



# Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia

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The amount (composition) and spatial arrangement (configuration) of forest patches in fragmented landscapes influence the accessibility, as well as the abundance and diversity of resources available to bats. Moreover, tropical fruit and insect abundance differ seasonally in response to changes in precipitation, and many bats in the family Phyllostomidae employ seasonal reproductive strategies. Because reproductive activities involve constraints on time and energy as well as increased nutritional demands, foraging behavior and home range size may differ between wet and dry seasons. Nonetheless, seasonal variation in response to landscape structure by bats has not been examined previously. Consequently, population-, ensemble- and assemblage-level responses of phyllostomids to landscape composition and configuration were quantified separately during the wet and dry season at three circular focal scales (1, 3 and 5 km radii) for 14 sites in fragmented lowland Amazon forest. Responses to landscape characteristics were scale-dependent, species-specific, and seasonal. Abundances of frugivores responded to landscape composition in the dry season and to landscape configuration in the wet season. Conversely, abundances of animalivores responded to landscape configuration in the dry season and to landscape composition in the wet season. Divergent responses to landscape structure between seasons suggest that variation in resource abundance and diversity play a significant role in structuring population-, ensemble- and assemblage-level patterns. As such, considerations of the effects of dietary flexibility and reproductive constraints on foraging strategies and habitat use may be important when designing management plans that successfully promote long-term persistence of biodiversity in fragmented landscapes.

Evaluating the consequences of fragmentation on biodiversity is facilitated by an explicit landscape framework. This allows variation in characteristics of biodiversity to be related to variation in attributes of habitat patches that are derived from relationships among multiple cover classes within a focal area (McGarigal and Cushman 2002, Fahrig 2003). Few studies have compared population characteristics among focal areas with different degrees of fragmentation (i.e. landscapes that differ in the size, number, or spatial arrangement of patches). Moreover, studies that have analyzed population- and community-level responses to fragmentation at the landscape-level generally quantify responses and landscape characteristics at a single, arbitrarily delineated focal scale. This is problematic because metrics of biodiversity and landscape structure vary with area in non-linear and potentially uncorrelated ways (McGarigal and McComb 1995, Turner et al. 2001), and species differ in the scales at which they perceive the environment, secure resources, or respond to heterogeneity (With and Crist 1995, Turner et al. 2001).

## Seasonal variation

Whereas temperate regions are seasonal in temperature, seasonality in the wet tropics is defined by differences in precipitation (MacArthur 1972). Because of its vast size,

variation in the degree of seasonality (e.g. differences in mean monthly precipitation between dry and wet seasons) exists within the Amazon Basin, and regions differ in the timing, length or magnitude of seasonal variation in precipitation (Marengo et al. 2008). Rainfall in the northern Amazon Basin peaks in March–May, whereas in southern Amazonia the wet season occurs in December–February. Seasonal fluctuation in rainfall influences the phenology of fruiting, flowering, and new leaf production in tropical forests (Janzen 1967). Peaks in fruit abundance usually coincide with peaks in rainfall in most tropical regions and generally fewer food resources for frugivores exist during the dry season (Smythe 1986). Canopy fruits are produced in larger crops, are larger in size, contain larger seeds, and are more seasonal in occurrence than are fruits from understory plants and early successional trees, which generally have extended fruiting periods but offer smaller daily fruit crops (Smythe 1970, Foster and Janson 1985).

A strong link also exists between insect abundance and rainfall patterns in tropical rainforests. Insect populations typically exhibit seasonal variation in abundance, associated with rainfall and the availability of food resources, such as new leaves or fruit (Wolda 1978, Frith and Frith 1985). Plants have evolved defense mechanisms against herbivory and mature leaves often have high concentrations of toxins

and low nutritional value. Consequently, seasonal cycles of insect abundance are strongly correlated with leaf production because young leaves often lack such defenses and have higher nutritional content compared to mature leaves (Wolda 1978). In general, leaf production peaks at the beginning of the wet season and is low during the dry season. Accordingly, dry season abundance of most insects is low in tropical sites with a pronounced dry season. In regions without a severe dry season, insects decrease in abundance during the dry season and increase during the wet season (Wolda 1978, Frith and Frith 1985).

## Bats

Because of their local abundance, richness and ecological diversity, bats are a promising indicator group for studying population and community responses to landscape structure in fragmented forests of the Neotropics (Fenton et al. 1992, Kalko 1998, Jones et al. 2009). Bats increase in richness toward the equator, and achieve highest taxonomic, functional and phenetic diversity at tropical sites (Stevens and Willig 2002, Stevens et al. 2006). Some taxa are highly mobile and travel long distances between roosts and foraging sites, making them efficient seed dispersers, pollinators, or predators of insects and small vertebrates (Findley 1993). Furthermore, frugivorous bats (Phyllostomidae) facilitate succession and revegetation of deforested areas by dispersing seeds of pioneer plant species in the genera *Piper*, *Solanum* and *Cecropia* (Fleming 1988).

The responses of bats to habitat fragmentation in the Neotropics are variable (Fenton et al. 1992, Schulze et al. 2000) and the responses to landscape structure remain understudied (Gorresen and Willig 2004, Gorresen et al. 2005, Meyer and Kalko 2008, Klingbeil and Willig 2009). Historically, studies have relied on dichotomous and qualitative descriptions of habitats (e.g. disturbed vs undisturbed, Fenton et al. 1992, fragmented vs continuous forest, Schulze et al. 2000) or simple indices of landscape composition. However, these approaches cannot assess relationships between the degree of habitat fragmentation and variation in aspects of biodiversity (Fahrig 2003). In highly fragmented interior Atlantic Forest, moderately fragmented Amazon rainforest, and fragmented tropical forest islands, the population-level responses of bats to a suite of landscape characteristics were species-specific and scale-dependent (Gorresen and Willig 2004, Gorresen et al. 2005, Meyer and Kalko 2008, Klingbeil and Willig 2009). In lowland Amazonia, abundances of frugivorous species respond to changes in compositional characteristics, whereas abundances of gleaning animalivores respond to changes in configurational characteristics in the dry season (Klingbeil and Willig 2009).

