species needed to produce the value of an empirical metric). This concept was extended to phylogenetic and functional dimensions using proportional phylogenetic divergence (Scheiner 2012) and proportional functional distance (Presley *et al.* 2014) to weight species presences, thereby estimating phylogenetic and functional diversity, respectively. The use of Hill numbers ensures that all metrics are in the same units (effective number of

species) and are on the same scale (from 1 to species richness; Chao *et al.* 2014). The general form of Hill numbers is:

$${}^qD = \left(\sum_{i=1}^S x_i^q \right)^{1/(1-q)}, \quad (1)$$

where S is species richness; x_i is proportional abundance, proportional lineage divergence, or proportional functional distance of species i , depending on dimension; and q is the order of the diversity metric that determines the weighting of relative proportions. The measure is undefined when $q = 1$, requiring a limit formulation:

$${}^1D = \lim_{q \rightarrow 1} {}^qD = \exp \left(- \sum_{i=1}^S x_i \log x_i \right). \quad (2)$$

As the value of q increases, the relative contributions of more abundant, more evolutionarily divergent, or more functionally distinct species increase. We used $q = 1$, which weights species based on their relative abundance, lineage divergence, or functional dissimilarity because we had no *a priori* reason to otherwise weight interspecific differences (*e.g.*, Scheiner 2012, Chao *et al.* 2014).

Abundance diversity, ${}^qD(A)$, reflects variation in relative abundances of species and has a maximum value of S for a community with a perfectly even distribution of individuals among species (Hill 1973). Communities with one dominant species have low diversity, with ${}^1D(A)$ approaching 1.0 as the proportional abundance of the dominant species increases. Phylogenetic diversity, ${}^qD(P)$, measures the variation in the proportional lineage divergences of species and has a maximum value of S when phylogenetic relationships are perfectly symmetrical, resulting in all species having equal proportional lineage divergence (Scheiner 2012). Any deviations from symmetry will decrease ${}^qD(P)$. ${}^qD(P)$ is lowest in a phylogenetic tree that has many closely related species and one distantly related species. Functional trait diversity, ${}^qD(T^*)$, measures variation in the proportional functional distances of species (*i.e.*, the sum of all pairwise functional distances for a particular species) and has a maximum value of S when all species have equal functional distances. ${}^qD(T^*)$ decreases as variation among species in total functional distance increases and is lowest in a community with one species that is highly distinct from all other species, which themselves are functionally similar. Competitive displacement is expected to equalize the functional distinctiveness among species resulting in a maximal value for ${}^qD(T^*)$.

CONFIDENCE ENVELOPES.—We employed a randomization procedure to create 95% confidence envelopes that define 2-dimensional regions of null expectation for diversity based on random selection. Separately for each season, data from all sites were combined to create a regional species pool. For each value of S from 1 to the number of species in the species pool for that season, species were selected at random, without replacement, 1000 times. Attributes (abundances, phylogenetic positions, functional

traits) associated with the selected species were used to calculate ${}^1D(A)$, ${}^1D(P)$, ${}^1D(T^*)$ for each randomly generated community, and values from the 1000 communities were used to create null distributions for each diversity metric. Species abundance attributes for each season were based on all sites combined, as the combined species abundance distribution represents the best estimate of relative abundances of species in the region. Confidence limits were defined by the lowest 2.5% and greatest 2.5% of values in the null distribution (*i.e.*, a 95% confidence interval). Upper and lower confidence limits for each value of S were plotted and used to estimate 95% confidence envelopes that define the region of null expectation based on random selection. An empirical value within the confidence envelope is consistent with random selection or a balance of mechanisms that promote overdispersion and underdispersion. An empirical value outside the confidence envelope suggests that assembly of the community is dominated by mechanisms that result in more or less diversity than expected by chance (*i.e.*, overdispersion or underdispersion, respectively).

