



# Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity

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## ABSTRACT

**Aim** To identify characteristics of a human-modified landscape that promote taxonomic (TD), functional (FD) and phylogenetic (PD) dimensions of bat biodiversity.

**Location** Caribbean lowlands of northeastern Costa Rica.

**Methods** During the dry and wet seasons, we quantified TD (Simpson's diversity), as well as FD and PD (Rao's quadratic entropy) of phyllostomid bat assemblages at 15 sites that represented a forest loss and fragmentation gradient. FD was estimated separately for each of seven functional components that reflect particular niche axes (e.g. diet, foraging strategy) and for all functional components combined (FD<sub>all</sub>). PD was based on relatedness of species derived from a supertree. We identified the best explanatory landscape characteristics of each dimension using hierarchical partitioning.

**Results** Landscape effects were dimension and season specific. During the dry season, TD and PD increased with increasing proportions of pasture or size of forest patches, whereas FD<sub>all</sub> decreased with increasing size of forest patches. During the wet season, TD increased with increasing forest patch size, whereas FD<sub>all</sub> and PD increased with increasing compactness of forest patches and decreasing proximity. Decomposition of FD into separate functional components revealed different landscape effects on ecological aspects of assemblages.

**Main conclusions** One dimension of biodiversity was not a good surrogate for another. Rather, decomposition of biodiversity into different dimensions and functional components facilitated identification of the aspects of assemblages that are most affected by forest conversion and fragmentation. Areas with intermediate amounts of forest and pasture during the dry season harboured highest diversity from taxonomic, functional and phylogenetic perspectives. During the wet season, areas with large, compact forest patches promoted the dimensions of biodiversity. Placement of areas with even amounts of forest and pasture adjacent to large, compact forest patches (e.g. reserves) may maintain high biodiversity of bats and the ecosystem functions that they provide throughout the year.

## Keywords

Chiroptera, Costa Rica, fragmentation, functional diversity, phylogenetic diversity, taxonomic diversity.

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## INTRODUCTION

Humans have reshaped over 77% of the terrestrial biosphere (Ellis *et al.*, 2010). Forty percentage of the terrestrial

biosphere is used directly by humans for agriculture and settlements; the remaining area (~ 37%) includes natural (e.g. primary or mature forest) or semi-natural (e.g. secondary forest) lands embedded within a mosaic of land converted

for human use. These embedded natural and semi-natural lands comprise more ice-free land than pristine areas (i.e. landscapes with no human impact; ~ 22%) and are prominent world-wide. Consequently, the success of biodiversity conservation and management of ecosystem functions and services depends on an understanding of the value and contributions of human-modified landscapes to conservation goals (Chazdon *et al.*, 2009).

Although considerable effort has been devoted to understanding the factors that affect community assembly in human-modified landscapes, most studies have focused on the taxonomic dimension (TD) of biodiversity (e.g. species richness and species diversity; Fahrig, 2003; Sodhi & Ehrlich, 2010; Tschardt *et al.*, 2012). TD considers species to be equally distinct and is insensitive to ecological and evolutionary attributes of species. Because the effects of environmental variation, including that produced by land conversion, are mediated by species characteristics (e.g. physiological constraints, habitat requirements, dispersal abilities), consideration of TD alone may provide an incomplete or misleading impression about the consequences of human activities on local or regional biodiversity. Furthermore, landscape modification likely creates new environmental filters that favour particular attributes that may be obligatory for species persistence, thereby altering the mechanistic bases of assembly, such as those reflecting interspecific competitive ability or niche partitioning (Mayfield *et al.*, 2010). Inclusion of species attributes, such as ecological functions or evolutionary histories, into biodiversity assessments should provide insights into the mechanisms that drive community assembly and disassembly to better inform conservation efforts.

Estimates of biodiversity based on ecological functions and evolutionary histories of species describe the functional dimension (FD) and phylogenetic dimension (PD), respectively. FD measures variability in ecological attributes among species and provides a mechanistic link to ecosystem resistance, resilience and functioning (Petchev & Gaston, 2006). PD measures the evolutionary differences among species based on times since divergence from a common ancestor (Faith, 1992) and sometimes represents a comprehensive estimate of phylogenetically conserved ecological and phenotypic differences among species (Cavender-Bares *et al.*, 2009). This dimension may represent the long-term evolutionary potential of a biota to respond or adapt to current and future environments.

