

# Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest

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## Summary

1. Habitat loss and fragmentation are serious threats to biodiversity, especially in the Amazon Basin, where biodiversity is greatest and deforestation is continuing at an alarming rate. Nonetheless, little is known about the responses of biotas to spatially explicit aspects of landscape structure.
2. Bats are a promising indicator group for studying consequences of forest fragmentation in the Neotropics. Therefore, population- and assemblage-level responses of bats to landscape composition and configuration were quantified at each of three focal scales (circles of 1-, 3-, and 5-km radii) at 14 sites in lowland Amazonia.
3. Responses to landscape characteristics were scale-dependent. Abundance and richness were higher in moderately fragmented forest than in continuous forest. Moreover, the abundance of each of nine frugivorous species decreased with increasing forest cover.
4. The abundance of frugivores probably responded to landscape composition (e.g. percentage forest, mean patch density) because of an increase in early successional fruits and flowers in areas with reduced canopy cover. In contrast, abundances of gleaning animalivores responded to landscape configuration (e.g. edge density), probably by exploiting low-contrast edges (i.e. closed canopy forest patches embedded in secondary forest) while foraging and travelling between higher quality resource patches.
5. *Synthesis and applications.* Species- and ensemble-specific responses to aspects of landscape structure suggest that both compositional and configurational aspects need to be managed effectively in conservation planning. However, conservation decisions based on associations of biodiversity metrics (e.g. richness, diversity and rarity) with landscape structure may be problematic as they are composite characteristics that mask individual responses and potentially reflect only patterns of the dominant species or groups.

**Key-words:** Amazon, biodiversity, conservation, Chiroptera, ensemble, forest fragmentation, frugivore guild, gleaning animalivore guild, landscape structure, scale

## Introduction

Deforestation and fragmentation of tropical forests continue at alarming rates (FAO 2003). In the Amazon, >2 million ha are deforested annually (Fearnside *et al.* 2005), and this rate will probably increase as more paved roads are constructed within the region's core. Indeed, habitat fragmentation is a pervasive feature of modern landscapes and is currently the most serious threat to species persistence in tropical forests (Ewers & Didham 2006). The primary consequences of

fragmentation are loss of original habitat, creation of forest edge habitats, reduction in size and isolation of habitat patches, all of which may influence species composition (Wilcox & Murphy 1985). Moreover, remnant forest patches often experience altered disturbance regimes and microclimate, invasion by exotic plant and animal species, and increased human exploitation such as hunting, burning, grazing, and extraction of resources (Turner & Corlett 1996).

Few studies have compared population characteristics among multiple landscapes with different degrees of fragmentation (i.e. landscapes that differ in the size, number, or spatial arrangement of patches). Moreover, studies that have analysed

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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 & McComb 1995; Villard, Trzcinski & Merriman 1999; Turner, Gardner & O'Neill 2001).

#### BATS AND CONSERVATION

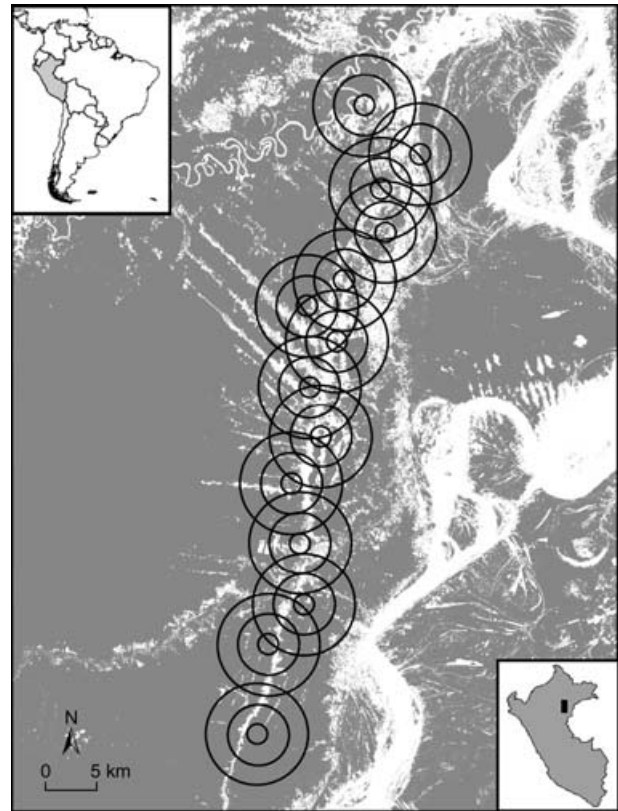
Because of their local abundance, species richness, and ecological diversity, bats are a promising indicator group for studying consequences of habitat fragmentation in the Neotropics (Fenton *et al.* 1992; Kalko 1998; Medellín, Equihua & Amin 2000). Bats increase in species richness with decreasing latitude (Willig & Selcer 1989), and achieve their highest taxonomic, functional (i.e. all trophic groups represented), and phenetic diversity at sites in tropical regions (Stevens & Willig 2002; Stevens, Willig & Strauss 2006). Some species are highly mobile and may travel long distances between roosts and foraging sites, making them efficient seed dispersers, pollinators, and 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 response of bats to habitat fragmentation in the Neotropics are equivocal (Fenton *et al.* 1992; Cosson, Pons & Masson 1999; Medellín *et al.* 2000; Schulze, Seavy & Whitacre 2000). 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 (e.g. size of forest fragments; Cosson *et al.* 1999). 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, the population-level responses of bats to a suite of landscape characteristics were species-specific and scale-dependent (Gorresen & Willig 2004; Gorresen, Willig & Strauss 2005). Consequently, associations between biodiversity and simple characterizations of landscape structure may be inadequate for understanding biotic responses to fragmentation. We predict that both compositional and configurational aspects of landscape structure will affect the abundance of species and thus, biodiversity. Because of differences in foraging patterns and food resources, we predict that species will respond in a guild-specific way to the composition and configuration of landscapes.