## Objectives

Despite seasonal differences in the landscape distribution of resources, analyses of species responses to fragmentation generally combine data across seasons and years or are conducted within a single season. Failure to account for seasonal differences in population-level or assemblage-level characteristics of species that exploit seasonal resources may obscure important changes in foraging strategies associated with times

of food abundance or scarcity. In particular, studies identifying seasonal differences in animal species responses to landscape structure are few, and those that exist are confined to temperate zones and examine behavioral differences between the breeding season and non-breeding season (Vergara and Marquet 2007). Although differences in foraging behavior (i.e. reproductive and non-reproductive states) provide much needed natural history data on bats, quantitative assessment of how energetic constraints associated with reproduction may affect species relationships to landscape structure has yet to be undertaken. Similarly, no studies have investigated how populations or communities respond to seasonal fluctuations in resources at a range of landscapes characterized by differences in composition and configuration. Because abundance of food resources and energy budgets of bats fluctuate seasonally in the Neotropics, we predict that responses to landscape structure will also differ in nature and focal scale between seasons. Moreover, differences in foraging mode are linked to differences in prey type. Consequently, we expect guilds (frugivores and gleaning animalivores) to respond differently from each other in both seasons.

## Material and methods

### Study area

Research was conducted in unflooded (terra firme) Amazonian rain forest, southwest of Iquitos ( $-3^{\circ} 44' 55'$ ,  $-73^{\circ} 14' 58'$ ) in northeastern Peru (Fig. 1). Elevation ranges from sea level to 200 m (Kalliola and Flores 1998). The climate is relatively constant with monthly temperatures of 25–27°C, and average high and low temperatures of 32°C and 21°C, respectively (Madigosky and Vatnick 2000). Precipitation patterns in the Amazon basin exhibit strong variation from year to year and may increasingly be affected by human activities (Marengo et al. 2008) but generally, the wettest months are between February and May in the Iquitos region (Madigosky and Vatnick 2000). Total monthly precipitation during the study period (September 2004 – May 2005) ranged from 198 mm to 534 mm. September received the least and February received the greatest precipitation (NCDC 2009).

### Experimental design

Fourteen sampling sites were established along the road being constructed from Iquitos to Nauta (Fig. 1). Site centers were located within 3 km from the road, on both sides. The number and placement of sites were determined so that sampling locations were >4 km apart, to minimize the influence of spatial autocorrelation and included a representative range of habitat configurations (i.e. continuous forest and forest fragmented by agriculture, development and logging). Although a range of landscape structures was captured by the selected sites, logistical constraints precluded us from capturing two potentially important landscapes. Our study does not include (1) a landscape that contains 100 percent forest at all three focal scales that is also embedded within a greater expanse of forest, or (2) a landscape that contains