Few studies have explored the influences of human-modified landscapes on FD or PD (Tschardt *et al.*, 2012), most of which have focused on plant assemblages (Mayfield *et al.*, 2005, 2006; Laliberté *et al.*, 2010; Arroyo-Rodríguez *et al.*, 2012). The spatial scale at which plants are influenced by landscape modification may differ from those that influence taxa that disperse farther, which may produce different patterns of biodiversity among taxa. Bats are important for assessing the effects of human-modified landscapes on ecological and evolutionary aspects of assemblages because they are diverse from taxonomic and functional perspectives

(Patterson *et al.*, 2003). In the Neotropics, bats are generally the most species rich and locally abundant mammalian group, comprise species from a variety of feeding guilds, and differ greatly in dispersal abilities (Patterson *et al.*, 2003). Moreover, bats provide important ecological services, such as seed dispersal, pollination and regulation of insect populations (Kunz *et al.*, 2011). To date, no study has simultaneously assessed taxonomic, functional and phylogenetic dimensions of bat biodiversity within a human-modified landscape.

In general, studies of the response of Neotropical bats to land conversion (Estrada *et al.*, 1993; Cosson *et al.*, 1999; Medellín *et al.*, 2000; Bernard & Fenton, 2002; Faria & Baumgarten, 2007; Willig *et al.*, 2007) have compared sites that differed in the degree of disturbance (e.g. forest vs. logged forest). Although this approach has been instrumental in understanding the influences of human-modified systems on bat assemblages, it ignores the landscape context of sites that has critical implications for community assembly or disassembly (Gorresen & Willig, 2004; Klingbeil & Willig, 2009, 2010). Anthropogenic modifications of landscapes are spatially complex, as natural land cover is fragmented and replaced by a variety of land cover types designed to serve human needs (i.e. landscape matrix). Furthermore, matrix environments are not completely inhospitable to biota, and the degree of permeability and resource availability in matrix environments are species specific (Kupfer *et al.*, 2006; Perfecto & Vandermeer, 2008). Accordingly, land conversion affects the quantity and diversity of available resources in the landscape, as well as the connectivity among resource patches.

In general, three processes associated with landscape modification affect patterns of biodiversity: loss of native vegetation, fragmentation per se (i.e. breaking apart of native vegetation) and matrix permeability or utility (Tschardt *et al.*, 2012). Loss of native vegetation and matrix effects are associated with the presence and proportion of natural and anthropogenically modified land cover types, independent of their spatial arrangement (i.e. landscape composition), whereas fragmentation per se affects connectivity and spatial arrangement (i.e. landscape configuration) of resource patches (Bennett *et al.*, 2006). Comprehensive understanding of the effects of native vegetation loss, fragmentation per se and the matrix on various aspects of assemblages requires explicit consideration of compositional and configurational characteristics of landscapes.

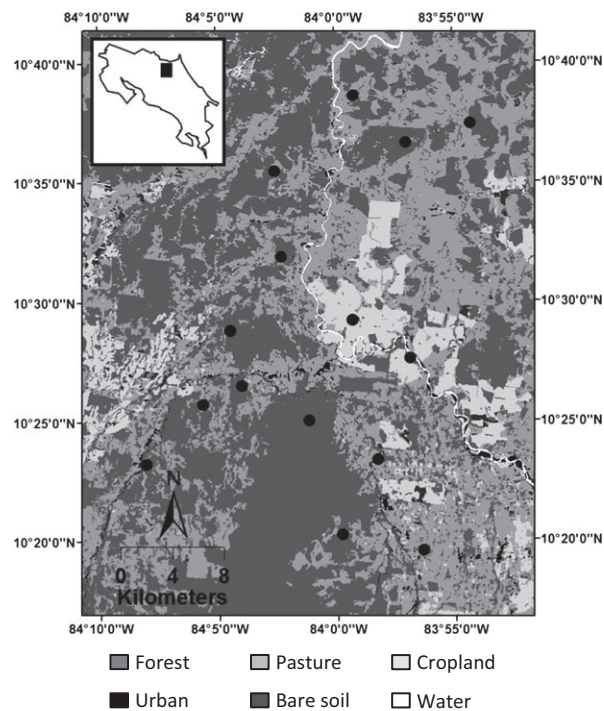
We quantified taxonomic, functional and phylogenetic dimensions of bat biodiversity within a human-modified landscape. Our objective was to identify compositional and configurational characteristics of the landscape that best accounted for variation in each dimension of biodiversity. We expected that TD would be most affected by landscape characteristics that reflect the amount of forest (composition), based on the assumption that species richness and total abundance are correlated positively with resource quantity. Conversely, we predicted that FD and PD would be

most affected by compositional and configurational characteristics, based on the assumption that diversity of species characteristics is correlated positively with diversity of resources, and that functional characteristics are conserved phylogenetically.