Abundances may affect the potential strength of interactions between species and associated mechanisms that structure communities. Therefore, we used an abundance-weighted diversity metric rather than species richness to better evaluate phylogenetic or functional dispersion of communities. Using ${}^1D(A)$ instead of S , this approach describes the relationships between the effective number of equally abundant species and the effective number of equally functionally distinct species or the effective number of equally divergent lineages. Metrics were calculated and simulations were conducted with script files written in Matlab 7.14.0.739 (available on line at <http://faculty.tarleton.edu/higgins/biological-diversity.html> and Appendices S2–S6).

SUPPORTING ANALYSES.—To determine if phylogenetic or functional dispersion was associated with percent forest cover, we conducted a series of analyses of variance that compared the percent forest cover between communities that exhibit random versus non-random dispersion (*i.e.*, underdispersion). Analyses were conducted separately for each combination of season and spatial scale. Because dispersion was season specific for communities, the category a community belonged to could differ between seasons.

We calculated the correlation of each functional trait with each axis from NMDS and determined the significance of each correlation with the `envfit` function from the R package “vegan” (Oksanen *et al.* 2013). Relationships between dimensions for each season were evaluated via Spearman rank correlations. As we had an *a priori* expectation that correlations between dimensions would be positive, these were conducted as one-tailed tests. All analyses were evaluated at an α -level of 0.05.

RESULTS

A total of 1293 bats were captured during the dry season, representing 30 species and five subfamilies. During the wet season, 1158 bats were captured, representing 33 species and five

subfamilies. Functional attributes representing 5 of the 6 functional components (*i.e.*, diet, foraging location, foraging strategy, body size, masticatory mode, and aerodynamics) were associated with the first axis from NMDS for the dry season, and attributes representing all six functional components were associated with the first NMDS for the wet season (Table 1). Clearly, the first dimension from NMDS represented a broad array of functional attributes for each season.

Six communities during the dry season and seven communities during the wet season exhibited phylogenetic underdispersion, whereas no communities exhibited phylogenetic overdispersion (Fig. 2A,B). Nine communities exhibited functional underdispersion each season, whereas no communities exhibited functional overdispersion (Fig. 2C,D). Communities characterized by phylogenetic ($t = 4.13$, $P = 0.001$) or by functional ($t = 2.51$, $P = 0.024$) underdispersion had greater abundance diversity than

did communities consistent with random selection, whereas during the wet season abundance diversity was not greater in underdispersed communities than in communities consistent with random selection (phylogenetic underdispersion, $t = 1.07$, $P = 0.302$; functional underdispersion, $t = 1.81$, $P = 0.092$).

During the dry season, percent forest cover was not significantly different between sites with communities characterized by underdispersion and sites with communities characterized by random assembly (Table 2). In contrast, during the wet season percent forest cover was significantly greater for communities characterized by underdispersion (75% at 1 km, 66% at 3 km, and 60% at 5 km) than for communities characterized by random assembly (43% at 1 km, 35% at 3 km, and 39% at 5 km). Pairs of dimensions were positively and significantly correlated regardless of season (Fig. 2).

DISCUSSION

In general, responses of Caribbean lowland bat communities were season-specific, suggesting that seasonal variation in resource availability drive relationships between (1) biodiversity (*n.b.*, all dimensions are positively correlated) and the degree of functional or phylogenetic underdispersion, and (2) forest cover and functional or phylogenetic underdispersion. As the relationships between season, dispersion, and biodiversity are complex, we summarize these relationships and then explore details in subsequent sections. Regardless of season, about half of bat communities exhibited functional or phylogenetic underdispersion, with remaining communities being consistent with random selection (Fig. 2). In addition, underdispersion always represented greater functional or phylogenetic redundancy and not less diversity, *per se*. More specifically, underdispersion increased with increasing biodiversity during the dry season (Fig. 2A,C), but was unrelated to biodiversity during the wet season (Fig. 2B,D). Forest loss did not result in underdispersion during either season. Rather, during the dry season the amount of forest cover did not differ between sites with bat communities characterized by underdispersion and those characterized by random selection, whereas during the wet season communities characterized by underdispersion occurred at sites with significantly greater forest cover than did other sites (Table 2). Taken together, these patterns indicate that when resources were limiting (*i.e.*, dry season) forest loss was not associated with underdispersion or with changes in biodiversity of communities, but increasing underdispersion and biodiversity were highly correlated. In contrast, when resources were plentiful (*i.e.*, wet season), underdispersion was not associated with biodiversity, but communities characterized by underdispersion occurred in landscapes with greater forest cover than other communities.