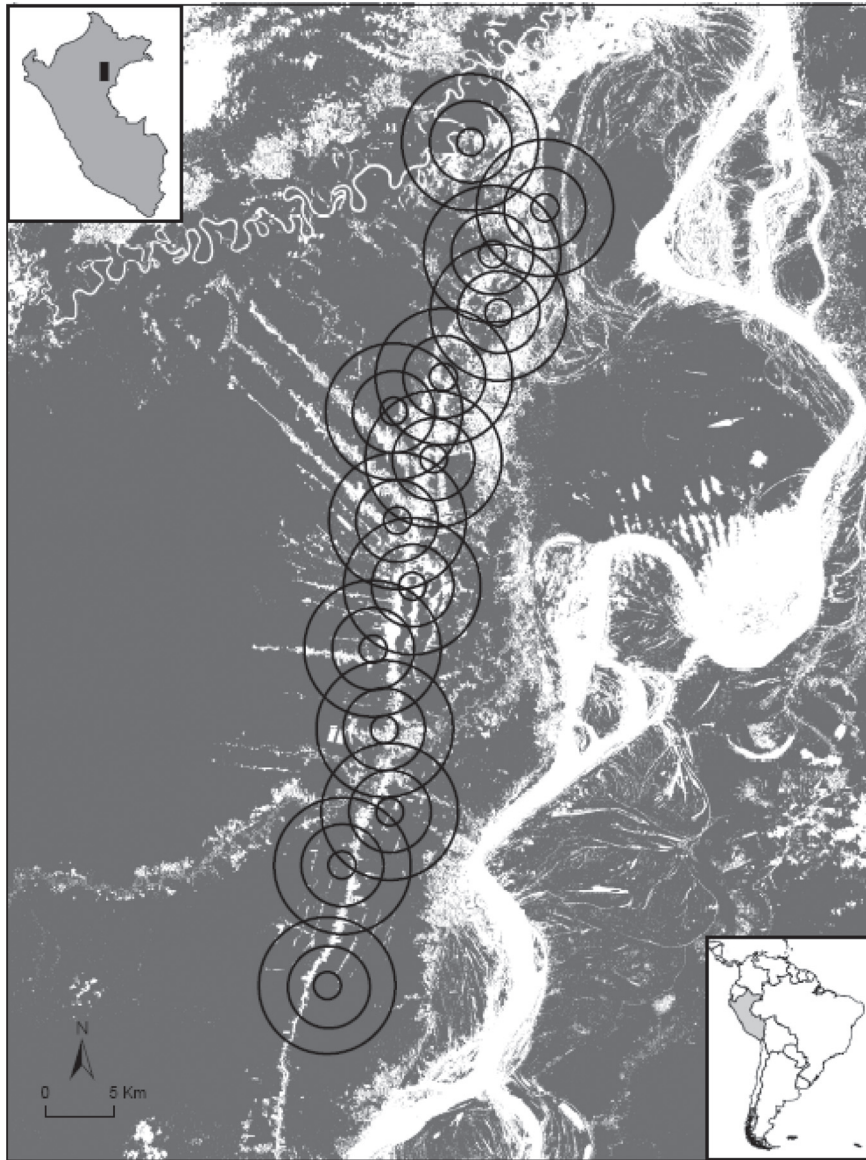


Figure 1. Classified image of study area displaying concentric focal scales (1, 3 and 5 km radii) centered on each of 14 sites (after Klingbeil and Willig 2009). Forest class is displayed in gray whereas non-forest class is displayed in white. Location of Peru (Gray) in South America is displayed in the lower-right corner of the map. Image in the upper-left corner shows location of the study area (black rectangle) in Peru. Study sites from north to south, with geographic coordinates are: Arboretum ( $-3^{\circ} 49' 48''$ ,  $-73^{\circ} 22' 12''$ ), Km 12 ( $-3^{\circ} 52' 48''$ ,  $-73^{\circ} 19' 48''$ ), Km 18 ( $-3^{\circ} 54' 0''$ ,  $-73^{\circ} 22' 12''$ ), Km 21 ( $-3^{\circ} 57' 0''$ ,  $-73^{\circ} 22' 12''$ ), Km 28 ( $-3^{\circ} 58' 52''$ ,  $-73^{\circ} 24' 36''$ ), Km 31.5 ( $-4^{\circ} 0' 0''$ ,  $-73^{\circ} 27' 0''$ ), Km 34 ( $-4^{\circ} 2' 24''$ ,  $-73^{\circ} 25' 48''$ ), Km 39.5 ( $-4^{\circ} 4' 12''$ ,  $-73^{\circ} 27' 36''$ ), Km 44 ( $-4^{\circ} 7' 12''$ ,  $-73^{\circ} 27' 0''$ ), Km 49 ( $-4^{\circ} 9' 36''$ ,  $-73^{\circ} 28' 48''$ ), Km 55 ( $-4^{\circ} 12' 36''$ ,  $-73^{\circ} 29' 24''$ ), Km 60 ( $-4^{\circ} 15' 36''$ ,  $-73^{\circ} 29' 24''$ ), Km 66.5 ( $-4^{\circ} 18' 0''$ ,  $-73^{\circ} 31' 48''$ ) and Km 75 ( $-4^{\circ} 22' 12''$ ,  $-73^{\circ} 33' 0''$ ).

100 percent forest at all three focal scales embedded within anthropogenically altered habitats. The first shortcoming is a consequence of the length of time and difficulty associated with travel to such a site and the second is because no such site existed within the study area.

The bat fauna at each site was sampled with 12 ground-level mist nets ( $12 \times 2.6$  m) in the dry season (3 September 2004 – 18 January 2005; 56 808 net meter hours) and wet season (29 January 2005 – 30 May 2005; 53 712 net meter hours). Seasons were defined based on actual precipitation in the study area during the study period and are consistent with general historical patterns in the Iquitos region

(Madigosky and Vatnick 2000, Marengo et al. 2008). Each site was surveyed six nights in each season. Nets were opened at dusk and remained open for approximately 5.5 h each night except during severe weather. To minimize biases associated with the use of ground-level mist-nets to sample bat assemblages, analyses of the response of bats to landscape structure were restricted to phyllostomids, consistent with approaches undertaken in a number of recent studies (Kalko 1998, Gorresen and Willig 2004, Willig et al. 2007). Phyllostomids were classified into broad foraging guilds (i.e. frugivores, nectarivores, gleaning animalivores and sanguinivores; Table 1) based on published

Table 1. Summary statistics (mean, standard deviation and range) of population-level (abundance of each phyllostomid species), ensemble-level (abundance of frugivores and animalivores), and assemblage-level (indices of biodiversity) characteristics of bats in Iquitos, Peru (n=14 in all cases). Taxa in bold were analyzed at the population-level. Taxa with an asterisk are rare in the study area. All phyllostomids were included in assemblage-level analyses. For ensembles: F=frugivore, GA=gleaning animalivore, N=nectarivore, S=sanguinivore.