## METHODS

### Study area and sites

Research was conducted in a human-modified landscape in the Caribbean lowlands of northeastern Costa Rica (Fig. 1). The 160,000 hectare landscape encompasses fragments of wet tropical forest at various successional stages, a variety of agricultural plantations (e.g. banana and pineapple), cattle pastures and logged areas. The climate is warm and moist, with relatively constant temperatures throughout the year (mean daily temperature: 31.0 °C; range: 30.2–31.9 °C) and appreciable rainfall every month (mean annual precipitation: 4374.6 mm; range: 2809.3–6164.0 mm; Organization for Tropical Studies, 2012). In general, a drier period occurs from January until late April, with mean monthly rainfall of 223.7 mm, followed by a wet period from early May to December, with mean monthly rainfall of 435.0 mm. Because of changes in resource availability and resource requirements of bats between seasons (Frankie *et al.*, 1974; Kurta *et al.*, 1989; Tschapka, 2004), analyses were conducted separately for the dry and wet seasons.



**Figure 1** Location of the 15 sampling sites (black dots) within the study landscape represented by a 2011 land cover map. Location of the study landscape (black rectangle) in Costa Rica is displayed in the upper-left corner of the land cover map.

Fifteen circular sites (5 km radius) were established across the landscape so that centres were positioned within forest patches and were separated by at least 3.5 km (Fig. 1). These sites represent a gradient of forest loss and fragmentation that encompasses the current range in composition and configuration of land cover in the study area (see Table S1 in Supporting Information). Site selection was not stratified or randomized because of limitations associated with gaining permission from land owners.

### Biological surveys and landscape structure

Bats were surveyed using ground-level mist nets during the dry season (January to April) and wet season (May to September) of 2010. Each site was surveyed four times each season. For each survey, 12 mist nets (12 m × 2.5 m) were opened for 6 h from dusk until midnight (mist nets were inspected every 30 min). Mist nets were deployed in trails and flyways in closed-canopy forest within 1 km of the centre of each site, and mist net configurations and locations differed among survey periods within seasons. Sampling was not conducted during the presence of a moon that was ≥ 90% full due to reduced bat activity associated with high lunar illumination (Morrison, 1978) or during severe weather because of health risks to bats from exposure to low temperatures associated with strong winds or rain. To identify recaptures within a sampling period, hair was trimmed on the back of each bat before release. The use of ground-level mist nets effectively samples species from the family Phyllostomidae (Kalko, 1997), but may under-represent other families (Kalko & Handley, 2001). Accordingly, analyses were limited to phyllostomids.

Landscape structure was quantified at each site using a land cover map that represented the landscape of 2011 (see Fagan *et al.*, 2013 for map construction). The original 13 cover types were reclassified into seven cover types: forest = mature forest, swamp forest, native reforestation and exotic tree plantations; cropland = banana, sugarcane, heart of palm and pineapple; and pasture, bare soil, urban, water and masked area were retained as unique categories (see Figure S1 for the contributions of the original cover types to the total forest or cropland cover types). Because only 0.6% of the pixel values of the land cover surrounding the sites were designated as masked areas (i.e. areas obscured by cloud or Landsat 7 line errors), masked area was manually changed to other pixel values using the area fill tool in ERDAS IMAGINE 2013. Masked area pixels were changed to the pixel value within which they were embedded or to pixel values based on a 2005 land cover map of the study area (Fagan *et al.*, 2013). In the reclassified land cover map, the six cover types occupied the following proportions of the study area: forest, 0.502; pasture, 0.376; cropland, 0.096; bare soil, 0.015; water, 0.006; and urban, 0.005.

Five compositional (i.e. percentage forest, percentage pasture, mean forest patch size, forest patch density and Simpson's diversity of cover types; see Table S2) and four

configurational (i.e. mean forest proximity, mean forest nearest neighbour, mean forest patch shape and forest edge density; see Table S2) indices were quantified using FRAGSTATS version 4 (McGarigal *et al.*, 2012). Composition refers to the proportions of different types of land cover within a site, whereas configuration specifies the geometric arrangement of land cover within a site. All indices were quantified using forest as the focal land cover type, except for percentage pasture and Simpson's diversity of cover types. Because spatial patterns are scale dependent, and the scale at which bats use and respond to the environment is species specific (Gorresen *et al.*, 2005; Klingbeil & Willig, 2009), all landscape characteristics were quantified at each of three spatial scales (circles of 1, 3 or 5 km radius) to account for interspecific differences in bat home range size and behaviour.

### Quantification of dimensions of biodiversity

#### Data

To evaluate TD, bat species abundances were obtained at each site separately for each season (recaptures were not included in abundance totals; site-by-species abundance matrices are available at <http://biofrag.wordpress.com/>). We followed the taxonomy of Simmons (2005) for classifying the 34 phyllostomid species recorded from the Caribbean lowlands of northeastern Costa Rica.