PHYLOGENETIC AND FUNCTIONAL UNDERDISPERSION.—Local bat biodiversity was consistent with random selection or with mechanisms associated with phylogenetic or functional underdispersion (Fig. 2). This corroborates previous studies on phylogenetic structure of bat communities (Riedinger *et al.* 2013, Patrick &

TABLE 1. Pearson product moment correlations (R) and P-values for associations between each of 21 functional traits and the first dimension from non-metric multidimensional scaling. Correlations that were significant ($P \leq 0.05$) or that approached significance ($0.05 < P \leq 0.10$) are bold, indicating an appreciable contribution of a particular trait to interspecific variation in function.

Functional component functional trait	Dry season		Wet season	
	R	P	R	P
Aerodynamics				
Aspect ratio	0.003	0.779	0.014	0.504
Wing loading	0.044	0.253	0.555	0.001
Body size				
Forearm length	0.356	0.001	0.625	0.001
Mass	0.207	0.009	0.623	0.001
Diet				
Blood	0.176	0.001	0.035	0.233
Fruit	0.002	0.825	0.051	0.227
Invertebrates	0.064	0.197	0.006	0.655
Nectar	0.099	0.076	0.015	0.492
Vertebrates	0.032	0.343	0.122	0.039
Location				
Canopy	0.004	0.748	0.434	0.001
Subcanopy	0.030	0.350	0.131	0.046
Understory	0.269	0.001	0.078	0.115
Masticatory mode				
Breadth across molars	0.152	0.020	0.598	0.001
Breadth of braincase	0.206	0.005	0.579	0.001
Condylobasal length	0.098	0.078	0.469	0.001
Greatest length of skull	0.185	0.017	0.433	0.001
Maxillary tooththrow	0.015	0.494	0.192	0.007
Postorbital constriction	0.081	0.103	0.127	0.050
Strategy				
Glean	0.567	0.001	0.230	0.004
Hover	0.567	0.001	0.230	0.004
Pounce	0.176	0.001	0.035	0.233