Taxon	Guild	Dry season			Wet season		
		Mean	SD	Range	Mean	SD	Range
Population-level							
<b>Artibeus anderseni</b>	F	0.8	1.19	0–4	1.0	1.75	0–6
<i>Artibeus concolor</i> *	F	0.4	0.63	0–2			
<b>Artibeus gnomus</b>	F	1.7	1.73	0–6	1.1	1.46	0–4
<b>Artibeus lituratus</b>	F	3.9	4.67	0–18	2.1	2.16	0–6
<b>Artibeus obscurus</b>	F	10.5	6.55	2–25	5.4	2.92	1–9
<b>Artibeus planirostris</b>	F	22.3	13.97	2–51	13.7	10.28	0–40
<b>Carollia benkeithi</b>	F	8.4	8.76	0–27	4.4	3.95	0–16
<b>Carollia brevicauda</b>	F	39.7	20.11	17–92	36.3	21.76	11–85
<b>Carollia perspicillata</b>	F	73.0	28.93	38–138	40.9	18.74	18–78
<i>Chiroderma trinitatum</i> *	F	0.1	0.27	0–1	0.3	0.83	0–3
<i>Chiroderma villosum</i> *	F	0.1	0.27	0–1	0.2	0.58	0–2
<i>Choeroniscus minor</i> *	N	0.3	0.61	0–2	0.1	0.36	0–1
<i>Chrotopterus auritus</i> *	GA	0.2	0.43	0–1	0.4	0.63	0–2
<i>Desmodus rotundus</i> *	S	0.4	0.94	0–3	0.5	0.85	0–3
<b>Glossophaga soricina</b>	N	1.3	1.33	0–4	2.0	4.00	0–15
<i>Glyphonycteris daviesi</i> *	GA	0.3	0.61	0–2			
<i>Glyphonycteris sylvestris</i> *	GA	0.3	0.47	0–1	0.4	0.65	0–2
<b>Lonchophylla thomasi</b>	N	2.6	2.34	0–7	1.3	1.44	0–4
<i>Lophostoma brasiliense</i> *	GA	0.1	0.27	0–1	0.1	0.53	0–2
<i>Lophostoma carrikeri</i> *	GA				0.1	0.27	0–1
<b>Lophostoma silvicolum</b>	GA	1.6	1.50	0–5	1.2	1.58	0–6
<b>Mesophylla macconelli</b>	F	5.3	4.16	0–13	2.6	1.87	0–6
<i>Micronycteris megalotis</i> *	GA				0.1	0.27	0–1
<i>Micronycteris minuta</i> *	GA	0.4	0.85	0–3			
<b>Mimon crenulatum</b>	GA	4.3	4.78	0–19	2.1	2.50	0–10
<i>Phylloderma stenops</i> *	GA	0.4	0.50	0–1	0.3	0.61	0–2
<b>Phyllostomus elongatus</b>	GA	2.9	3.88	0–15	1.4	1.02	0–3
<b>Phyllostomus hastatus</b>	GA	4.2	4.41	0–17	3.4	5.23	0–20
<i>Platyrrhinus brachycephalus</i> *	F	0.2	0.43	0–1	0.3	0.61	0–2
<i>Platyrrhinus helleri</i> *	F	0.4	0.63	0–2	1.0	2.39	0–9
<i>Platyrrhinus infuscus</i> *	F				0.1	0.27	0–1
<b>Rhinophylla fischeriae</b>	F	1.8	1.42	0–4	1.3	1.27	0–4
<b>Rhinophylla pumilio</b>	F	10.1	5.42	1–20	6.5	5.68	0–23
<b>Sturnira lilium</b>	F	6.6	8.86	0–29	6.7	7.94	0–23
<b>Sturnira magna</b>	F	1.7	1.90	0–7	0.9	1.07	0–4
<b>Sturnira tildae</b>	F	3.4	5.23	0–19	5.2	10.07	0–39
<b>Tonatia saurophila</b>	GA	1.3	1.14	0–3	1.3	1.77	0–5
<i>Trachops cirrhosus</i> *	GA	0.6	0.74	0–2	0.7	1.38	0–5
<i>Trinycteris nicefori</i> *	GA	0.1	0.36	0–1			
<b>Uroderma bilobatum</b>	F	1.1	1.33	0–4	1.1	1.00	0–3
<i>Uroderma magnirostrum</i> *	F				0.7	0.91	0–3
<b>Vampyressa bidens</b>	F	1.0	1.52	0–5	1.0	1.11	0–3
<i>Vampyressa brocki</i> *	F	0.4	0.84	0–3	0.7	0.91	0–3
<b>Vampyressa thylene</b>	F	2.5	4.65	0–18	2.1	1.86	0–6
<i>Vampyrodes caraccioli</i> *	GA	0.1	0.27	0–1			
<i>Vampyrum spectrum</i> *	GA	0.1	0.27	0–1	0.2	0.58	0–2
Ensemble-level							
Abundance of frugivores		195.6	61.3	98–276	135.8	50.29	76–249
Abundance of animalivores		16.4	9.84	3–30	11.4	7.62	3–33
Assemblage-level							
Cumulative abundance of phyllostomids		216.7	66.54	105–294	151.1	53.85	83–266
Richness (S)		22.6	3.69	14–28	21.57	4.09	14–28
Diversity (H')		2.2	0.27	1.93–2.89	2.24	0.31	1.71–2.72
Dominance (D)		3.0	0.66	2.06–4.34	3.71	1.15	2.3–6.0
Evenness (PIE)		0.8	0.04	0.73–0.88	0.83	0.06	0.71–0.91
Number of rare species		15.3	3.69	6–21	14.29	3.77	7–20

recommendations (Gardner 1977). Local representatives of these guilds compose ensembles, sensu Fauth et al. (1996). Details on nomenclature can be found in Klingbeil and Willig 2009.

## Landscape structure

Measurement of landscape characteristics involved processing Landsat 5 Thematic Mapper data (path 6, row 63, recorded 25 February 2004) with ERDAS IMAGINE (Leica Geosystems), and creating digital vegetation coverages at each of three focal scales (i.e. circles of 1, 3 and 5 km radius) for each site using ArcInfo 9.1 (ESRI). Image classification based on differences in spectral reflectance properties of surfaces resulted in five landcover classes (closed canopy forest, secondary forest, agriculture and cleared areas, water, or roads and urban areas). However, an accuracy assessment of the classification identified inconsistencies between aerial photographs and spectral-based classification of secondary forest and agriculture. To avoid misrepresentation of land cover classes, only the distinction between closed canopy forest and other habitats (hereafter nonforest) was retained in analyses. Consequently, a digital vegetation coverage using two cover types was created in ArcMap (Fig. 1) and used to quantify landscape structure via FRAGSTATS ver. 3.3 (McGarigal et al. 2002).

The relationship between aspects of biodiversity and landscape characteristics may be weak or non-existent if landscape attributes are quantified at focal scales that are different from those at which species perceive environmental variation. Unfortunately, little is known about the sizes of bat home ranges and species likely differ in the scales at which they interact with the environment because of differences in their mobility, habitat requirements, and life history attributes (With and Crist 1995). Consequently, landscape characteristics should be quantified at a range of relevant scales. As done elsewhere (Gorresen and Willig 2004, Klingbeil and Willig 2009), landscape characteristics were quantified at three spatial scales defined by the radius of a circle (1, 3 and 5 km radius). The smallest of three focal scales (1 km) was chosen to encompass the home ranges of smaller phyllostomids that occur in the study area (e.g. *Glossophaga soricina* and *Mesophylla macconnelli*) as well as home ranges of glean-ing insectivores that forage short distances from their roosts (e.g. *Lophostoma silvicolum*; Kalko et al. 1999). Because of logistical constraints, focal scales greater than 5 km radius were not examined as those areas would overlap substantially, producing spatial autocorrelation.