FD was estimated using species abundances and two types of data: categorical (binary) and mensural attributes (Table 1). For each data type, a suite of functional attributes were used to describe particular niche axes (i.e. functional components). Categorical components were associated with (1) diet, (2) foraging location, (3) foraging strategy and (4) roost type. Mensural components were associated with (1) body size, (2) masticatory mode (i.e. skull characteristics) and (3) aerodynamic mode (i.e. wing characteristics). These mensural components also reflect physiological constraints, diet and foraging behaviour, respectively. For each categorical attribute, a species received a '1' if it exhibited the characteristic or a '0' if it did not exhibit the characteristic. To best portray the variety of functions performed by a species, all attributes related to a particular functional component (e.g. all diet attributes) were considered together in defining the species' functions. For each mensural attribute, an average value was obtained for each species based on measurements of multiple male and female adults.

Information for all functional attributes was derived from the literature and restricted to records from Central America when possible (see Table S3). Measurements of size attributes were augmented by field measurements from the study area. Missing mensural data were estimated using linear regression, with mass as the independent variable and attribute values of other species from the same subfamily. Missing categorical data were replaced by values from congeners. Only 4.1% of species traits were estimated or replaced. Because the environmental gradient may affect particular functional

**Table 1** Functional attributes that reflect niche axes (functional components) were used to estimate functional diversity of bat assemblages from the Caribbean lowlands of Costa Rica. Mensural attributes were measured as described in sources (see Table S3).

Type of data	Functional component	Attribute	Trait value		
Categorical	Diet	Fruit or plant	0, 1		
		Nectar or pollen	0, 1		
		Invertebrates	0, 1		
		Vertebrates	0, 1		
		Blood	0, 1		
	Foraging location	Canopy	0, 1		
		Subcanopy	0, 1		
		Understory	0, 1		
		Gleaning	0, 1		
	Foraging strategy	Hover	0, 1		
		Pounce	0, 1		
		Foliage	0, 1		
	Roost type	Bark or roots	0, 1		
		Tree hole or termite nest	0, 1		
		Man-made structures	0, 1		
		Culvert or under large rocks	0, 1		
		Cave, tunnels, mines or sewers	0, 1		
		Mensural	Size	Mass	Mean (g)
				Forearm length	Mean (mm)
	Skull		Greatest length of skull	Mean (mm)	
Condylbasal length			Mean (mm)		
Length of maxillary toothrow			Mean (mm)		
Breadth across upper molars			Mean (mm)		
Width across post-orbital constriction			Mean (mm)		
Breadth of braincase			Mean (mm)		
Wing			Wing loading	Mean (mm)	
			Aspect ratio	Mean (mm)	

components differently, integration of ecological attributes into a single multivariate measure may obscure important patterns (Spasojevic & Suding, 2012; Cisneros *et al.*, 2014). Accordingly, mean functional differences among species were estimated for each functional component separately (Table 1), as well as for all functional components combined (each component was weighted equally despite having unequal number of attributes).

We evaluated PD based on species abundances and branch lengths from a species-level supertree of bats (Jones *et al.*, 2005). For each species that was missing from the supertree (i.e. five of the 34 species), the closest congener present in the supertree that was not present in the study area was substituted. Although a number of phylogenetic trees are available for bats, the supertree developed by Jones *et al.*



(2005) represents the most complete and accurate tree. Moreover, assessment of PD is robust with respect to variation in the resolution of nodes near terminal branches of the tree (Webb, 2000) and variation among trees would not likely affect conclusions in this study.

#### Biodiversity indices

At each site, TD was quantified using Simpson's diversity index (Simpson, 1949), and FD and PD were quantified using Rao's quadratic entropy (Botta-Dukát, 2005). These metrics facilitate comparison among the three dimensions because Rao's Q is an extended form of Simpson's index that includes information on species dissimilarities (Simpson's index considers all species to be equally distinct). Rao's Q is the sum of the distances (functional or phylogenetic) between all possible pairs of species, weighted by the product of their relative abundances, and conceptually is the abundance-weighted average difference among species (Weihner, 2011). Functional and phylogenetic distances between species were obtained from pairwise dissimilarity matrices for each of the seven functional components separately, for all of the functional components combined, and for the phylogenetic approach. Functional pairwise dissimilarity matrices were calculated using the Gower metric from the R package 'clusters' (Maechler *et al.*, 2012). The Gower metric can quantify dissimilarities when considering categorical and mensural attributes at the same time (Botta-Dukát, 2005). The phylogenetic pairwise dissimilarity matrix was calculated via the 'cophenetic' function of the R package 'ape' (Paradis *et al.*, 2004).

To promote meaningful comparisons among dimensions, each metric was transformed into its effective number of species (hereafter numbers equivalent). The numbers equivalent is the number of maximally dissimilar species with equal abundances that is required to produce the empirical value of a metric (Jost, 2006; Villéger *et al.*, 2012). This transformation facilitates intuitive interpretation of differences among assemblages because indices are expressed in the same units (Jost, 2006). R functions developed by de Bello *et al.* (2010) quantified Simpson's index and Rao's Q as numbers equivalent.