## Materials and methods

#### STUDY AREA

Research was conducted in unflooded (*terra firme*) Amazonian rainforest, southwest of Iquitos (3°46'30"S, 73°24'33"W) in north-eastern Peru (Fig. 1). Altitude ranges from sea level to 200 m above sea level



**Fig. 1.** Classified image of study area displaying concentric focal scales (1-, 3-, and 5-km radii) centred on each of 14 sites. The forest class is displayed in grey whereas the non-forest class is displayed in white. Location of Peru (grey) in South America is displayed in the upper-left corner of the map. The image in the bottom-right corner shows the location of the study area (black rectangle) in Peru. Study sites from north to south, with geographical coordinates in decimal degrees are: Arboretum (−3.83, −73.37), Km 12 (−3.88, −73.33), Km 18 (−3.90, −73.37), Km 21 (−3.95, −73.37), Km 28 (−3.98, −73.41), Km 31.5 (−4.00, −73.45), Km 34 (−4.04, −73.43), Km 39.5 (−4.07, −73.46), Km 44 (−4.12, −73.45), Km 49 (−4.16, −73.48), Km 55 (−4.21, −73.49), Km 60 (−4.26, −73.49), Km 66.5 (−4.30, −73.53), and Km 75 (−4.37, −73.55).

(Kalliola & Flores 1998). The climate is tropical, humid and almost aseasonal, with mean monthly temperatures of 25–27 °C, and average high and low temperatures of between 32 °C and 21 °C, respectively. Total annual precipitation ranges from 2600 to 3100 mm (Madigosky & Vatnick 2000).

#### EXPERIMENTAL DESIGN

Fourteen sampling sites were established along the highway from Iquitos to Nauta (Fig. 1). The number and placement of sites were determined so that sampling locations were >4 km apart, included a representative range of habitat configurations, were accessible by field crews, and were located on either side of the highway. The centres of sampling sites were located using a Global Positioning System (Garmin® GPS 12 Personal Navigator®, Kansas, USA).

The bat fauna at each site was sampled with ground-level mist nets (56 808 net metre-hours) between September 2004 and January 2005. Biases associated with the use of ground-level mist nets to sample bat communities have been addressed by a number of authors (e.g. Handley 1967; Kunz & Brock 1975; Kalko 1998).

Consequently, analyses of the response of bats to landscape structure in this study were restricted to phyllostomids, consistent with approaches undertaken in a number of recent studies (Kalko 1998; Gorresen & Willig 2004; Willig *et al.* 2007).

At each site, 12 mist nets (12 × 2.6 m) were erected in forest habitat and positioned across trails and flyways on each sampling night. Bats were captured during three two-night surveys, totalling 84 sampling nights. Each survey was separated by 35 to 55 days. Sampling was not conducted on nights immediately before, during, or following a full moon (i.e. when the moon is ≥90% illuminated), as decreased activity of some species is associated with high illumination (i.e. lunar phobia; Morrison 1975). Nets were opened from dusk to 23:30 h (approximately 5.5 h) each night, except during severe weather (i.e. strong wind or rain) to avoid health risks to bats. Nets were checked continually, with a maximum of 30–45 m between visits to particular nets. Hair was trimmed on the back of each captured bat to facilitate identification of recaptures. Voucher specimens facilitated accurate taxonomic identification and were deposited at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, Peru. Nomenclature follows Simmons (2005), except for recognizing *Carollia benkeithi* (Solari & Baker 2006) rather than *C. castanea*, and *Artibeus planirostris* rather than *A. jamaicensis* (Lim *et al.* 2004). Phyllostomids were classified into broad foraging guilds (i.e. frugivores, nectarivores, gleaning animalivores, and sanguinivores; Table 1) based on published recommendations (Gardner 1977; Willig 1986). Local representatives of these guilds represent ensembles, *sensu* Fauth *et al.* (1996).