Landscape structure can be characterized by composition or configuration (McGarigal and McComb 1995). Landscape composition is sensitive to relative proportions of different habitat types, without reference to location or connectivity. Landscape configuration describes the spatial arrangement of habitat types or patches. Because many metrics of landscape structure are correlated strongly and reflect redundant information (Turner et al. 2001, McGarigal et al. 2002), a subset of indices associated with the presence and abundance of species in previous studies (for birds, McGarigal and McComb 1995; for bats, Gorresen and Willig 2004, Klingbeil and Willig 2009) were selected to quantify landscape structure at each focal scale. Percent

cover (cover), mean patch size (size), mean patch density (density), and Simpson's diversity (diversity) characterized landscape composition. Edge density (edge), mean shape index (shape), mean nearest-neighbor distance (nearest), and a mean proximity index (proximity) characterized landscape configuration (for a description of the indices and associated formulas, McGarigal et al. 2002, Klingbeil 2007). As in most fragmentation research, forest was the focal habitat type for all measures of landscape structure.

## Biodiversity and landscape structure

We evaluated effects of landscape structure on taxonomic components of biodiversity, as well as on abundances of ensembles or particular species. Consideration of measures of biodiversity based on relative abundance (i.e. evenness, dominance, rarity and diversity; Stevens and Willig 2002), in addition to richness, is critical because different aspects of biodiversity do not vary with habitat fragmentation in the same manner (Gorresen and Willig 2004). Richness ( $S$ ) was calculated as the number of species captured at each site. The Shannon index estimated species diversity. Hurlbert's probability of interspecific encounter estimated evenness. The Berger-Parker index estimated dominance. Rarity equaled the number of species at a site whose relative abundance in the study area was  $\leq 1/S_{\text{total}}$  where  $S_{\text{total}}$  is the number of unique species regardless of site. These indices (Magurran 2004, Klingbeil and Willig 2009) were calculated separately for the wet and dry seasons.

Measures of landscape structure are correlated with the area of focal patch type (McGarigal and McComb 1995). To avoid confounded assessments of relationships between species abundance and landscape characteristics, the effects of forest area should be removed from each measurement of landscape structure using linear regression approaches. Consequently, residuals of each characteristic of composition and configuration, except percent forest cover (which was used in its original form), were used as independent variables in subsequent analyses (Gorresen and Willig 2004).

To minimize the influence of multi-collinearity among landscape characteristics and to identify the most important factors influencing seasonal patterns of biodiversity, we employed hierarchical partitioning analysis (Chevan and Sutherland 1991) at each focal scale to assess the independent effects of eight landscape characteristics on each biotic response characteristic. Hierarchical partitioning is a regression technique in which all possible linear models are jointly considered in an attempt to identify the most likely explanatory factors, providing a measure of the effect of each characteristic that is largely independent from that of others (Chevan and Sutherland 1991, Mac Nally 2000). Patterns of species abundance, richness and rarity were modeled using Poisson errors with goodness of fit based on  $R^2$ . Because data for species diversity, evenness and dominance were not counts, they were modeled using Gaussian errors with goodness of fit based on  $R^2$ . If a species was captured less than ten times in either season, it was not analyzed at the population level. However, all phyllostomid species, regardless of abundance, were included in estimates of biodiversity for assemblage-level analyses or for estimates of ensemble abundance. The total deviance explained by a generalized linear model with all eight

landscape characteristics was calculated as the sum of their independent contributions to the total explained variance, and equals the goodness of fit measure ( $R^2$ ) of the full model minus the goodness of fit of the null model. Corrections to control for experiment-wise error rates when multiple related tests are performed were not implemented. Use of methods to limit type I errors are controversial in ecology, are extremely conservative, resulting in a high potential for type II errors, and require arbitrary decisions about what constitutes a “family” of analyses (Moran 2003). These adjustments are not recommended for exploratory studies (Roback and Askins 2005). Consequently, we chose not to adjust significance levels, rather, we interpret the results of all analyses based on p-values estimated via randomization procedures with 1000 iterations and an alpha level of 0.05 (Mac Nally 2002). Hierarchical partitioning and associated randomization tests were executed using the hier.part package in the R computing environment (R Development Core Team 2005).

## Results

We captured 5139 individuals representing 46 species, 25 genera and six subfamilies of phyllostomid bat during the study. Most species were captured in both seasons with the exception of nine rare taxa. Four species (i.e. *Lophostoma carrikeri*, *Micronycteris megalotis*, *Platyrrhinus infuscus*, *Uroderma magnirostrum*) were captured only in the wet season, whereas five species (i.e. *Artibeus concolor*, *Glyphonycteris daviesi*, *Micronycteris minuta*, *Trinycteris nicefori*, *Vampyrodes caraccioli*) were captured only in the dry season. Cumulative abundance, richness, and the number of rare phyllostomids was lower in the wet season (2115 individuals, 33 of the 41 species were rare) than in the dry season (3024 individuals, 35 of 42 species were rare; Table 1).

Relationships between abundance and landscape characteristics were species-specific, scale-dependent, and differed between seasons (Table 2). Forest cover and mean nearest neighbor distance were associated most frequently with abundances of particular species and were the only landscape characteristics associated with assemblage-level characteristics (i.e. richness, evenness and diversity) in the wet season. Forest cover was related to abundance more often at small and medium scales, whereas mean nearest neighbor distance was related to abundance more often at medium and large scales (Table 2). Mean nearest neighbor distance was the only significant predictor of abundance of frugivores at the ensemble level and abundance of gleaning animalivores was associated only with mean patch density.

The abundances of frugivorous species were associated more commonly with landscape characteristics at the smallest focal scale in the dry season (11 species) compared to the wet season (six species). The abundance of only one species, *Carollia perspicillata*, had an equivalent response to landscape structure (i.e. negative association with forest cover at 1 km focal scale) in the dry and wet season (Table 2). The abundance of two other understory frugivores (*Vampyressa bidens* and *Mesophylla macconelli*) responded negatively to forest cover in the dry season but positively to forest cover in the wet season. More species exhibited scale-independent responses to landscape characteristics in

the dry season (*Artibeus obscurus*, *A. planirostris*, *Carollia brevicauda*, *Sturnira lilium*, *Vampyressa thuyone*, *Glossophaga soricina*, *Mimon crenulatum*) than in the wet season (*Mesophylla macconelli*, *Vampyressa bidens*, *Phyllostomus elongatus*).