#### Quantitative analyses

Hierarchical partitioning (Chevan & Sutherland, 1991) was employed to identify the landscape characteristics that best accounted for variation in each of the three dimensions of biodiversity at each of six combinations of season (dry and wet) and spatial scale (1, 3 or 5 km radius). Statistical significance of the independent contribution of each explanatory variable was determined using a randomization approach with 1000 iterations and an  $\alpha$ -level of 0.05 (Mac Nally, 2002). Hierarchical partitioning and associated randomization tests were executed using the R package 'hier.part' (Mac Nally & Walsh, 2004).

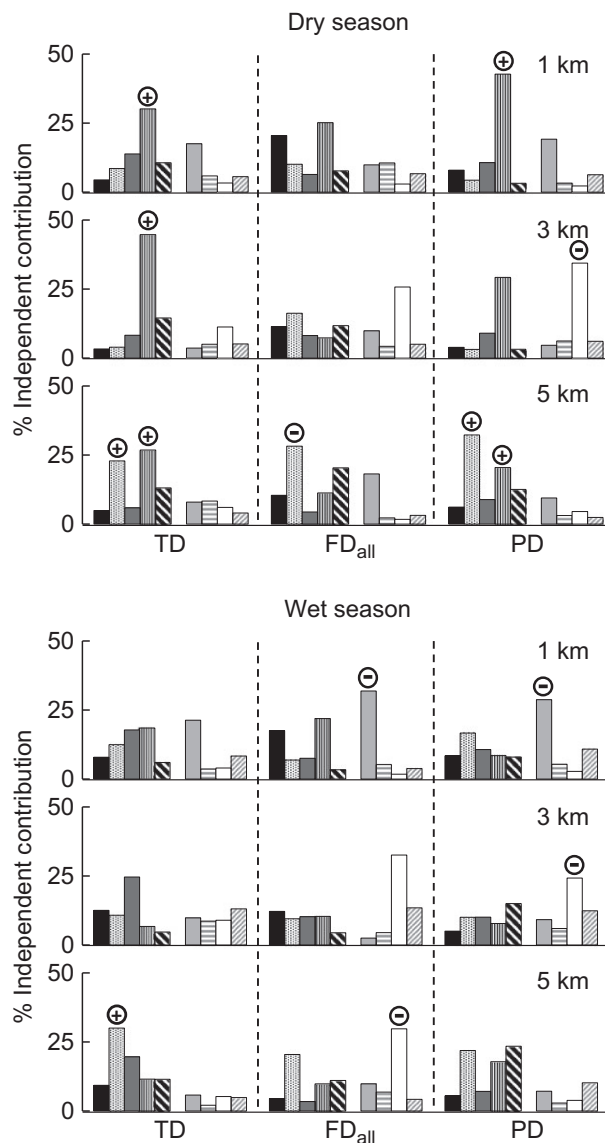
#### Phylogenetic signal

To facilitate ecological interpretation of phylogenetic patterns, we used the *D*-statistic (Fritz & Purvis, 2010) and Pagel's  $\lambda$  (Pagel, 1999; Freckleton *et al.*, 2002) to measure the strength of phylogenetic signals (i.e. statistical dependence among species' trait values due to phylogenetic affinities; Revell *et al.*, 2008) of categorical attributes and mensural attributes, respectively. These approaches evaluate if traits on a phylogeny are overdispersed, independent, consistent with a model of Brownian motion or conserved. If empirical patterns are consistent with a model of Brownian motion or conserved, traits reflect a phylogenetic signal and phylogenetic patterns can be interpreted with regard to those traits. Tests of phylogenetic signal were calculated with the R package 'caper' (Orme, 2012).

#### RESULTS

Based on 51,840 mist-net-metre-hours per season, we captured 1293 and 1158 phyllostomid bats during the dry and wet seasons, respectively. This assemblage comprised 30 species during the dry season and 33 species during the wet season. Most species were caught in both seasons. One species (*Lonchorhina aurita*) was only caught during the dry season and four species (*Chiroderma villosum*, *Lamproncycteris brachyotis*, *Lichonycteris obscura*, and *Trachops cirrhosus*) were only caught during the wet season.