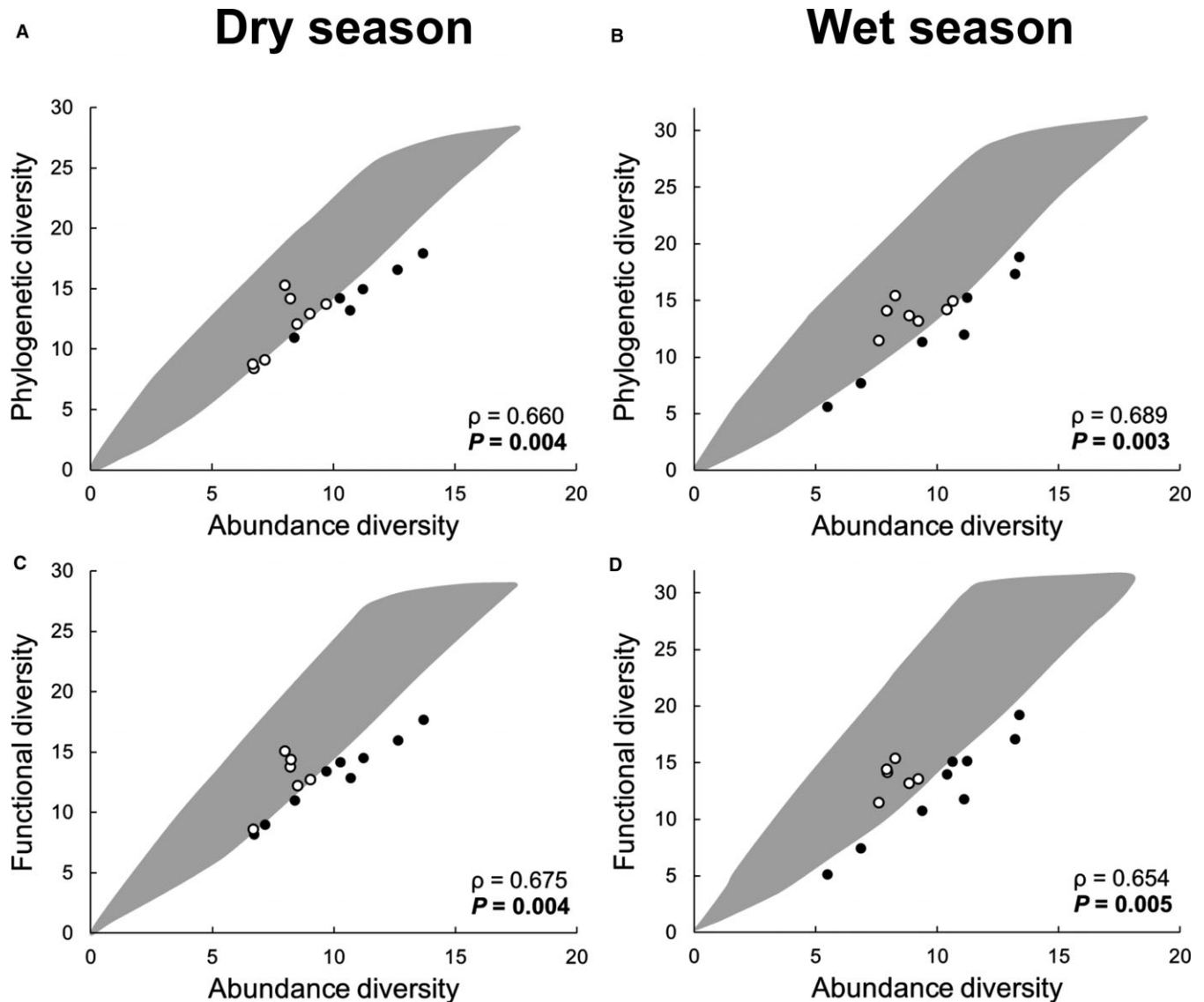


FIGURE 2. Relationships between phylogenetic and abundance diversity (A and B) or between functional and abundance diversity (C and D) for bats from the Caribbean lowlands of Costa Rica during dry and wet seasons. Shaded areas represent 95% confidence envelopes for pairwise considerations of dimensions. Communities with biodiversity values inside confidence envelopes, indicating structure consistent with random selection, have open circles (○); communities with biodiversity values outside confidence envelopes, indicating structure consistent with underdispersion, have solid circles (●). Results from Spearman rank correlation analyses indicate the degree of positive association between pairs of dimensions. Significant ($P \leq 0.05$) correlations are bold.