## Discussion

We expected seasonal differences in the scale and landscape characteristics to which species respond for two reasons. First, seasonal patterns in reproduction and behavior impose different energetic and nutritional constraints on habitat use by individuals (Racey and Entwistle 2000). Second, the abundance and spatial distribution of food types differ between wet and dry seasons, affecting foraging patterns and behavior.

### Reproduction and behavior

Insect and fruit abundance peak during the wet season in the tropics (Janzen 1967, Smythe 1970), and data on the reproductive biology of Neotropical phyllostomid bats (although heavily skewed towards frugivores) indicate that most species are seasonal breeders, with reproductive activities timed so that times with the highest energetic demands on bats correspond to times when food abundance is greatest (Fleming et al. 1972, Wilson 1979, Charles-Dominique 1991, Estrada and Coates-Estrada 2001). Data on reproductive patterns of frugivorous bats in the Iquitos region are consistent with those from other sites in the neotropics, and indicate that the greatest proportion of individuals are pregnant at the end of the dry season (i.e. between October and December; Willig unpubl.). As a consequence, energetic demands on bats are highest towards the end of the dry season and beginning of the wet season, when food abundance is low but increasing. This enhances the likelihood that adequate food sources are present during lactation or when juveniles begin to forage independently (Racey and Entwistle 2000, Estrada and Coates-Estrada 2001). These times ostensibly place the greatest resource demands on the environment. Generally, bat pups are not capable of sustained flight and foraging until they achieve adult wing dimensions, or at least 70% of adult body mass (Kunz and Stern 1995). Consequently, pups require milk and remain nutritionally dependent on their mothers for relatively longer periods of time than do the young of many terrestrial mammals (Kunz and Stern 1995). Transport of pups by foraging bats has been reported for several frugivorous and nectarivorous bat species (e.g. *C. perspicillata*, *A. lituratus* and *G. soricina*), which increases wing loading and energy expenditure, and decreases maneuverability and foraging efficiency of nursing mothers (Kunz and Hood 2000). In *C. perspicillata*, lactating females required 1.5–2 times as much energy compared to non-breeding females (Fleming 1988). Many males may exhibit seasonal changes in behavior as well. In tropical regions, males of some species (e.g. *C. perspicillata*, *P. hastatus* and *A. jamaicensis*) defend roosts or harems, investing considerable time and energy when females are pregnant and young are present (Kunz and Hood 2000). As a consequence, higher energetic demands associated with reproduction or

Table 2. Landscape characteristics with significant ( $p < 0.05$ ) independent effects on population-level (species abundances), assemblage-level (richness, diversity, dominance, evenness, and rarity), and ensemble-level (total abundances of species in guilds) characteristics at each of three focal scales in the dry and wet seasons separately. Only the landscape characteristic with the greatest independent effect at each focal scale is displayed. The direction of the relationship (+, -) is shown before the characteristic.  $R^2_{dev}$  shown in parentheses, is the total deviance explained by a generalized linear model with all eight landscape characteristics. It is the sum of the independent contribution of all eight landscape characteristics to the total explained variance, and equals the goodness of fit measure ( $R^2$ ) of the full model minus the goodness of fit of the null model. Landscape characteristics in bold represent configurational characteristics, compositional characteristics are not bold

	Dry season			Wet season		
	1 km	3 km	5 km	1 km	3 km	5 km
Population-level						
Frugivores						
<i>Artibeus anderseni</i>						+ <b>proximity (0.61)</b>
<i>Artibeus gnomia</i>		+ <b>proximity (0.71)</b>				
<i>Artibeus lituratus</i>	- cover (0.79)	+ <b>edge (0.74)</b>	- <b>shape (0.66)</b>		+ <b>shape (0.59)</b>	
<i>Artibeus obscurus</i>	- cover (0.82)	- cover (0.90)	- cover (0.56)		+ <b>edge (0.76)</b>	
<i>Artibeus planirostris</i>	- cover (0.58)	- cover (0.42)	- cover (0.46)		+ density (0.71)	+ <b>shape (0.73)</b>
<i>Carollia benkeithi</i>	+ diversity (0.84)					- <b>nearest (0.69)</b>
<i>Carollia brevicauda</i>	- cover (0.61)	- cover (0.64)	- cover (0.78)	- cover (0.48)	- <b>nearest (0.82)</b>	
<i>Carollia perspicillata</i>	- cover (0.49)			- cover (0.53)		
<i>Mesophylla macconelli</i>	- cover (0.72)		- cover (0.41)	- cover (0.79)	+ cover (0.82)	+ cover (0.75)
<i>Rhinophylla fischeriae</i>			- <b>shape (0.66)</b>		+ cover (0.57)	
<i>Rhinophylla pumilio</i>		- <b>nearest (0.90)</b>				
<i>Sturnira lilium</i>	- cover (0.54)	- cover (0.72)	- cover (0.75)	- cover (0.48)	- <b>nearest (0.90)</b>	- <b>nearest (0.63)</b>
<i>Sturnira magna</i>	+ <b>edge (0.63)</b>			+ diversity (0.95)		- <b>proximity (0.86)</b>
<i>Sturnira tildae</i>	+ <b>edge (0.76)</b>				+ density (0.76)	
<i>Uroderma bilobatum</i>		- cover (0.35)	- cover (0.54)		- <b>nearest (0.78)</b>	
<i>Vampyressa bidens</i>		- cover (0.76)	- cover (0.86)	+ cover (0.68)	+ cover (0.65)	+ cover (0.61)
<i>Vampyressa thuyone</i>	- density (0.75)	- density (0.85)	- density (0.84)			- <b>nearest (0.74)</b>
Nectarivores						
<i>Glossophaga soricina</i>	- cover (0.79)	- cover (0.73)	- cover (0.51)		+ <b>nearest (0.56)</b>	+ <b>nearest (0.79)</b>
<i>Lonchophylla thomasi</i>					- cover (0.63)	+ <b>shape (0.66)</b>
Animalivores						
<i>Lophostoma silvicolium</i>			- diversity (0.80)	+ density (0.82)		- diversity (0.88)
<i>Mimon crenulatum</i>	+ <b>edge (0.50)</b>	+ <b>edge (0.54)</b>	+ <b>edge (0.54)</b>	+ <b>edge (0.62)</b>	+ <b>edge (0.31)</b>	
<i>Phyllostomus elongatus</i>		+ <b>nearest (0.47)</b>	+ <b>nearest (0.83)</b>	+ cover (0.75)	+ cover (0.55)	+ cover (0.64)
<i>Phyllostomus hastatus</i>		+ <b>edge (0.67)</b>			+ density (0.78)	
<i>Tonatia saurophila</i>					+ cover (0.79)	+ cover (0.75)
Assemblage-level						
Richness					- <b>nearest (0.62)</b>	- <b>nearest (0.76)</b>
Evenness		- <b>nearest (0.85)</b>	- <b>nearest (0.82)</b>			+ cover (0.75)
Dominance			- <b>nearest (0.78)</b>			
Rarity						
Diversity					+ cover (0.47)	+ cover (0.75)
Ensemble-level						
Frugivore abundance	- cover (0.79)	- cover (0.69)	- cover (0.72)		- <b>nearest (0.84)</b>	- <b>nearest (0.55)</b>
Animalivore abundance	+ <b>edge (0.45)</b>	+ <b>edge (0.49)</b>			+ density (0.79)	