Relationships between landscape characteristics and dimensions of biodiversity were season and dimension specific; nevertheless, significant landscape relationships with each dimension occurred at all three spatial scales. During the dry season, variation in TD and PD across sites was best accounted for by proportion of pasture and mean forest patch size, such that each dimension increased with increasing proportions of pasture and forest patch size (Fig. 2). Variation in FD based on all functional components (FD<sub>all</sub>) was best accounted for by mean forest patch size during the dry season; however, FD<sub>all</sub> decreased with increasing forest patch size (Fig. 2). Decomposition of FD into separate functional components revealed considerable heterogeneity of landscape relationships with different ecological characteristics of assemblages during the dry season (Table 2). In general, diversity of foraging location and foraging strategy attributes was associated negatively with forest cover and forest patch size and was associated positively with landscape heterogeneity (measured by Simpson's diversity of land cover types). Diversity of wing morphology was associated positively with the amount of pasture. Interpretation of the associations between landscape characteristics and the aforementioned functional components is similar because as pasture increases, forest decreases, and even representation of the two cover types results in greater landscape heterogeneity. In addition, decreasing distances between forest patches was associated with increasing diet diversity.



**Figure 2** The percentage independent contribution of each landscape characteristic derived by hierarchical partitioning on each dimension of biodiversity (taxonomic, TD; functional, FD<sub>all</sub>; phylogenetic, PD) for each combination of season and scale. Functional diversity is based on all attributes, with each functional component weighted equally. Phylogenetic diversity is based on a supertree (Jones *et al.*, 2005). For each combination, compositional characteristics are grouped to the left (percentage forest, ■; mean forest patch size, □; forest patch density, ▨; percentage pasture, ▨; Simpson's diversity of land cover, ▨) and configurational characteristics are grouped to the right (mean forest proximity, □; mean forest nearest neighbour, ▨; mean forest patch shape, □; forest edge density, ▨). Significant results ( $P \leq 0.05$ ) are indicated by a circle with a positive or negative sign that indicates the direction of the correlation between the dimension of biodiversity and the landscape characteristic.

During the wet season, variation in TD was best accounted for by mean forest patch size, whereas FD<sub>all</sub> and PD increased as proximity between forest patches and shape

irregularity of forest patches decreased (i.e. increasing compactness of patches; Fig. 2). Landscape relationships with particular functional components were different from those on FD<sub>all</sub>. Diet diversity was associated positively with proximity among forest patches; foraging strategy diversity had a negative association with forest cover and a positive association with land cover diversity; and skull and wing attributes were more diverse in areas with greater proportions of pasture (Table 2).

Phylogenetic signals were significant for all categorical attributes (see Table S4). However, the signal strength was greater in attributes associated with diet, foraging strategy and roost type. In contrast, phylogenetic signal was only significant for 3 of 10 mensural attributes (see Table S5).

## DISCUSSION

### Dimension-specific landscape relationships

Unique combinations of landscape characteristics were associated with spatial variation in each dimension of biodiversity. Regardless of season, variation in TD was best accounted for by compositional characteristics, whereas variation in FD and PD were best accounted for by a combination of compositional and configurational characteristics (Fig. 2 and Table 2). This demonstrates the complex ways in which anthropogenic disturbance can affect different dimensions of biodiversity.

The positive relationships between TD and forest patch size or proportion of pasture for bats of Costa Rica were not consistent with landscape relationships observed in other Neotropical localities (Gorresen & Willig, 2004; Paraguay; Meyer & Kalko, 2008; Panama; Klingbeil & Willig, 2009, 2010; Peru; Avila-Cabadilla *et al.*, 2012; Mexico). Although positive associations between native vegetation cover and different aspects of TD were consistently observed at each of the aforementioned Neotropical localities, the relative importance of configurational characteristics (e.g. distance between forest patches, forest patch shape) and the direction of their relationships with TD were inconsistent. These contrasting results may arise because of differences in the extent of landscape modification (Pardini *et al.*, 2010), differences in the permeability and utility of the matrix (i.e. non-forested areas) to bats (Harvey *et al.*, 2006; Harvey & González Villalobos, 2007), or differences in regional species pools. Responses to landscape configuration are complex. Configurational characteristics affect bat TD at Neotropical localities with less modification (Klingbeil & Willig, 2009, 2010) and with more modification (Meyer & Kalko, 2008) than that observed in the Caribbean lowlands of Costa Rica, indicating that the extent of landscape modification does not fully explain differences in relationships between landscape characteristics and TD. Landscape matrices differed greatly among these Neotropical localities, from water to agriculture and pasture. The importance of configurational characteristics of forest may be a consequence of their correlation with other

**Table 2** Landscape characteristics with significant ( $P < 0.05$ ) independent contributions on functional diversity based on separate consideration of each functional component are displayed for each combination of season and scale.

