Season-specific and guild-specific effects of anthropogenic landscape modification on metacommunity structure of tropical bats

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Summary

1. Fragmentation *per se* due to human land conversion is a landscape-scale phenomenon. Accordingly, assessment of distributional patterns across a suite of potentially connected communities (i.e. metacommunity structure) is an appropriate approach for understanding the effects of landscape modification and complements the plethora of fragmentation studies that have focused on local community structure. To date, metacommunity structure within human-modified landscapes has been assessed with regard to nestedness along species richness gradients. This is problematic because there is little support that species richness gradients are associated with the factors moulding species distributions. More importantly, many alternative patterns are possible, and different patterns may manifest during different seasons and for different guilds because of variation in resource availability and resource requirements of taxa.

2. We determined the best-fit metacommunity structure of a phyllostomid bat assemblage, frugivore ensemble, and gleaning animalivore ensemble within a human-modified landscape in the Caribbean lowlands of Costa Rica during the dry and wet seasons to elucidate important structuring mechanisms. Furthermore, we identified the landscape characteristics associated with the latent gradient underlying metacommunity structure.

3. We discriminated among multiple metacommunity structures by assessing coherence, range turnover, and boundary clumping of an ordinated site-by-species matrix. We identified the landscape characteristics associated with the latent gradient underlying metacommunity structure via hierarchical partitioning.

4. Metacommunity structure was never nested nor structured along a richness gradient.

5. The phyllostomid assemblage and frugivore ensemble exhibited Gleasonian structure (range turnover along a common gradient) during the dry season and Clementsian structure (range turnover and shared boundaries along a common gradient) during the wet season. Distance between forest patches and forest edge density structured the phyllostomid metacommunity during the dry and wet seasons, respectively. Proportion of pasture and forest patch density structured the frugivore metacommunity during the dry season.

6. Gleaning animalivores exhibited chequerboard structure (mutually exclusive species pairs) during the dry season and random structure during the wet season.

7. Metacommunity structure was likely mediated by differential resource use or interspecific relationships. Furthermore, the interaction between landscape characteristics and seasonal variation in resources resulted in season-specific and guild-specific distributional patterns.

Key-words: Chiroptera, Costa Rica, forest loss, fragmentation, interspecific competition, niche trade-offs, range turnover, species distribution, temporal dynamics, tropical wet forest

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Introduction

Human-modified landscapes occupy over 77% of the terrestrial biosphere (Ellis *et al.* 2010). These landscapes are increasing in extent in the tropics, where forest loss has continued to increase over the past decade (Hansen *et al.* 2013). In addition, the proportion and arrangement of land cover types (e.g. agricultural land, pasture, regenerating forest) in tropical landscapes frequently change due to increasing and shifting demands for natural resources, developing infrastructure and changing land-use policy (Mayaux *et al.* 2005; Fagan *et al.* 2013). Responses of biota to these spatially complex and temporally dynamic landscapes depend on the connectivity among patches of native vegetation or on the permeability and resource characteristics of anthropogenically produced land cover. Loss of connectivity among resource patches will affect not only local community structure, but also large-scale patterns and dynamics of interacting populations and communities.

MESOSCALE ECOLOGY

Most investigations of the effects of human-modified landscapes on species assembly or disassembly have focused on local variation in species richness, diversity or composition (Fahrig 2003; Sodhi & Ehrlich 2010). By focusing on the local scale, effects of processes that operate at the landscape scale (e.g. environmental heterogeneity, landscape connectivity, dispersal limitation; Leibold 2011) as well as cross-scale interactions (Peters *et al.* 2004) are ignored. Assessment of metacommunity structure (i.e. distributional patterns across a suite of sites that are potentially connected through dispersal; Wilson 1992; Leibold & Mikkelson 2002) is an appropriate approach for understanding the effects of landscape modification on ecological communities that complement local-scale approaches at the community level.

Many models of metacommunity structure (chequerboard, Diamond 1975; nested, Patterson & Atmar 1986; Clementsian, Clements 1916; Gleasonian, Gleason 1926; evenly spaced, Tilman 1982) have been recognized (Leibold & Mikkelson 2002). Originally, these distributional patterns were individually evaluated to explore the operation of particular structuring mechanisms. For example, mutually exclusive species pairs that respond independently to a gradient with regard to other such species pairs (i.e. chequerboard pattern) suggest that interspecific competition may strongly structure the metacommunity. Nested structures in which species with narrow environmental ranges are embedded within the ranges of more broadly distributed species may arise because of species-specific differences in dispersal ability, extinction risk or habitat specialization (Wright *et al.* 1998). Similarly, structures that are characterized by replacement of species distributions with other species distributions along an environmental gradient (e.g. Gleasonian, Clementsian, evenly spaced distributions) may arise due to differential performances in different environments or niche trade-offs.

FOREST LOSS AND FRAGMENTATION GRADIENT

The effects of forest loss and fragmentation on metacommunity structure have been assessed in terms of nestedness (Cutler 1991; Atmar & Patterson 1993; Fischer & Lindenmayer 2005; Meyer & Kalko 2008; Hill *et al.* 2011; Menezes & Fernandez 2013) along gradients of species richness. Although nested structures are commonly detected in human-modified landscapes (Whittaker 1992; Louzada *et al.* 2010; Hill *et al.* 2011), two constraints of common nestedness approaches limit interpretations. First, most approaches limit comparisons to nested structure vs. non-nested structure. This is problematic because empirical structure is assigned to one of two categories when a number of alternative patterns are possible. Secondly, most approaches evaluate structure along an environmental gradient that is identified *a priori*. Most often, species richness is assumed to be the gradient of interest (Atmar & Patterson 1993), although a few studies have explored other environmental gradients, such as forest patch size or forest patch isolation (Mac Nally, Horrocks & Bennett 2002; Louzada *et al.* 2010). Richness-based gradients are linked to island biogeographic theory and the species–area relationship, in which larger islands (or forest patches) support more species than do smaller islands or patches. Unlike the situation for oceanic island systems, land cover surrounding forest patches (i.e. the matrix) in human-modified landscapes is not completely inhospitable to biota, and the degree of permeability and resource availability in such matrix environments are species specific (Kupfer, Malanson & Franklin 2006; Perfecto & Vandermeer 2008). Consequently, forest patch size and isolation may not be the only factors affecting metacommunity structure, as other landscape characteristics (e.g. mix of land cover types surrounding forest) affect resource availability and patch connectivity. For many taxa, especially those in tropical environments, landscape characteristics that most affect species distributions are poorly understood; consequently, *a priori* decisions about the identity of dominant gradients may be poorly supported by empirical or theoretical evidence.