#### SATELLITE IMAGERY

Measurement of landscape characteristics involved processing Landsat 5 Thematic Mapper data (path 6, row 63, recorded 25 February 2004) with ERDAS IMAGINE (Leica Geosystems, Georgia, USA), creating a digital vegetation coverage at each of three focal scales (i.e. circles of 1-, 3-, and 5-km radii) using ArcInfo 9.1 (ESRI, Georgia, USA). Image data originally were classified into five land-cover classes (closed canopy forest, secondary forest, agriculture and cleared areas, water, or roads and urban areas) based on spectral reflectance properties. However, inconsistencies between aerial photographs and spectral classification existed for secondary forest and agriculture classes at the largest focal scale. 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 version 3.3 (McGarigal *et al.* 2002).

#### LANDSCAPE STRUCTURE

The relationship between biodiversity and landscape characteristics may be weak or non-existent if landscape attributes are quantified at a focal scale that is different from that at which species perceive environmental variation. Unfortunately, little is known about the sizes of bat home ranges, and species probably differ in the scales at which they interact with the environment because of differences in their mobility, habitat requirements, and life-history characteristics, (Kotliar & Wiens 1990; Andr n 1994; With & Crist 1995). Consequently, landscape characteristics should be quantified at a range of relevant scales. As done elsewhere (Gorresen & Willig 2004), 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

**Table 1.** Summary statistics (mean, standard deviation, and range) of population-level (abundance of each species) and assemblage-level (indices of biodiversity) characteristics for all 14 sites in Iquitos, Peru. Taxa in bold were analysed 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

	Ensemble	Mean	Standard deviation	Range
Population-level				
<i>Carollia brevicauda</i>	F	39.7	20.11	17–92
<i>Carollia benkeithi</i>	F	8.4	8.76	0–27
<i>Carollia perspicillata</i>	F	73.0	28.93	38–138
<i>Rhinophylla fischeriae</i> *	F	1.8	1.42	0–4
<i>Rhinophylla pumilio</i>	F	10.1	5.42	1–20
<i>Desmodus rotundus</i> *	S	0.4	0.94	0–3
<i>Choeroniscus minor</i> *	N	0.3	0.61	0–2
<i>Glossophaga soricina</i> *	N	1.3	1.33	0–4
<i>Lonchophylla thomasi</i> *	N	2.6	2.34	0–7
<i>Chrotopterus auritus</i> *	GA	0.2	0.43	0–1
<i>Glyphoncyteris daviesi</i> *	GA	0.3	0.61	0–2
<i>Glyphoncyteris sylvestris</i> *	GA	0.3	0.47	0–1
<i>Lophostoma brasiliense</i> *	GA	0.1	0.27	0–1
<i>Lophostoma silvicolum</i> *	GA	1.6	1.50	0–5
<i>Micronycteris minuta</i> *	GA	0.4	0.85	0–3
<i>Mimon crenulatum</i> *	GA	4.3	4.78	0–19
<i>Phylloderma stenops</i> *	GA	0.4	0.50	0–1
<i>Phyllostomus elongatus</i> *	GA	2.9	3.88	0–15
<i>Phyllostomus hastatus</i> *	GA	4.2	4.41	0–17
<i>Tonatia saurophila</i> *	GA	1.3	1.14	0–3
<i>Trachops cirrhosus</i> *	GA	0.6	0.74	0–2
<i>Trinycteris nicefori</i> *	GA	0.1	0.36	0–1
<i>Vampyrus spectrum</i> *	GA	0.1	0.27	0–1
<i>Artibeus concolor</i> *	F	0.4	0.63	0–2
<i>Artibeus lituratus</i> *	F	3.9	4.67	0–18
<i>Artibeus obscurus</i>	F	10.5	6.55	2–25
<i>Artibeus planirostris</i>	F	22.3	13.97	2–51
<i>Chiroderma trinitatum</i> *	F	0.1	0.27	0–1
<i>Chiroderma villosum</i> *	F	0.1	0.27	0–1
<i>Dermanura anderseni</i> *	F	0.8	1.19	0–4
<i>Dermanura gnoma</i> *	F	1.7	1.73	0–6
<i>Mesophylla macconnelli</i> *	F	5.3	4.16	0–13
<i>Platyrrhinus brachycephalus</i> *	F	0.2	0.43	0–1
<i>Platyrrhinus helleri</i> *	F	0.4	0.63	0–2
<i>Sturnira lilium</i>	F	6.6	8.86	0–29
<i>Sturnira magna</i> *	F	1.7	1.90	0–7
<i>Sturnira tildae</i> *	F	3.4	5.23	0–19
<i>Uroderma bilobatum</i> *	F	1.1	1.33	0–4
<i>Vampyressa bidens</i> *	F	1.0	1.52	0–5
<i>Vampyressa brocki</i> *	F	0.4	0.84	0–3
<i>Vampyressa thylene</i> *	F	2.5	4.65	0–18
<i>Vampyrodes caraccioli</i> *	F	0.1	0.27	0–1
Assemblage-level				
Cumulative abundance of phyllostomids		216.7	66.54	105–294
Richness (S)		22.6	3.69	14–28
Diversity (H')		2.2	0.27	1.93–2.89
Dominance (D)		3.0	0.66	2.06–4.34
Evenness (PIE)		0.8	0.04	0.73–0.88
Number of rare species		15.3	3.69	6–21