	Dry season			Wet season		
	1 km	3 km	5 km	1 km	3 km	5 km
Diet		– <i>Nearest</i>			+ <i>Proximity</i>	+ <i>Proximity</i>
Foraging location	– <b>Forest</b>		– <b>Forest</b>			
Foraging strategy	– <b>Forest</b>		– <b>Size</b> + <b>Diversity</b>	– <b>Forest</b>	+ <b>Diversity</b>	+ <b>Diversity</b>
Roost type						
Size						
Skull morphology				+ <b>Pasture</b>		
Wing morphology	+ <b>Pasture</b>	+ <b>Pasture</b>	+ <b>Pasture</b>	+ <b>Pasture</b>	+ <b>Pasture</b>	+ <b>Pasture</b>

Blank areas indicate non-significant landscape contributions. The direction of correlation between the landscape characteristic and functional diversity is shown by a ‘+’ if positive and a ‘–’ if negative. Codes for landscape characteristics are forest, percent forest; size, mean forest patch size; pasture, percent pasture; diversity, Simpson’s diversity; proximity, mean forest proximity; nearest, mean forest nearest neighbour. Compositional landscape characteristics are in boldface and configurational characteristics are in italics.

characteristics of the matrix. Explicit assessment of the influences of the matrix on TD is needed to elucidate these landscape relationships in future studies.

More importantly, it is critical to recognize that the number and abundance of species (TD) is an outcome of community assembly processes (Mayfield *et al.*, 2010) that operate on species characteristics. Because regional species pools differ among the Neotropical localities, the proportions of different functional and phylogenetic traits of the regional pool likely differ. Differences in regional functional and phylogenetic composition can result in different TD due to ecological filters that promote species with particular traits. Consequently, better understanding of the association between landscape structure and TD may be realized through assessment of the effects of human-modified landscapes on functional and phylogenetic aspects of assemblages.

The identification of landscape relationships with the structure of assemblages was dependent on particular functional components (Table 2). Variation in diversity of body size and roost attributes was not associated with landscape structure, suggesting that community assembly or disassembly after landscape modification is not moulded primarily by physiological constraints or roost availability. Conversely, landscape structure affected variation in diversity of diet and foraging behaviour attributes. Diet diversity increased with increasing proximity between forest patches. Greater diet diversity was driven by more even abundances of species with different diets at sites with forest patches in close proximity (Laura M. Cisneros (L.C.)). Sites with highly separated forest patches were primarily dominated by frugivores (i.e. species that are often good dispersers). This suggests that more individuals of species from multiple feeding guilds may be able to cross the matrix to use resources from multiple forest patches if those patches are in close proximity.

Decreasing forest cover and increasing diversity of land cover were associated with increasing FD based on resource

acquisition attributes, and increasing proportion of pasture was associated with increasing FD based on wing or skull attributes. Consequently, areas characterized with even amounts of forest and pasture (areas with high land cover diversity) harboured a diversity of attributes associated with foraging behaviour (i.e. foraging location/strategy and wing attributes) as well as diet (i.e. skull attributes). These diverse landscapes comprise a variety of habitat types in addition to forest and pasture, such as regenerating forests and edge environments (i.e. environments with higher production and persistence of fruits than in the interior forest; Levey, 1988). Moreover, riparian forests and live fences (fences made of live woody species) thread throughout pastures (Harvey *et al.*, 2011), and support moderate species richness and abundance from a number of feeding guilds (Harvey *et al.*, 2006). This suggests that a diverse set of species with regard to resource acquisition characteristics was able to use these diverse landscapes due to of a greater variety of resources associated with a diversity of habitat types and habitat physiognomies.

Variation among sites in  $FD_{all}$  reflects the interactions of multiple landscape characteristics. Indeed, significant independent contributions of landscape characteristics on  $FD_{all}$  were different from those on individual components (Fig. 2 and Table 2). Although identifying landscape relationships using  $FD_{all}$  obscured landscape relationships on particular components, this approach may be more practical for landscape management because it identifies a few landscape characteristics that promote a diversity of characteristics along multiple niche axes. For bats in the Caribbean lowlands, landscapes associated with relatively small forest patches or landscapes associated with more compact-shaped forest patches with greater distance between patches harboured high  $FD_{all}$  values. In essence, heterogeneous landscapes harboured high  $FD_{all}$  values. Similarly, heterogeneous landscapes were associated with high diversity with regard to many of the individual functional components.

Phylogenetic relatedness is often used as a proxy for functional similarity (Webb, 2000; Swenson, 2013). However, the effectiveness of PD as a surrogate for  $FD_{all}$  is dependent on the strength of the phylogenetic signal exhibited by functional attributes. Not all functional attributes exhibited a phylogenetic signal (see Tables S4 and S5). Furthermore, PD may represent differences in attributes that were not measured in this study. As a result, PD was not consistently a good proxy of  $FD_{all}$  (or TD) because variation in PD was affected by landscape characteristics that influenced TD during the dry season and was affected by landscape characteristics that influenced  $FD_{all}$  during the wet season (Fig. 2). Because community assembly processes operate on ecological characteristics, responses of species to environmental variation may be best captured by functional attributes that were measured (FD) or by characteristics that were not measured (PD). Accordingly, consideration of all three dimensions together can provide a general idea of factors affecting biodiversity, and we use this approach in the following section.