The analytical methods of Leibold & Mikkelson (2002) and the conceptual framework of Presley, Higgins & Willig (2010) provide a means to simultaneously discriminate among a number of metacommunity structures along a latent environmental gradient. Moreover, this approach does not require *a priori* identification of salient environmental factors to which constituent species respond. Although a number of studies have employed this approach, most have been conducted at continental or regional scales or along elevational gradients (Presley & Willig 2010; Keith *et al.* 2011; Willig *et al.* 2011; López-González *et al.* 2012; Presley *et al.* 2012). To date, no study has distinguished among multiple alternative metacommunity structures in a human-modified landscape.

STUDY TAXON

Bats are useful for assessing the effects of human-modified landscapes on ecological characteristics of assemblages because they are diverse from taxonomic and functional perspectives (Patterson, Willig & Stevens 2003). In the Neotropics, bats are generally the most species-rich and locally abundant mammalian group, comprise species from a variety of feeding guilds (e.g. frugivores, gleaning animalivores) and vary greatly in dispersal abilities. More-over, bats provide important ecological services, such as seed dispersal, pollination and regulation of insect populations (Kunz *et al.* 2011).

The effects of forest loss and fragmentation on local community structure of bats are known to be season specific and guild specific (Klingbeil & Willig 2009, 2010; García-Morales, Badano & Moreno 2013). Assessment of these effects has provided critical insights on structuring mechanisms associated with temporal variation in resource availability and resource requirements of taxa that would have been obscured otherwise. Nevertheless, assessments of mesoscale structure of bats within human-modified landscapes have been primarily based on data that represent combined guilds or seasons, and have been limited to considerations of only nestedness (Meyer & Kalko 2008; Struebig *et al.* 2008). These prior assessments detected nested structure for bats along species richness gradients; however, it remains to be tested whether nestedness is the best-fit model for bats when multiple structures are considered simultaneously, as well as whether the best-fit metacommunity structure varies between seasons and among guilds.

The primary objective of this study was to evaluate the effects of human-modified landscapes on metacommunity structure of an assemblage of Neotropical bats (family Phyllostomidae) and of two of its constituent ensembles (frugivores and gleaning animalivores) during different seasons. The secondary objective of this study was to test whether nestedness is the best-fit model of bat metacommunities within a human-modified landscape when considering multiple alternative patterns.

Materials and methods

STUDY AREA AND SITES

Research was conducted in the Caribbean lowlands of north-eastern Costa Rica (Fig. 1). The 160 000 hectare landscape
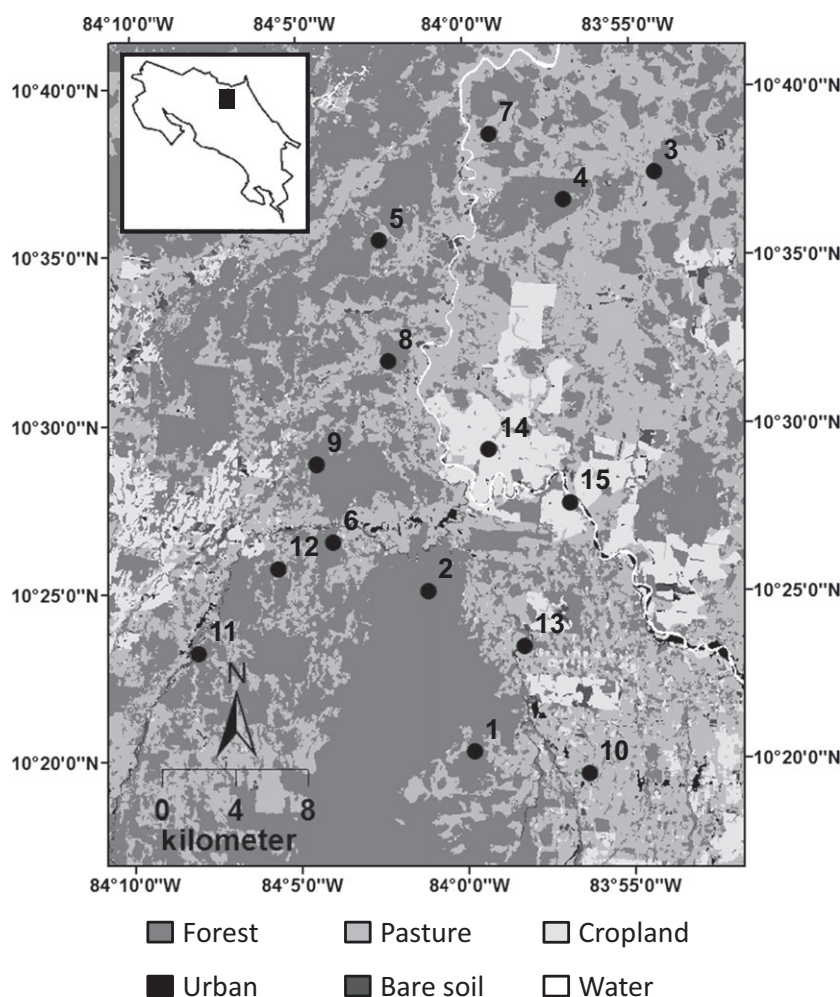

Fig. 1. Location of the 15 sampling sites (black dots) within the study landscape represented by a 2011 land cover map. Location of the study landscape (black rectangle) in Costa Rica is displayed in the upper-left corner of the land cover map. Numerical site codes indicate the placement of sites along a landscape modification gradient based on Simpson's diversity index of land cover quantified at the 5 km focal scale (Fig. S1, Supporting Information).

encompasses fragments of wet tropical forest at various successional stages (e.g. old-growth and secondary forests), a variety of agricultural plantations (e.g. heart of palm, 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. Nevertheless, the dry and wet seasons during the year of this study (2010) were less distinct (i.e. mean monthly rainfall was 353·8 mm in the dry season and 431·4 mm in the wet season).

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 (Table S1, 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. 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, unaccompanied by other sampling methods, effectively samples species from the family Phyllostomidae (Kalko 1997), but may under-represent other families (Kalko & Handley 2001). Accordingly, analyses were limited to phyllostomids. The protocol for animal use of this research was approved by the IACUC at the University of Connecticut (IACUC number: A09-014).

Landscape structure was quantified at each site using a land cover map that represented the landscape of 2011 (Fagan *et al.* 2013). 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. 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 (Intergraph Corporation, Madison, AL, USA). 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).