roost defense may result in a seasonal decrease in home range size. For example, *C. perspicillata* shorten the duration of flights when pregnant or lactating, possibly to compensate for the metabolic cost of producing milk or the increased weight of carrying a fetus (Charles-Dominique 1991). Similarly, if male bats spend more time defending resources, less time can be allocated to searching and securing resources. Consequently, the focal scale at which landscape characteristics are important may be smaller during periods associated with pregnancy, lactation, or roost

defense. Indeed, almost twice as many frugivores were significantly associated with landscape characteristics at the 1 km scale in the dry season as compared to the wet season (Table 2). Conversely, landscape characteristics at the 3 km scale were related to species abundances most often in the wet season. A change in the scale of response may indicate the severity of energetic and parental constraints associated with reproduction or that greater food abundance enables bats to spend more time exploring larger areas for higher quality food sources and roost sites.

## Animalivore ensemble

Seasonal differences in the particular landscape characteristic to which a species responds may reflect seasonal differences in the abundance or diversity of food sources. During times of peak insect abundance in the wet season, gleaning animalivores likely have a greater number and diversity of food sources concentrated within a shorter distance of roost sites. Animalivores are proficient flyers in highly cluttered environments and exploit closed canopy forest for roosting, feeding, and protection (Kalko et al. 1999, Kunz and Lumsden 2003). Indeed, positive associations with forest cover are expected when resources are plentiful and many studies have identified positive relationships between abundance of animalivores and extent of forest habitat (Fenton et al. 1992, Schulze et al. 2000, Gorreson and Willig 2004, Meyer and Kalko 2008, this study). However, when food resources are scarce and widely dispersed, as may be the case in the dry season, a mix of profitable and less profitable foraging patches for animalivores may exist. To meet dietary needs, bats may visit habitats of lower quality (i.e. edge) with greater predation risk or forage over a greater area, exploiting habitat boundaries as flyways. Consequently the spatial arrangement and configuration of forest patches, rather than the composition of the landscape may be more important in the dry season.

## Frugivore ensemble

Similar to the situation for insectivorous bats, the abundance and diversity of food sources available to frugivorous bats is higher in the wet season (Janzen 1967, Smythe 1986, Mello et al. 2004, Mello 2009); however the importance of particular landscape characteristics differ between the two ensembles (Table 2). Although animalivores respond to landscape composition in the wet season, frugivores respond to landscape configuration. A response to configuration may be an indication of the diversity of food sources available in the wet season rather than the abundance of fruit per se. Frugivores respond negatively to forest cover (indicating a preference for gap and secondary forest habitats) in the dry season but respond negatively to nearest neighbor distance of forest patches (indicating a preference for multiple closely spaced forest patches with little secondary forest habitat) in the wet season. This may indicate a seasonal change in foraging strategy or fruit species for a number of bat species (Fleming 1988, Mello et al. 2004). Frugivores respond to temporal and spatial availability of resources, and diets of some frugivores change over the course of the year and throughout their geographic ranges as the abundance and availability of different fruit species changes (Bonaccorso 1979, Giannini 1999, da Silva et al. 2008).

Bats that rely on figs for a substantial portion of their diet may need to incorporate fruit from shrubs and trees common in successional forest and gaps (i.e. *Cecropia*) during the dry season, especially in fragmented forest ecosystems because they are more abundant and less spatially dispersed than are figs. Bat species from the tribe Ectophillini (including the genera *Artibeus*, *Vampyressa*, *Uroderma* and *Mesophylla* from this study) are often considered fig specialists (Fleming 1986, Giannini and Kalko 2004) and all genera contained

species that responded negatively to forest cover in the dry season but not in the wet season. In particular, *M. macconelli* and *V. bidens* responded negatively to forest cover in the dry season but positively to forest cover in the wet season. These bats are two of the smallest in the tribe and consequently may be affected most severely by a seasonal decrease in fig abundance or diversity (i.e. can not travel long distances in a night due to energetic constraints). This decrease may force individuals in fragmented forests to include a less profitable but more abundant fruit source in their diet.