### Season-specific landscape relationships

Influences of landscape characteristics on multiple dimensions of biodiversity were season specific. During the dry season, diversity for each dimension was greatest in areas with intermediate amounts of forest and pasture (Fig. 2). During the wet season, diversity for each dimension was greatest in areas with forest patches that were large and compact in shape (e.g. square forest patches; Fig. 2).

Seasonal difference in landscape relationships may occur because of changes in resource requirements of bats associated with reproductive phenology or with changes in resource availability. In the Caribbean lowlands, bat species from frugivorous, nectarivorous and gleaning animalivorous guilds exhibit a peak in pregnancy and lactation during the mid- to late dry season (Durant *et al.*, 2013). Additionally, bat species that primarily consume plant material evince a second peak in pregnancy and lactation during the mid-wet season (Durant *et al.*, 2013). Because reproduction in bats may be more energetically demanding than in other terrestrial mammals (Kurta *et al.*, 1989), it is critical that such activities coincide with periods of high food productivity and reliability or that bats change their behaviour to meet daily caloric requirements. Flowering by plants used by bats occurs from the mid-wet season to mid-dry season in the Caribbean lowlands (Tschapka, 2004). In addition, the prime fruiting period occurs during the middle of the wet season (Frankie *et al.*, 1974). Consequently, the mid- to late dry season offers lesser quantities and varieties of food resources for bats that consume plant material.

To satisfy energetic demands during the dry season, frugivorous and nectarivorous species expand their diet to comprise a greater number of fruit species and greater quantities of arthropods than they do during the wet season (Lopez & Vaughan, 2007). To acquire a diversity of resources, bats may use a greater variety of land cover during times of low

resource availability, such as the dry season in Costa Rica. Thus, landscapes that comprise a diversity of environments (e.g. areas with even amounts of forest and pasture, which are associated with riparian areas, live fences, and edge environment) have greater bat diversity during the dry season than the wet season. In contrast, resources are more plentiful during the wet season and core forest may be sufficiently productive to maintain high abundances of species with different ecological characteristics regardless of energy demands associated with reproduction.

### Summary and recommendations

Decomposition of biodiversity into different dimensions and functional components facilitates identification of the aspects of assemblages that are most affected by forest conversion and fragmentation. For bats, attributes associated with diet and foraging behaviour, as opposed to other functional characteristics, were most associated by variation in landscape structure. Areas with intermediate amounts of forest and pasture, and shorter distances between forest patches were associated a greater diversity of functional attributes. Furthermore, areas with large compact forest patches harboured greater diversity from taxonomic, functional and phylogenetic perspectives during the wet season. To increase the likelihood of maintaining ecosystem function within a human-modified landscape, it is critical that areas characterized with even amounts of forest and pasture are maintained adjacent to large, compact forest patches (e.g. reserves) so that high biodiversity is maintained throughout the region and throughout the year.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1** Mean, standard deviation, and range of landscape characteristics quantified at the 15 sampling sites.

**Table S2** Indices that quantified landscape structure at sampling sites.

**Table S3** Sources of information for functional attributes of bat species.

**Table S4** Phylogenetic signal present in categorical functional attributes of the 34 bat species.

**Table S5** Phylogenetic signal present in mensural functional attributes of the 34 bat species.

**Figure S1** Percentage contributions of the original cover types to the total forest and cropland cover types.

## BIOSKETCHES

**Laura M. Cisneros, PhD** is faculty member in the Department of Natural Resources and the Environment. She is interested in the consequences of human activities on ecological and evolutionary components of mammalian assemblages. Additionally, she is interested in linking anthropogenic effects on assemblages to ecosystem services provided by species.

**Matthew E. Fagan, PhD** is a NASA postdoctoral fellow at Goddard Space Flight Center. His research examines the effects of agricultural expansion on forests using ecological fieldwork and remote sensing. His PhD research evaluated the impact of landscape conservation policies on deforestation, reforestation, and habitat connectivity in north-eastern Costa Rica.

**Michael R. Willig, PhD** is a professor of ecology and evolutionary biology. His research interests include population, community and metacommunity dynamics in response to spatial and environmental gradients caused by anthropogenic (e.g. land use change) or natural disturbances (e.g. hurricanes). In addition, his work examines scale-dependence and assumes long-term perspectives.

Author contributions: L. Cisneros and M. Willig designed the field experiment and analysis of biological data, as well as collaborated in the writing of the manuscript. In addition, L. Cisneros conducted the field work and executed statistical analyses. M. Fagan analyzed remotely sensed data to derive land cover maps that informed landscape metrics, and reviewed the manuscript for accuracy, format, and style.

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