Five compositional (i.e. per cent forest, per cent pasture, mean forest patch size, forest patch density and Simpson's diversity of cover types; Table S2, Supporting Information) and four configurational (i.e. mean forest proximity, mean forest nearest neighbour, mean forest patch shape and forest edge density; Table S2, Supporting Information) indices were quantified using FRAGSTATS version 4 (McGarigal, Cushman & Ene 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 per cent pasture and Simpson's diversity of cover types. Spatial patterns are scale-dependent, and the scale at which bats use and respond to the environment is species specific (Gorresen, Willig & Strauss 2005). Thus, all landscape characteristics were quantified at each of three spatial scales (circles of 1, 3 and 5 km radius) to account for interspecific differences in bat home range size and behaviour.
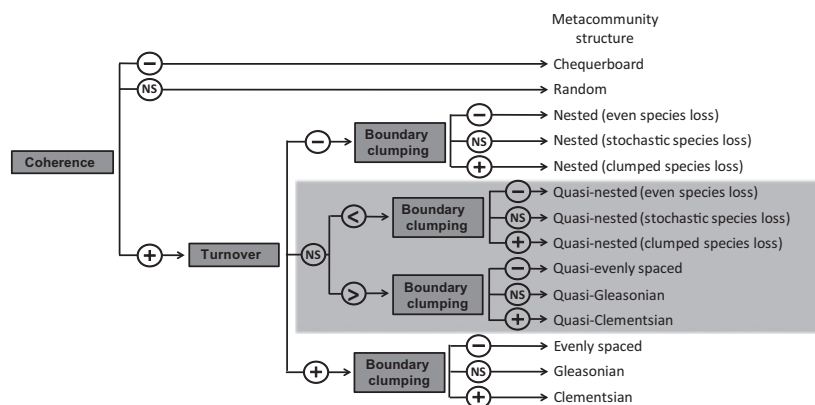
QUANTITATIVE ANALYSES

Metacommunity structure

Using the analytical methodologies of Leibold & Mikkelson (2002) and Presley, Higgins & Willig (2010), we evaluated metacommunity structure for the phyllostomid assemblage, the frugivore ensemble and the gleaning animalivore ensemble during the dry and wet seasons, separately. Structure was determined via assessment of coherence, species range turnover and boundary clumping of an ordinated site-by-species incidence matrix (Fig. 2). To simultaneously optimize the proximity of sites with similar species compositions and the proximity of species with similar environmental distributions, both empirical and null matrices were ordinated via reciprocal averaging. The arrangement of sites along the first axis of ordination represents a latent environmental gradient that moulds species distributions (Gauch 1982; Leibold & Mikkelson 2002). Consequently, no *a priori* assumptions are needed concerning the environmental factors to which species respond.

Coherence was evaluated by comparing the number of embedded absences in the ordinated empirical incidence matrix to a distribution of embedded absences derived from 1000 ordinated null matrices. We employed a null model that constrained species richness of each site to be equal to empirical species richness and allowed species occurrences to be equiprobable. This null model creates a biologically realistic null space for the analysis of coherence and has more desirable combination of Type I and Type II error properties than do alternative models (Gotelli 2000; Presley, Higgins & Willig 2010).

Non-significant coherence (i.e. the number of empirical embedded absences is not greater than or <97·5% of the null values) characterizes random distributions (Fig. 2), indicating that the preponderance of species is not responding to a common environmental gradient. Negative coherence (i.e. more embedded absences than expected by chance) is the defining characteristic of chequerboard (Fig. 2; Tilman 1982) which results from mutually exclusive species pairs that respond independently to the gradient with regard to other such species pairs. Fewer embedded absences than expected by chance indicate positive coherence. A positively coherent metacommunity signifies that species distributions arise in response to a common environmental gradient. If the metacommunity exhibits positive coherence, embedded absences were

Fig. 2. A decision tree (modified from Presley, Higgins & Willig 2010) representing the hierarchical analysis of characteristics of metacommunity structure (dark grey boxes) that differentiate among eight idealized structures and six quasi-structures (light grey region). Results of the tests appear within circles (positive significance, +; non-significance, NS; negative significance, −; non-significant result in which observation is less than that produced by randomizations, <; non-significant result in which observation is greater than that produced by randomizations, >).

filled in (i.e. replaced by 1 s), and turnover and boundary clumping were assessed subsequently.

Species range turnover was quantified by counting the number of replacements of one species by another, considering all possible pairs of species in an ordinated matrix. Significance was determined by comparing the number of empirical replacements to a distribution of like values from 1000 null matrices, constructed by randomly shifting ranges. Less turnover than 97·5% of null values (i.e. negative turnover) is indicative of nested subsets (Fig. 2). In a nested metacommunity, most species are present at one end of the gradient and species are progressively lost towards the other end of the gradient. Conversely, positive range turnover (i.e. more turnover than 97·5% of null values) is a characteristic of Clementsian, Gleasonian and evenly spaced distributions (Fig. 2).

Clumping of species distributional boundaries was assessed using Morisita's index (I; Hurlbert 1990). Significance was determined by a chi-square test that compared the empirical distribution of boundaries to an expected uniform distribution. Significantly and positively clumped boundaries are signalled by a significant chi-square test with $I > 1$, whereas hyper-dispersed boundaries (significant negative clumping) are signalled by a significant chi-square test with $I < 1$. Species distributions that occur independently and idiosyncratically with respect to each other are indicated by a non-significant chi-square test with $I \sim 1$. The degree of boundary clumping distinguishes among Clementsian, Gleasonian and evenly spaced distributions (Fig. 2). Analyses of coherence, species range turnover and boundary clumping were conducted with algorithms written in MATLAB 7.5.0.342 (script files for MATLAB are available at http://faculty.tarleton.edu/higgins/metacommunity-structure.html), and site component scores of ordination were derived from the correspondence analysis option in MINITAB 16 (Minitab, State College, PA, USA).

Assessment of the underlying environmental gradient

Hierarchical partitioning (Chevan & Sutherland 1991) was employed to identify the landscape characteristics that were associated with the latent environmental gradient underlying metacommunity structure (represented by the site component scores of the first ordination axis from reciprocal averaging) for metacommunities that exhibited positive coherence. Many regression techniques, such as multiple regression, suffer from problems of collinearity among explanatory variables and the need to specify *a priori* the form of a model. Hierarchical partitioning provides a means to minimize the influences of multicollinearity by considering

all possible linear models that involve a suite of explanatory variables and determine the independent contribution of each explanatory variable to the response variable (Chevan & Sutherland 1991). The independent contribution is the average improvement in fit upon addition of a particular variable to a model. Accordingly, the importance of a particular explanatory variable in accounting for the response variable, independent of other variables, can be quantified. For each combination of season (dry and wet) and spatial scale (1, 3, 5 km radius), analyses were conducted separately for the phyllostomid assemblage, the frugivore ensemble and gleaning animalivore ensemble.

When multiple related statistical tests are performed, the probability of rejecting the null hypothesis when it is inappropriate to do so (Type I error) increases as the number of tests increases. Nevertheless, methods that reduce Type I errors are conservative and increase Type II errors (Moran 2003), resulting in trade-offs from a design perspective. Furthermore, the decision for partitioning analyses into subsets for which adjustments in P-values can be undertaken is controversial (Moran 2003), and the appropriateness of adjustments for multiple tests is still debated depending on the nature of the study (i.e. hypothesis generating or hypothesis confirming; Roback & Askins 2005). For exploratory studies or hypothesis generating studies (such as this one), failure to reject a false null hypothesis has greater repercussions for scientific advancement than does rejection of a true null hypothesis (Roback & Askins 2005). Consequently, statistical significance of the independent contribution of each explanatory variable was determined using a randomization approach with 1000 iterations and an α-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).