Fruits of *Cecropia* species are often present in the diet of ectophilline bats and may be the dominant fruit consumed in some regions where *Ficus* trees are not abundant (Lobova et al. 2003, Sampaio 2003, da Silva et al. 2008). *Cecropia* and *Ficus* are both common, diverse, and available year round in the Amazon, but generally are present in different abundances, exhibit different fruiting strategies and populations are likely affected differently by forest fragmentation (Milton et al. 1982, Gorchov et al. 1993, Olea-Wagner et al. 2007). Plants in the genus *Cecropia* are pioneer species, with a continuous fruiting strategy, providing abundant fruit year round in the Neotropics (Bonaccorso 1979, Estrada et al. 1984). Trees are generally common in gap, successional, and recently deforested habitats and increase in abundance as a result of forest fragmentation (Gorchov et al. 1993, Lobova et al. 2003). Plants in the genus *Ficus* are colonizing species, present in primary and secondary forest, exploiting natural gaps as well as forest edges. Trees tend to have clumped distributions, are present in low densities, exhibit an asynchronous fruiting strategy within the population, and produce large crops of fruit one or more times a year that are present for a short number of days (Janzen 1979, Milton et al. 1982). The abundance and proximity of fruiting *Ficus* trees likely decreases as a consequence of forest fragmentation and may be especially low during the dry season. Larger bats in the Ectophillini (*Artibeus lituratus*, *A. planirostris*, *A. obscurus* and *Uroderma bilobatum*) generally responded to landscape configuration at intermediate to large focal scales in the wet season, indicating that the shape and spatial arrangement of forest patches were more important than was landscape composition. Fruit bats forage based on olfactory cues and may be exploiting spatial features of the landscape to minimize long distance travel over open areas when commuting to spatially dispersed resources found in distant forest patches. Additionally, bats undertake multiple trips between resource patches (i.e. fruiting *Ficus* trees) and nearby feeding roosts each night, and may exploit spatial features (e.g. shape or distance to nearby forest patches) to avoid predation.

Seasonal responses to landscape structure were similar for *S. lilium*, *Carollia brevicauda*, *C. perspicillata* and *C. benkeithi*, (Table 1), and differences between species may be a consequence of degrees of dietary specialization. Fruit preferences influence foraging behavior or strategy, and consequently mold species responses to landscape structure. The degree of importance of *Piper* in the diets of *Carollia* is species-specific, with *C. benkeithi* exploiting primarily *Piper*, *C. brevicauda* and *C. perspicillata* incorporating greater proportions of *Vismia*, *Cecropia* and *Solanum*, and *C. brevicauda* being the most euryphagic of the congeners (Fleming 1988, 2004, Thies and Kalko 2004). Additionally, *C. perspicillata* primarily exploits species of *Piper* found in

gaps and secondary forest, rather than the forest *Piper* species that are more prevalent in the diet of *C. benkeithi* (Thies and Kalko 2004). This specialization on gap species of *Piper*, in addition to other fruits primarily found in successional forest, likely accounts for the consistent negative response to forest cover, regardless of season, for *C. perspicillata*.

*Sturnira lilium* is best considered to be a generalist, opportunistic frugivore, exploiting fruits from *Solanum*, *Piper*, *Vismia*, *Cecropia* and *Ficus* species (Gorchov et al. 1995, Giannini 1999, Olea-Wagner et al. 2007). Similar to *C. perspicillata* and *C. brevicauda*, *S. lilium* is often one of the most abundant bat species throughout the Neotropics (Estrada et al. 1993, Galindo-Gonzalez et al. 2000) and is less sensitive to forest fragmentation than are many other phyllostomids. Despite the incorporation of *Ficus* in its diet, and sometimes being grouped with canopy frugivores like *Artibeus* and most other stenodermatines (Gardner 1977), *S. lilium* is more similar to species of *Carollia* than to *Artibeus* in its nightly foraging distances (Loayza and Loiselle 2008) and may exemplify an extreme generalist among frugivores. The response of *S. lilium* to landscape structure was most similar to *C. brevicauda*, which may be an indication that the generalist nature of their diets is driving their responses to landscape structure.

## Biodiversity

Bat biodiversity (i.e. richness, evenness, dominance, rarity, and species diversity) was similar in wet and dry seasons (Table 1) but relationships of particular characteristics with landscape structure were season-specific (Table 2). Seasonal responses to composition and configuration at the assemblage level are likely a consequence of changes in the size of local populations rather than changes in assemblage composition per se. Consistent with patterns at other neotropical localities, differences in the abundance of phyllostomids were observed between seasons (Mello 2009), however the proportion of frugivores and animalivores remained constant (Table 1). Despite differences in diet and particular mode of foraging, many neotropical bats take advantage of multiple short-term roosts in trees or foliage, and exploit ephemeral resource patches that are linked to seasonal variation in precipitation (Kalko and Handley 2001, Kunz and Lumsden 2003, Mello 2009). Consequently, spatially explicit interactions of assemblages with landscapes are constantly changing as a function of roost locations, food abundance, and time of year. As a result, identifying ecologically meaningful responses at the assemblage level may require a larger spatial context compared to responses at the population- and ensemble-level, especially in assemblages characterized by high taxonomic and functional diversity. Indeed, assemblage-level characteristics were not significantly associated with landscape characteristics at the smallest focal scale in either season.

## Overview

The successful design of conservation reserves may be predicated on a deeper understanding of seasonal dynamics in the use of space by different guilds. Seasonal variation in resource abundance and diversity, in conjunction with

changes in time and energy budgets imposed by reproductive constraints, likely influence the foraging behavior of neotropical phyllostomids throughout the year. Changes in the abundance, diversity, and proximity of preferred resources (i.e. roost and food) as a consequence of forest fragmentation may intensify the severity of seasonal changes in resource availability, necessitating shifts in foraging strategy that may not otherwise be needed in unfragmented landscapes. Identifying seasonal shifts in habitat use and dietary composition, especially in tropical regions that have a history of forest conversion to agriculture, may provide critical information to account for variation in local assemblage structure as well as responses of species abundances to landscape structure throughout the year. Future work will benefit from the inclusion of additional sites and landscapes that have been subject to a wider range of anthropogenic effects, and as a consequence, exhibit a greater diversity of forest fragmentation patterns. Additionally, long-term studies that include sampling in more than two seasons have the potential to identify population-, ensemble-, and assemblage-level responses to landscape structure that arise because of differences in precipitation and food abundance.

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