gleaning insectivores that forage short distances from their roosts (e.g. *Lophostoma silvicolum* may travel only 500 m from roosts while searching for prey; Kalko *et al.* 1999). Focal scales greater than a 5-km radius were not examined because those areas would overlap substantially, producing spatial autocorrelation. Moreover, the selected focal scales facilitate comparison with previous research on scale-dependent associations of bats with landscape structure (Gorresen & Willig 2004; Gorresen *et al.* 2005).

Landscape structure can be characterized by composition or configuration. 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 (Riitters *et al.* 1995; 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, Rolstad 1991; McGarigal & McComb 1995; Villard *et al.* 1999; for bats, Gorresen & Willig 2004) were selected to quantify landscape structure at each focal scale. Percentage 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-neighbour distance (Nearest), and a mean proximity index (Proximity) characterized landscape configuration. Forest was the principal habitat type for all measures of landscape structure and nonforest represented the matrix within which forest patches were dispersed.

#### BIODIVERSITY AND LANDSCAPE STRUCTURE

Taxonomic components of biodiversity and the abundance of ensembles or particular species assessed the effects of land use characteristics. Consideration of measures of biodiversity based on relative abundance (i.e. evenness, dominance, rarity, and diversity; Purvis & Hector 2000; Stevens & Willig 2002; Wilsey *et al.* 2005), in addition to richness, is critical because different measures do not vary with habitat fragmentation in the same manner (Gorresen & Willig 2004). Richness (S) was calculated as the number of species captured at each site. The Shannon index (Pielou 1975) was used to estimate diversity. Hurlbert's probability of interspecific encounter (PIE; Hurlbert 1971) was used to estimate evenness. The index of Berger & Parker (1970) was used to estimate dominance. Rarity equalled the number of species at a site whose relative abundance in the study area was  $\leq S^{-1}$  (Camargo 1992).

Measures of landscape structure are correlated with the area of focal patch type (Rolstad 1991; McGarigal & McComb 1995). To avoid confounded assessments of relationships between species abundance and landscape characteristics, it was necessary to remove the effects of forest area from each measurement of landscape structure using regression approaches. The residuals were used together with forest cover in its original form, as independent variables in subsequent analyses (Gorresen & Willig 2004).

To minimize the influence of multi-collinearity among landscape characteristics and to identify the most important factors influencing patterns of biodiversity, we employed hierarchical partitioning analysis (Chevan & 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 & Sutherland 1991; Mac

Nally 2000). Patterns of species abundance, richness and rarity were modelled using Poisson errors with goodness of fit based on *r*-square. Because data for species diversity, evenness and dominance were not counts, they were modelled using Gaussian errors with goodness of fit based on *r*-square. If a species was captured less than 10 times, it was not analysed at the population level. However, all 42 phyllostomid species, regardless of abundance, were included in estimates of biodiversity for assemblage-level analyses or for estimates of ensemble abundance.

Significance ( $\alpha = 0.05$ ) was estimated using Mac Nally's (2002) randomization test with 1000 iterations. Hierarchical partitioning and associated randomization tests were executed using the hier.part package in the R computing environment (R Development Core Team 2005).