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. During the dry season, this assemblage comprised 30 species: 14 were frugivores and 10 were gleaning animalivores. During the wet season, the phyllostomid assemblage comprised 33 species: 15 were frugivores and 11 were gleaning animalivores. Most species were caught in both seasons. One species (gleaning animalivore, *Lonchorhina aurita*) was only caught during the dry season and four species (frugivore, *Chiroderma villosum*; gleaning animalivore, *Lampronycteris brachyotis*,

Trachops cirrhosus; and nectarivore, *Lichonycteris obscura*) were only caught during the wet season.

Regardless of season, the phyllostomid assemblage and the frugivore ensemble exhibited positive coherence and positive range turnover, whereas the gleaning animalivore ensemble was never coherent with fewer embedded absences than expected by chance (Table 1). Positive turnover indicates that sites at opposite ends of the latent gradient have different species compositions. For the phyllostomid and frugivore metacommunities, sites at one end of the gradient were associated with low-to-moderate landscape modification (e.g. areas dominated by forest) and sites at the opposite end of the gradient were associated with moderate-to-high landscape modification (e.g. areas with a diversity of forest and anthropogenically produced land cover; Fig. 3a,b,d,e). With regard to the phyllostomid assemblage, a number of gleaning animalivores generally were restricted to less modified or highly forested sites (Table 2). Conversely, a number of frugivores and nectarivores were restricted to more modified sites (Table 2).

Metacommunity structure differed between seasons for the phyllostomid assemblage as well as for each of the two ensembles (Table 1). A transition from Gleasonian structure during the dry season to Clementsian structure during the wet season characterized the phyllostomid assemblage and frugivore ensemble. In contrast, a transition from chequerboard pattern during the dry season to random structure during the wet season characterized the gleaning animalivore ensemble.

In addition to the Gleasonian–Clementsian transition, seasonal changes occurred in the phyllostomid metacommunity with regard to the positioning of feeding ensembles along the latent gradient as well as with respect to the size of species ranges (Fig. 3a,d). During the dry season, species of gleaning animalivore primarily resided at sites with low-to-moderate landscape modification at one end of the gradient, whereas frugivorous and nectarivorous species primarily resided at sites with moderate-to-high landscape modification at other end of the gradient (Fig. 3a). Conversely, species were more evenly distributed along the latent gradient during the wet season regardless of ensemble (Fig. 3d). Additionally, species ranges generally encompassed a greater number of sites during the dry season than they did during the wet season (Fig. 3a,d).

The relationships between the latent environmental gradients (represented by site component scores of the first ordination axis) and landscape characteristics were season and ensemble specific (Table 3). Configurational characteristics consistently best represented the underlying gradient of the phyllostomid metacommunity; distances between forest patches were important during the dry season, and the density of forest edges was important during the wet season. Conversely, compositional characteristics best represented the latent gradient of the frugivore metacommunity; proportion of pasture and density of forest patches were important during the dry season. No landscape characteristic significantly accounted for the latent gradient underlying the frugivore metacommunity during the wet season.

Discussion

NON-NESTED STRUCTURE WITHIN A HUMAN-MODIFIED LANDSCAPE

Nested subsets did not manifest for the phyllostomid assemblage or for two of its constituent ensembles. This is contradictory to findings that have arisen from common nestedness analyses for a variety of taxa, including bats, within human-modified landscapes (Whittaker 1992; Meyer & Kalko 2008; Struebig *et al.* 2008; Louzada *et al.* 2010; Hill *et al.* 2011). For nested assemblages to occur,

Table 1. Results of analyses of coherence, species range turnover and range boundary clumping (Morisita's index, *I*) for bat metacommunities within a human-modified landscape in the Caribbean lowlands of Costa Rica

	Coherence			Species turnover			Boundary clumping		
	Number of absences			Number of replacements					
	Empirical	Mean	*P*	Empirical	Mean	*P*	*I*	*P*	Metacommunity structure
Dry season									
All phyllostomids	133	176·5	**< 0·01**	1109	678·1	**0·02**	1·25	0·09	Gleasonian
Frugivores	27	55·8	**< 0·01**	177	78·0	**0·01**	0·87	0·50	Gleasonian
Gleaning animalivores	59	34·0	**< 0·01**	83	106·8	0·64	1·15	0·28	Chequerboard
Wet season									
All phyllostomids	151	202·0	**< 0·01**	1404	716·7	**< 0·01**	1·75	**< 0·01**	Clementsian
Frugivores	24	66·5	**< 0·01**	266	117·0	**< 0·01**	2·89	**0·01**	Clementsian
Gleaning animalivores	34	39·0	0·42	250	190·7	0·34	1·24	0·19	Random

Analyses were performed separately for all phyllostomid species, as well as for each of two constituent feeding ensembles (i.e. frugivores and gleaning animalivores). Empirical values (empirical) and mean randomized values (mean) are shown for coherence and species range turnover analysis. Significant results *(P < 0·05)* are in boldface.

Table 2. Species of frugivores, nectarivores and gleaning animalivores that were restricted to half of the latent gradient associated with less landscape modification (less modified) and species that were restricted to half of the latent gradient associated with more landscape modification (more modified) of the phyllostomid metacommunity and frugivore metacommunity

	Phyllostomid metacommunity		Frugivore metacommunity	
	Less modified	More modified	Less modified	More modified
Dry season				
Frugivore	*Vampyressa thyone*	*Sturnira lilium*	*Mesophylla macconnelli*	*Platyrrhinus helleri*
		Vampyressa nymphaea	*Vampyressa thyone*	*Sturnira lilium*
Nectarivore		*Lonchophylla robusta*		
Gleaning animalivore	*Lophostoma silvicolum*	*Phyllostomus hastatus*		
	Micronycteris hirsuta			
	Mimon crenulatum			
	Tonatia saurophila			
	Trinycteris nicefori			
Wet season				
Frugivore	*Mesophylla macconnelli*	*Chiroderma villosum*	*Mesophylla macconnelli*	*Chiroderma villosum*
	Vampyressa thyone	*Ectophylla alba*	*Vampyressa thyone*	*Ectophylla alba*
		Sturnira lilium		*Platyrrhinus helleri*
				Sturnira lilium
Nectarivore	*Lichonycteris obscura*	*Lonchophylla robusta*		
Gleaning animalivore	*Lampronycteris brachyotis*	*Phyllostomus hastatus*		
	Lophostoma brasiliense	*Trinycteris nicefori*		
	Micronycteris schmidtorum			
	Trachops cirrhosus			

Species listed are associated with distributional profiles in Fig. 3a,b,d and e.

at least three conditions must be met: (i) a common source of species or common evolutionary history of sites; (ii) similar vegetative structure at sites and (iii) hierarchical organization of niche relationships of species (Patterson & Brown 1991; Wright *et al.* 1998). Given the absence of appreciable latitudinal or elevational variation within the study landscape and that sites occurred within forest with closed canopies, conditions 1 and 2 are likely met.