Stevens 2014), which observed a general trend toward phylogenetic underdispersion or random assembly, with no evidence of overdispersion. Although phylogenetic community ecology suggests that habitat filtering should lead to underdispersion for analyses at large spatial scales and that interspecific interactions (*e.g.*, intraclade competition) should lead to overdispersion at small spatial scales (*e.g.*, Webb *et al.* 2002, Weiher *et al.* 2011), phylogenetic structure of bat communities exhibits underdispersion at both large (Riedinger *et al.* 2013, Patrick & Stevens 2014) and small (this study) spatial scales. Patterns consistent with random selection can be interpreted in two ways: (1) a balance between mechanisms that promote overdispersion and

mechanisms that promote underdispersion, or (2) a lack of strong effects from any such mechanism. There was no support for the prediction that landscapes with the most forest loss would evince phylogenetic or functional underdispersion (Table 2). Rather, underdispersion characterized communities from landscapes with greater forest cover. Similarly, there was no support for the prediction that landscapes with intermediate amounts of forest loss evince phylogenetic or functional overdispersion. Finally, contrary to predictions, results were not consistent with intraclade competition being greater during the dry season than the wet season. Rather, it remained relatively unimportant regardless of season, with no evidence of overdispersion.

TABLE 2. Results (P-values) for analysis of variance comparing percent forest cover between sites that exhibited phylogenetic or functional underdispersion and sites that were consistent with random selection. Analyses were conducted separately for combination of each season and spatial scale. Significant ($P \leq 0.05$) results are bold. % difference in forest cover = difference between mean % forest cover at underdispersed sites and mean % forest cover at random sites (i.e., positive differences indicate greater mean % forest cover at sites characterized by underdispersion).

	1 km		3 km		5 km	
	P	% Difference in forest cover	P	% Difference in forest cover	P	% Difference in forest cover
Dimensions of biodiversity						
Dry season						
Phylogenetic diversity	0.852	-3.16	0.991	0.13	0.934	0.68
Functional diversity	0.988	0.25	0.982	0.27	0.762	2.47
Wet season						
Phylogenetic diversity	0.038	31.79	0.002	31.02	0.001	21.60
Functional diversity	0.142	23.82	0.023	24.87	0.003	20.48

Although phylogenetic or functional underdispersion is consistent with predictions based on interclade competition, abiotic filtering, or biotic filtering, some of these mechanisms are more likely than are others to be applicable to bats in the Caribbean lowlands. Abiotic characteristics that are important for determining Neotropical bat distributions (e.g., humidity, temperature, López-González *et al.* 2012, 2015) do not differ appreciably among our sites (Organization for Tropical Studies 2012), making it unlikely that abiotic filtering is directly responsible for the local assembly of forest communities from the regional species pool. Alternatively, habitat filtering is a common explanation for underdispersion when species pools are derived from multiple habitat types within a region (e.g., Horner-Devine & Bohannon 2006, Willis *et al.* 2010, Patrick & Stevens 2014). Our study area is a complex mosaic of forest and human modified habitats (Fig. S1). Despite all study sites being in Caribbean lowland forest, land cover types surrounding each site can affect the composition of forest bat communities (Cisneros *et al.* 2015a,b). Consequently, areas with a high amount of forest cover that support a lower diversity of habitats and resources than do more heterogeneous landscape mosaics may act as a biotic filter that results in phylogenetic or functional underdispersion in heavily forested areas. Indeed, during the wet season communities that exhibited underdispersion were from landscapes with the greatest amount of forest cover (Table 2). This suggests that landscape-level habitat filters associated with habitat or resource diversity are more likely mechanisms to explain phylogenetic and functional underdispersion than are the alternatives.

LANDSCAPE MOSAICS AND COMMUNITY STRUCTURE.—Caribbean lowlands in Costa Rica have been subjected to extensive forest loss and fragmentation during the past several decades (Fagan *et al.* 2013). Only ~25% of Costa Rica's original forest cover remains (McClearn *et al.* 2015), with bat communities from mature forest patches being embedded in a landscape dominated by pasture and plantations (Fig. S1). To date, the evaluation of phylogenetic or functional structure of systems exposed to anthropogenic disturbances suggests that underdispersion is common (e.g., Verdú

& Pausas 2007, Santos *et al.* 2010, 2014, Riedinger *et al.* 2013, Patrick & Stevens 2014). In the Neotropics, fragmentation of Amazonian and Atlantic forests results in phylogenetic underdispersion of trees (Santos *et al.* 2010, 2014). Because woody plants provide habitat and resources for phyllostomid bats, as well as habitat and resources for animals on which some bats prey (e.g., insects), a reduction in phylogenetic and functional dispersion of the forest flora may have a cascading effect on associated faunas (Duffy 2002, Vellend 2008). Consistent with these predictions, bats from Bavaria exhibit phylogenetic underdispersion, with underdispersion increasing as the proportion of landscape dominated by humans increases (Riedinger *et al.* 2013).