Conversely, non-hierarchical organization of niche relationships of species due to differences in preferred habitat may be a reason for the lack of nestedness. Originally, tropical wet forest was the primary habitat of phyllostomid bats before major anthropogenic modification of the landscape in the Caribbean lowlands of Costa Rica. However, in the contemporary human-modified landscape, dependence on forest varies among species because many critical resources may be obtained from human-impacted environments. In particular, forest edge environments increase abundance of early successional plants used by bats (Lobova *et al.* 2003; Thies & Kalko 2004), pastural 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). Consequently, nested subsets did not form as sites with greater anthropogenic modification comprised species not found at less modified sites and vice versa.

Moreover, nested metacommunity structure will only arise if the latent gradient moulding species distributions

is correlated with a species richness gradient. For a variety of systems and taxa, factors dictating the number of species in an assemblage are often not the same as those that affect the identity of species in an assemblage (e.g. Stevens *et al.* 2003; Mayfield *et al.* 2005; Cisneros *et al.* 2014). Indeed, the latent gradients underlying metacommunity structure of the phyllostomid assemblage, the frugivore ensemble and the gleaning animalivore ensemble were not correlated with a richness gradient during the dry season (all phyllostomids – $\rho = 0.14$, $P = 0.60$; frugivores – $\rho = 0.22$, $P = 0.44$; animalivores – $\rho = 0.38$, $P = 0.16$; Fig. 3a–c) or the wet season (all phyllostomids – $\rho = 0.32$, $P = 0.24$; frugivores – $\rho = 0.28$, $P = 0.31$; animalivores – $\rho = -0.17$, $P = 0.57$; Fig. 3d–f). This further demonstrates that assessment of metacommunity structure along an *a priori* species richness gradient may obscure the factors moulding species distributions and provide misleading insight about mesoscale patterns.

PHYLLOSTOMID ASSEMBLAGE

In both seasons, the phyllostomid metacommunity was structured along the latent gradient such that particular species were associated with less modified sites (e.g. sites dominated by forest land cover) at one end of the gradient and other species were associated with more modified sites (e.g. sites with a diversity of forest and anthropogenic land cover) at the opposite end of the gradient (Fig. 3a,d). In general, gleaning animalivores were associated with less modified or highly forested sites, whereas frugivores and nectarivores were associated with sites with
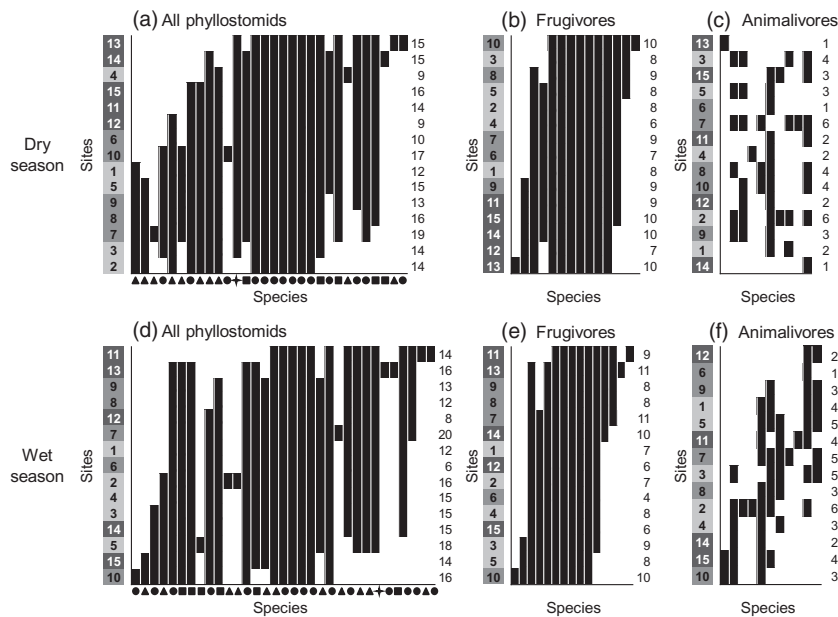
Fig. 3. Distributional profiles of species (black vertical bars) as ordered via reciprocal averaging for each combination of metacommunity (all phyllostomid species, frugivores and gleaning animalivores) and season. The order of sites (rows) and species (columns) differs among metacommunities. Embedded absences are only filled for positively coherent metacommunities (a, b, d and e). Numerical site codes in shaded boxes (left of graphs) correspond with those in Fig. 1. Levels of landscape modification at each site are indicated by shading (dark grey with white numbers: five most modified sites; medium grey with black numbers: five sites situated in the middle of the modification gradient; light grey with black numbers: five least modified sites). Non-shaded numbers (right of graphs) are species richness of sites. The feeding ensembles to which species belong are specified in the metacommunities with all phyllostomid species by symbols (frugivore, ●; gleaning animalivore, ▲; nectarivore, ■; sanguinivore, ✦).

more anthropogenic land cover (Table 2). These associations between particular bat ensembles and degrees of landscape modification have been documented throughout the Neotropics. Gleaning animalivores are commonly associated with the complex vegetation structure of old-growth or late successional forest, whereas frugivores and nectarivores often exhibit high abundances in moderately disturbed areas or agroforestry crop systems (Fenton *et al.* 1992; Medellín, Equihua & Amin 2000; García-Morales, Badano & Moreno 2013). Negative responses to landscape modification by gleaning animalivores (e.g. reduced frequency of occurrence) may be due to limited prey availability near forest edges (Meyer *et al.* 2008), loss of a complex understorey that provides prime foraging environment (Gorresen & Willig 2004) or an inability to use distant forest patches to acquire resources due to poor dispersal ability or small home range sizes (Meyer & Kalko 2008). Persistence of frugivorous and nectarivorous bats in the most modified sites is most likely related to greater abundance and diversity of food resources from early successional plants or Neotropical crops (Castro-Luna & Galindo-González 2011).

Despite these generalities, a number of characteristics of the phyllostomid metacommunity differed between seasons. First, the distribution of species range boundaries shifted from random during the dry season to clumped during the wet season (Table 1). Secondly, although gleaning animalivores generally resided at the opposite

end of latent gradient compared to frugivores and nectarivores, this pattern was more distinctive during the dry season (Fig. 3a). During the wet season, species from these three ensembles were more randomly distributed across the gradient with respect to each other (Fig. 3d). Thirdly, species distributions generally encompassed a greater number of sites during the dry season than during the wet season (Fig. 3a,d).

These seasonal changes can be explained by optimal patch use theory and optimal diet theory. Optimal patch use theory predicts that foragers should spend less time in habitat patches with lower resource availability and as a consequence use more habitat patches (Sih 2011). Optimal diet theory predicts that foragers should specialize on high-value food resources when those resources are abundant, but should have broad, generalized diets when high-value resources are rare (Sih 2011). In the Caribbean lowlands of Costa Rica, the dry season offers fewer and less abundant food resources to bats that consume plant material and arthropods, as fruits, flowers and arthropods peak in abundance during the wet season (Frankie, Baker & Opler 1974; Boinski & Fowler 1989; Tschapka 2004). The distributional characteristics of bats exhibited during this time of limitation suggest that species concentrate activities at particular ends of the gradient associated with the presence of their food resources. For example, sites with more core forest likely have greater arthropod abundance for gleaning animalivores and sites with agricultural

Table 3. Percentage of independent effects of landscape characteristics on the site component scores of the first ordination axis from reciprocal averaging for each combination of season and focal scale

		Compositional characteristics					Configurational characteristics			
	Scale	Per cent forest	Mean forest patch size	Forest patch density	Per cent pasture	Simpson's diversity	Mean forest proximity	Mean forest nearest neighbour	Mean forest patch shape	Forest edge density
Dry season										
All phyllostomids	1	21·4	16·4	5·2	2·6	9·4	15·0	**26·2**	1·5	2·2
	3	11·2	9·2	9·3	25·4	20·7	7·3	5·8	4·9	6·2
	5	9·9	13·3	7·2	16·4	22·0	15·7	6·3	5·4	3·8
Frugivores	1	6·9	9·4	**34·0**	8·8	10·2	5·3	11·9	8·4	5·1
	3	3·5	4·8	12·4	**43·2**	20·2	3·8	3·5	3·6	4·9
	5	11·2	9·8	10·9	**32·4**	20·1	4·7	3·5	5·1	2·4
Wet season										
All phyllostomids	1	20·6	5·7	12·3	5·0	13·6	5·5	4·9	11·7	20·7
	3	10·7	5·3	18·5	8·1	6·9	7·2	12·0	11·7	19·5
	5	18·9	6·1	13·9	6·1	5·3	9·3	8·3	2·4	**29·7**
Frugivores	1	4·0	5·3	27·6	6·4	11·7	3·9	3·6	17·2	20·2
	3	10·7	7·6	19·9	15·6	8·3	8·3	5·8	9·9	13·8
	5	19·4	7·4	14·2	12·0	7·8	10·5	6·8	4·4	17·6

Significant effects ($P \leq 0.05$) are in boldface. Results are not shown for the gleaning animalivore metacommunity because species did not respond to a common environmental gradient.

areas likely have greater abundance of fruits and flowers for frugivores and nectarivores. However, given limited resources at particular sites, species need to use a greater number of sites with similar land modification. In addition to using more sites, frugivorous and nectarivorous species expand their diet during the dry season to comprise a greater number of fruit species and greater quantities of arthropods than they do during the wet season (Lopez & Vaughan 2007). Because prey and plant species included in these expanded diets are most likely species specific, ranges occur independently of each other along the gradient during the dry season. When food resources were more plentiful, species from particular ensembles were not restricted to one end of the gradient and used fewer sites. Clumped boundaries most likely represent shared preferences in optimal habitat when resources were not limiting.

The importance of use of more sites during times of limited resources was further supported by the influences of distances between forest patches on metacommunity structure during the dry season (Table 3). Smaller distances between forest patches characterized the end of the gradient associated with less landscape modification, whereas larger distances characterized more modified sites. Species with poor dispersal ability or small home range sizes (e.g. many gleaning animalivores) were most associated with areas with smaller distances between forest patches than species with good dispersal ability or large home range sizes (e.g. many frugivores). Similarly, distance between forest patches significantly affected diversity of diet traits of phyllostomid assemblages in the Caribbean lowlands of Costa Rica (Cisneros, Fagan & Willig 2014b). Diet diversity increased with increasing proximity between forest patches, suggesting that multiple species from a number of ensembles may be able to cross the matrix to use resources from multiple forest patches if those patches are in close proximity. Consequently, connectivity among forest patches plays a critical role in dictating species distributions as well as the functional diversity of assemblages when resources are limiting.

Forest edge density had a stronger influence on metacommunity structure during the wet season than during the dry season (Table 3). Less modified sites were characterized by low edge density, whereas more modified sites were characterized by high edge density. Forest edges may significantly increase the diversity and abundance of fruits available during the prime fruiting season (i.e. mid-wet season in the Caribbean lowlands of Costa Rica; Frankie, Baker & Opler 1974) given that fruiting plants in gap environments have higher production of fruit and persistence of fruits for a longer period of time than do interior forest conspecifics (Levey 1988). Because many nectarivores and gleaning animalivores consume fruits (Giannini & Kalko 2004), a variety of species may benefit from forest edges during this time of year, although some species that do not consume fruits may remain edge sensitive.

FRUGIVORE ENSEMBLE

Similar to the situation for the phyllostomid assemblage, metacommunity structure of the frugivore ensemble shifted from Gleasonian structure during the dry season to Clementsian structure during the wet season (Table 1). Nonetheless, the particular landscape characteristics associated with spatial variation in species distributions differed between the two groups of bats (Table 3) because the responses of species from a variety of ensembles (i.e. gleaning animalivore, nectarivore and sanguinivore) in addition to frugivores contribute to the overall response of the phyllostomid metacommunity to landscape structure. Landscape characteristics only had significant influences on metacommunity structure of the frugivore ensemble during the dry season. This may mean that environmental characteristics at the local scale may be more important to the frugivore ensemble during the wet season or that important landscape characteristics were not included in the analysis.

During the dry season, the latent gradient underlying the frugivore metacommunity was associated with forest patch density and pasture (Table 3). At one end of the gradient, sites were characterized by greater patch density and more pasture (i.e. less modified sites), whereas at the other end, sites were characterized by less patch density and less pasture (i.e. more modified sites). Sites with less patch density and less pasture comprised large agricultural plantations of banana or pineapple and were more modified than sites with greater forest patch density and more pasture. Although the ranges of many frugivorous species spanned the entire gradient (i.e. species from the genera *Artibeus* and *Carollia*; Fig. 3b), two species were unique to less modified sites and two species were unique to more modified sites (Table 2, frugivore metacommunity during dry season). In general, frugivorous species are less sensitive to land conversion and often benefit from non-monoculture agricultural systems (García-Morales, Badano & Moreno 2013). Pasture also may not be a harsh matrix to frugivorous bats that are more sensitive to agricultural plantations, especially because pastures are often associated with riparian forests and live fences (i.e. barbed fences made of live woody species), which are used by a diversity of bat species (Harvey *et al.* 2006).