However, Costa Rican lowland forest bats exhibit the opposite response: functional and phylogenetic underdispersion is observed for bat communities from the least disturbed forested landscapes during the wet season and underdispersion was not associated with habitat loss during the dry season. Importantly, underdispersion is not synonymous with lower diversity, but indicates greater phylogenetic or functional redundancy than expected by chance. Multiple biotic filters potentially promote functional and phylogenetic redundancy as functional groups of phyllostomids exhibit different responses to habitat loss and fragmentation in the Neotropics (Klingbeil & Willig 2009, 2010, García-Morales *et al.* 2013, Cisneros *et al.* 2015a). Frugivores and nectarivores generally increase in abundance and in taxonomic diversity in response to low-to-moderate levels of deforestation because the plant species on which they rely for fruit and nectar thrive in forest openings and along forest edges (e.g., Willig *et al.* 2007, Klingbeil & Willig 2009, Castro-Luna & Galindo-González 2011). In contrast, gleaning phyllostomines typically decrease in abundance and diversity in response to the loss of mature forest (Klingbeil & Willig 2009, Farneda *et al.* 2015). Gleaning phyllostomines primarily forage in habitats between the canopy and understory (Fenton *et al.* 1992, Meyer *et al.* 2008), which are uncommon in human-modified and early successional forests. Depending on the time of year, moderately disturbed and less disturbed landscapes likely provide sufficient resources to support a greater number of species with similar functional traits or that belong to

specific guilds. These responses of functional groups to landscape modification are reflected in phylogenetic patterns as well (Fig. 2) due to a strong phylogenetic signal in many functional traits of phyllostomid bats (Cisneros *et al.* 2015b).

SEASONAL DIFFERENCES IN PHYLOGENETIC AND FUNCTIONAL STRUCTURE.—Mechanisms associated with competitive interactions should have a greater effect on community structure when resources are more limiting. During the dry season, resources in Caribbean lowlands are less diverse, less abundant, and more limiting for local bat populations that consume plant material and arthropods, as fruits, flowers, and arthropods peak in abundance during the wet season (Frankie *et al.* 1974, Tschapka 2004). As a result, we expected an increase in the strength of competitive interactions during the dry season to promote phylogenetic or functional overdispersion (Fig. 1). Although communities exhibited seasonal differences in phylogenetic and functional underdispersion, empirical differences were not consistent with predictions (Fig. 2).

During the dry season, only high-diversity communities exhibited phylogenetic or functional underdispersion, with the amount of deviation from null expectation increasing with diversity (Fig. 2). In contrast, during the wet season, the deviation from null expectation for communities that exhibited phylogenetic or functional underdispersion was not associated with increasing diversity. These season-specific responses are consistent with the relaxation of intraclade competition (*i.e.*, species that are functionally more similar or more closely related can coexist more easily) only in sites that support low-diversity communities when resource abundance is high.