Intermediate amounts of forest and pasture were also documented to have positive influences on local taxonomic, functional and phylogenetic diversity of phyllostomid bats in the Caribbean lowlands of Costa Rica (Cisneros, Fagan & Willig 2014b). Thus, both forest and pasture play critical roles in structuring mesoscale and local-scale patterns of phyllostomid bats.

GLEANING ANIMALIVORE ENSEMBLE

Unlike the situation for phyllostomids in general or the frugivore ensemble in particular, the metacommunity structure of the gleaning animalivore ensemble changed

from chequerboard structure during the dry season to random structure during the wet season (Table 1). This may indicate that a common environmental gradient does not affect the preponderance of species of this ensemble or may be an artefact associated with the rarity of many species in this ensemble. The chequerboard pattern during the dry season suggests that competitive exclusion between pairs of species is an important mechanism that structures this metacommunity during times of limited food resources (i.e. dry season).

Much debate surrounds the role of competition in structuring bat assemblages at a variety of scales (e.g. regional scale, local scale; Stevens & Willig 1999, 2000; Moreno, Arita & Solis 2006). At large geographic scales, such as along latitudinal gradients, there is little support for competitive interactions structuring bat assemblages based on character displacement of ecomorphological characteristics or density compensation (Stevens & Willig 1999, 2000). Environmental heterogeneity may facilitate co-occurrence among ecologically similar species at large scales. At local scales, overdispersion of ecomorphological characteristics of frugivorous bats suggests the operation of competitive exclusion among ecologically similar frugivorous species in Mexico (Moreno, Arita & Solis 2006). Within a land-bridge island system in Panama, Meyer & Kalko (2008) found that less vagile bats and gleaning animalivores occurred together less often than expected by chance, whereas more vagile species and frugivores did not exhibit such a pattern. These findings, in conjunction with the findings of this study, suggest that competitive interactions may play a significant role in species assembly of bats at landscape and local scales when resources are limiting and species dispersal abilities are poor, such as those of many species of gleaning animalivores.

CONCLUDING REMARKS

Metacommunity structure differed between seasons and among different groups of species. Furthermore, landscape characteristics that significantly affected metacommunity structure differed between seasons and among different groups of species. These differences are likely mediated by differential resource use or interspecific competition. Furthermore, seasonal differences emphasize the importance of interactions between landscape characteristics and seasonal variation in resource quantity and diversity in species assembly.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository http://doi.org/10.5061/dryad.9fp3g (Cisneros, Fagan & Willig 2014a).

References

Atmar, W. & Patterson, B.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, **96**, 373–382.

Boinski, S. & Fowler, N.L. (1989) Seasonal patterns in a tropical lowland forest. *Biotropica*, **21**, 223–233.

Castro-Luna, A. & Galindo-González, J. (2011) Enriching agroecosystems with fruit-producing tree species favors the abundance and richness of frugivorous and nectarivorous bats in Veracruz, Mexico. *Mammalian Biology*, **77**, 32–40.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *The American Statistician*, **45**, 90–96.

Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2014a) Data from: season-specific and guild-specific effects of anthropogenic landscape modification on metacommunity structure of tropical bats. *Dryad Digital Repository*, http://doi.org/10.5061/dryad.9fp3g

Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2014b) Effects of human-modified landscapes on taxonomic, functional, and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*.

Cisneros, L.M., Burgio, K.R., Dreiss, L.M., Klingbeil, B.T., Patterson, B.D., Presley, S.J. *et al.* (2014) Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. *Journal of Animal Ecology*, **83**, 1124–1136.

Clements, F.E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution, Washington, District of Columbia, USA.

Cutler, A. (1991) Nested faunas and extinction in fragmented habitats. *Conservation Biology*, **5**, 496–505.

Diamond, J.M. (1975) Assembly of species communities. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge, Massachusetts, USA.

Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 589–606.

Fagan, M.E., DeFries, R.S., Sesnie, S.E., Arroyo, J.P., Walker, W., Soto, C. *et al.* (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, **8**, 034017.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K. *et al.* (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica*, **24**, 440–446.

Fischer, J. & Lindenmayer, D.B. (2005) Nestedness in fragmented landscapes: a case study on birds, arboreal marsupials and lizards. *Journal of Biogeography*, **32**, 1737–1750.

Frankie, G.W., Baker, H.G. & Opler, P.A. (1974) Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *Journal of Ecology*, **62**, 881–919.

García-Morales, R., Badano, E.I. & Moreno, C.E. (2013) Response of Neotropical bat assemblages to human land use. *Conservation Biology*, **27**, 1096–1106.

Gauch, H.G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, Massachusetts, USA.

Giannini, N.P. & Kalko, E.K.V. (2004) Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos*, **105**, 209–220.

Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 7–26.

Gorresen, P.M. & Willig, M.R. (2004) Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *Journal of Mammalogy*, **85**, 688–697.

Gorresen, P.M., Willig, M.R. & Strauss, R.E. (2005) Multivariate analysis of scale-dependent associations between bats and landscape structure. *Ecological Applications*, **15**, 2126–2136.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A. et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850–853.

Harvey, C.A. & González Villalobos, J.A. (2007) Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. *Biodiversity and Conservation*, **16**, 2257–2292.

Harvey, C.A., Medina, A., Sánchez, D.M., Vílchez, S., Hernández, B., Saenz, J.C. et al. (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecological Applications*, **16**, 1986–1999.

Hill, J.K., Gray, M.A., Khen, C.V., Benedick, S., Tawatao, N. & Hamer, K.C. (2011) Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 3265–3276.

Hurlbert, S.H. (1990) Spatial distribution of the montane unicorn. *Oikos*, **58**, 257–271.

Kalko, E.K.V. (1997) Diversity in tropical bats. *Tropical Biodiversity and Systematics* (ed. H. Ulrich), pp. 13–43. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

Kalko, E.K.V. & Handley, C.O. (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319–333.

Keith, S.A., Newton, A.C., Morecroft, M.D., Golicher, D.J. & Bullock, J.M. (2011) Plant metacommunity structure remains unchanged during biodiversity loss in English woodlands. *Oikos*, **120**, 302–310.

Klingbeil, B.T. & Willig, M.R. (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. *Journal of Applied Ecology*, **46**, 203–213.

Klingbeil, B.T. & Willig, M.R. (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos*, **119**, 1654–1664.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1–38.

Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, **15**, 8–20.

Leibold, M.A. (2011) The metacommunity concept and its theoretical underpinnings. *The Theory of Ecology* (eds S.M. Scheiner & M.R. Willig), pp. 163–184. University of Chicago Press, Chicago, Illinois, USA.

Leibold, M.A. & Mikkelson, G.M. (2002) Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos*, **97**, 237–250.

Levey, D.J. (1988) Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology*, **69**, 1076–1089.

Lobova, T.A., Mori, S.A., Blanchard, F., Peckham, H. & Charles-Dominique, P. (2003) *Cecropia* as a food resource for bats in French Guiana and the significance of fruit structure in seed dispersal and longevity. *American Journal of Botany*, **90**, 388–403.

Lopez, J.E. & Vaughan, C. (2007) Food niche overlap among neotropical frugivorous bats in Costa Rica. *Revista de Biología Tropical*, **55**, 301–313.

López-González, C., Presley, S.J., Lozano, A., Stevens, R.D. & Higgins, C.L. (2012) Metacommunity analysis of Mexican bats: environmentally mediated structure in an area of high geographic and environmental complexity. *Journal of Biogeography*, **39**, 177–192.

Louzada, J., Gardner, T., Peres, C. & Barlow, J. (2010) A multi-taxa assessment of nestedness patterns across a multiple-use Amazonian forest landscape. *Biological Conservation*, **143**, 1102–1109.

Mac Nally, R. (2002) Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation*, **11**, 1397–1401.

Mac Nally, R., Horrocks, G. & Bennett, A.F. (2002) Nestedness in fragmented landscapes: birds of the box-ironbark forests of south-eastern Australia. *Ecography*, **25**, 651–660.

Mac Nally, R. & Walsh, C.J. (2004) Hierarchical partitioning public-domain software. *Biodiversity and Conservation*, **13**, 659–660.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H.-J. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 373–384.

Mayfield, M.M., Boni, M.F., Daily, G.R.C.D. & Ackerly, D.D. (2005) Species and functional diversity of native and human-dominated plant communities. *Ecology*, **86**, 2365–2372.

McGarigal, K., Cushman, S.A. & Ene, E. (2012) *FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps*. University of Massachusetts, Amherst, Massachusetts, USA. URL http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Medellín, R.A., Equihua, M. & Amin, M.A. (2000) Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology*, **14**, 1666–1675.

Menezes, J.F.S. & Fernandez, F.A.S. (2013) Nestedness in forest mammals is dependent on area but not on matrix type and sample size: an analysis on different fragmented landscapes. *Brazilian Journal of Biology*, **73**, 465–470.

Meyer, C.F.J. & Kalko, E.K.V. (2008) Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Diversity and Distributions*, **14**, 644–654.

Meyer, C.F.J., Fründ, J., Pineda Lizano, W. & Kalko, E.K.V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–391.

Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**, 403–405.

Moreno, C.E., Arita, H.T. & Solis, L. (2006) Morphological assembly mechanisms in Neotropical bat assemblages and ensembles within a landscape. *Oecologia*, **149**, 133–140.

Morrison, D.W. (1978) Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour*, **26**, 852–855.

Organization for Tropical Studies (2012) La Selva daily rainfall, 1963–2010 (May11 update). *Organization for Tropical Studies, Meteorlogical Data, GPS Data and Hydrological Data*. URL http://www.ots.ac.cr/meteoro/default.php?pestacion=2.

Patterson, B.D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, **28**, 65–82.

Patterson, B.D. & Brown, J.H. (1991) Nested patterns of species composition in granivorous rodent assemblages. *Journal of Biogeography*, **18**, 395–402.

Patterson, B.D., Willig, M.R. & Stevens, R.D. (2003) Trophic strategies, niche partitioning, and patterns of ecological organization. *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 536–579. University of Chicago Press, Chicago, Illinois, USA.

Perfecto, I. & Vandermeer, J. (2008) Biodiversity conservation in tropical agroecosystems: a new conservation paradigm. *Annals of the New York Academy of Sciences*, **1134**, 173–200.

Peters, D.P.C., Pielke, R.A. Sr, Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. & Havstad, K.M. (2004) Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences*, **101**, 15130–15135.

Presley, S.J., Higgins, C.L. & Willig, M.R. (2010) A comprehensive framework for the evaluation of metacommunity structure. *Oikos*, **119**, 908–917.

Presley, S.J. & Willig, M.R. (2010) Bat metacommunity structure on Caribbean islands and the role of endemics. *Global Ecology and Biogeography*, **19**, 185–199.

Presley, S.J., Cisneros, L.M., Patterson, B.D. & Willig, M.R. (2012) Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds. *Global Ecology and Biogeography*, **21**, 968–976.

Roback, P.J. & Askins, R.A. (2005) Judicious use of multiple hypothesis tests. *Conservation Biology*, **19**, 261–267.

Sih, A. (2011) Foraging theory. *The Theory of Ecology* (eds S.M. Scheiner & M.R. Willig), pp. 65–90. University of Chicago Press, Chicago, Illinois, USA.

Sodhi, N.S. & Ehrlich, P.R. (2010) *Conservation Biology for All.* Oxford University Press, New York, New York, USA.

Stevens, R.D. & Willig, M.R. (1999) Size assortment in New World bat communities. *Journal of Mammalogy*, **80**, 644–658.

Stevens, R.D. & Willig, M.R. (2000) Density compensation in New World bat communities. *Oikos*, **89**, 367–377.

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters*, **6**, 1099–1108.

Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A. & Rossiter, S.J. (2008) Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation*, **141**, 2112–2126.

Thies, W. & Kalko, E.K.V. (2004) Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos*, **104**, 362–376.

Tilman, D. (1982) *Resource Competition and Community Structure.* Princeton University Press, Princeton, New Jersey, USA.

Tschapka, M. (2004) Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. *Journal of Zoology (London)*, **263**, 7–21.

Whittaker, R.J. (1992) Stochasticism and determinism in island ecology. *Journal of Biogeography*, **19**, 587–591.

Wilkinson, G.S. (1985) The social organization of the common vampire bat. *Behavioural Ecology and Sociobiology*, **17**, 111–121.

Willig, M.R., Presley, S.J., Bloch, C.P., Castro-Arellano, I., Cisneros, L.M., Higgins, C.L. *et al.* (2011) Tropical metacommunities along elevational gradients: effects of forest type and other environmental factors. *Oikos*, **120**, 1497–1508.

Wilson, D.S. (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, **73**, 1984–2000.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia*, **113**, 1–20.

Supporting Information

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

Fig. S1. Position of sites along a landscape modification gradient (indicated by the numerical site codes) was based on Simpson's diversity index of land cover (i.e. forest, cropland, pasture, bare soil, urban, and water) quantified at the 5 km focal scale.

Table S1. Mean, standard deviation (SD), and range of each of nine landscape characteristics quantified at each of three focal scales (i.e. circles with a 1, 3 or 5 km radius) for sites in the Caribbean lowlands of Costa Rice (for definitions, formulae, and units of landscape metrics, see Table S2, Supporting information).

Table S2. Indices that quantified landscape structure at each of three focal scales for each of the 15 sampling sites based on a 2011 land cover map.