During the dry season, sites with intermediate forest loss had the greatest abundance, phylogenetic, and functional diversity (Cisneros *et al.* 2015b). These highly heterogeneous landscapes supported many species from each foraging guild and evolutionary lineage as they provided a variety of habitat types associated with different resources. For example, forest edge environments increase abundance of early successional plants used by bats (Lobova *et al.* 2003, Thies & Kalko 2004), pastoral lands are associated with an increase in cattle (a prey source for the common vampire bat, *Desmodus rotundus*; Wilkinson 1985), and agriculture offers a variety of fleshy fruits, pollen, or nectar that are consumed by bats (Harvey & González Villalobos 2007). It is also important to note that many nectarivores and gleaning animalivores consume fruits (Giannini & Kalko 2004) and frugivores and nectarivores are known to expand their diet during the dry season to comprise a greater number of fruit species and greater quantities of arthropods (Lopez & Vaughan 2007), which allows species from these functional groups to use a diversity of habitat and resource types when resources are limiting. Accordingly, during this time of low resource availability, biotic filtering occurs at the extremes of the disturbance gradient (*i.e.*, landscapes dominated by either forest or agriculture), resulting in greater concentrations of bat species in heterogeneous sites with intermediate disturbance. As underdispersion indicates greater phylogenetic or functional redundancy, underdispersion likely indicates

that ecosystem functioning of these communities is more resilient to species loss (Walker 1992, Vandewalle *et al.* 2010), as any single species is less likely to be the only one to provide a particular ecological function.

During the wet season, underdispersion was associated with landscapes dominated by forest. When resources are more plentiful, bats may be able to remain in optimal habitats. Although forest-dominated landscapes provide fewer distinct niches for bats compared to more heterogeneous landscapes (Frankie *et al.* 1974, Wilkinson 1985, Lobova *et al.* 2003, Thies & Kalko 2004, Tschapka 2004), increased resource abundance allowed more species of the same guild to co-exist, with greater redundancy in low- and intermediate-diversity communities compared to the dry season.

CONCLUSIONS

Extensive habitat loss and fragmentation throughout the Caribbean lowlands has created complex mosaics of habitats that provide greater habitat and resource diversity for bats than do large expanses of continuous mature forests. During the wet season when resources are more plentiful, heterogeneous landscapes that have mature forests, secondary forests, plantations, and plentiful forest edges harbored bat communities with phylogenetic and functional dispersion consistent with a random sampling from the regional fauna. This contrasts with bat faunas from temperate habitat mosaics in Bavaria, which exhibit greater phylogenetic underdispersion with increased anthropogenic activities (Riedinger *et al.* 2013). Alternatively, landscapes dominated by mature forest exhibited greater phylogenetic and functional redundancy than expected during the wet season, resulting in underdispersion but not necessarily less biodiversity. This effect may manifest only during the wet season because greater resource abundances allows bats to remain in preferred habitats, whereas reduced resource abundances during the dry season may force bats to range more widely in search of resources (Cisneros *et al.* 2015a). During the dry season, underdispersion increases with diversity regardless of the amount of forest in the landscape, suggesting that landscapes with low, intermediate, or high forest loss may be productive for bats and support highly diverse communities with phylogenetic or functional redundancy.

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DATA AVAILABILITY

Data deposited in the Dryad Repository: <https://doi.org/10.5061/dryad.9fp3g/1> (Cisneros *et al.* 2014b).

SUPPORTING INFORMATION

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

FIGURE S1. Maps showing the locations of sites in Sarapiquí, Costa Rica.

APPENDIX S1. A list of bat species captured in the Caribbean lowlands of Costa Rica and species-level functional traits associated with diet, foraging location, foraging strategy, and body mass.

APPENDIX S2. ScheinerMDBx.m: Matlab code to calculate abundance, phylogenetic, and functional biodiversity.

APPENDIX S3. ScheinerRand.m: Matlab code to perform randomizations to calculate confidence intervals for biodiversity measures.

APPENDIX S4. samplewor.m: Matlab code needed for randomization procedure.

APPENDIX S5. runscheinerdivx: Matlab script file that allows user to copy in necessary data to calculate biodiversity measures for local communities and associated confidence intervals based on a regional species pool.

APPENDIX S6. Example data for scheinerMDBx: excel file with example data necessary to calculate abundance, phylogenetic, and functional biodiversity measure.

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