#### SPATIAL AUTOCORRELATION

Abundance data often are autocorrelated spatially, violating assumptions of many statistical techniques. This may lead to inaccurate conclusions by biasing error rates (Legendre 1993). To address this, the construction of ecological and geographical distance matrices was based on percentage dissimilarity (Renkonen index) of species abundances between sites (Krebs 1989) and straight-line distances between geographical centres of sites, respectively. Because no a priori assumptions were made regarding the form of association between ecological and geographical distances, Spearman rank correlation (Sokal & Rohlf 1995) was used to quantify associations (Gorresen & Willig 2004).

### Results

A total of 56 808 mist-net metre-hours resulted in the capture of 3024 phyllostomids representing 42 species and 25 genera. Total abundance of particular species (Table 1) ranged over three orders of magnitude, from 1 (i.e. *Lophostoma brasiliense*, *Vampyrum spectrum*, *Chiroderma trinitatum*, and *Chiroderma villosum*) to 1022 (*Carollia perspicillata*). The majority of species (35 of the 42 species) were rare.

#### SPATIAL AUTOCORRELATION

Ecological and geographical distances were not associated significantly for sites (Spearman correlation:  $r = 0.1$ ,  $P = 0.714$ ). Consequently, spatial autocorrelation is minimal and corrective measures are unnecessary (Legendre 1993).

#### RESPONSE OF POPULATION- AND ASSEMBLAGE-LEVEL CHARACTERISTICS TO LANDSCAPE STRUCTURE

Relationships between abundance and landscape characteristics were species-specific and scale-dependent (Table 2). In general, abundances of frugivorous species responded significantly to characteristics of landscape composition more than to characteristics of landscape configuration. In contrast, abundances of gleaning animalivores responded significantly most often to characteristics of landscape configuration. Moreover, both negative and positive associations between abundance and landscape characteristics were observed at

**Table 2.** Percentage of independent effects of landscape characteristics on population-level (species abundances) and assemblage-level (richness, diversity, dominance, evenness, and rarity) characteristics at each of three focal scales. Values in bold represent significant effects ( $P < 0.05$ ). Significant effects that depict a negative relationship are shown in parentheses.  $R_{dev}^2$  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

	Scale	$R_{dev}^2$	Compositional characteristics				Configurational characteristics			
			Cover	Density	Size	Diversity	Edge	Shape	Nearest	Proximity
<b>Frugivores</b>										
<i>Carollia benkeithi</i>	1	0.84	5.2	5.5	11.8	<b>49.4</b>	13.1	5.2	6.5	3.3
	3	0.36	2.8	16.3	7.0	30.9	3.3	23.9	7.2	8.6
	5	0.61	10.6	13.9	4.3	11.8	5.2	22.0	10.8	21.4
<i>Carollia brevicauda</i>	1	0.61	<b>36.6(-)</b>	3.8	4.6	4.3	31.4	6.7	11.2	1.4
	3	0.64	<b>43.0(-)</b>	4.3	4.6	14.1	18.3	2.1	3.6	10.0
	5	0.78	<b>41.1(-)</b>	4.4	5.0	10.4	20.6	5.9	3.3	9.3
<i>Carollia perspicillata</i>	1	0.49	<b>47.1(-)</b>	9.4	6.2	13.4	1.9	6.7	12.5	2.9
	3	0.72	21.9	12.5	13.4	3.7	7.0	17.4	18.1	6.0
	5	0.75	19.1	20.6	10.4	3.7	15.0	3.0	23.4	4.7
<i>Artibeus anderseni</i>	1	0.44	27.1	16.9	11.9	9.5	22.6	7.4	2.3	2.4
	3	0.58	21.7	10.5	5.3	2.9	30.5	9.4	13.2	6.4
	5	0.75	20.8	4.0	13.5	11.4	25.1	13.0	5.3	6.9
<i>Artibeus gnoma</i>	1	0.49	10.1	7.3	5.7	17.1	26.7	3.3	3.2	26.8
	3	0.71	0.8	7.1	17.3	11.2	4.8	13.3	3.5	<b>41.9</b>
	5	0.31	6.6	10.3	5.2	4.5	39.3	5.1	7.5	21.4
<i>Artibeus lituratus</i>	1	0.79	<b>30.7(-)</b>	5.4	9.6	4.5	16.2	24.1	8.0	1.5
	3	0.74	19.3	16.2	9.1	2.6	<b>35.1</b>	11.4	1.5	4.8
	5	0.66	29.1	2.6	9.5	6.9	6.8	<b>30.9(-)</b>	5.3	9.0
<i>Artibeus obscurus</i>	1	0.82	<b>50.7(-)</b>	3.4	6.6	2.7	18.7	10.4	6.5	1.0
	3	0.90	<b>31.6(-)</b>	13.6	6.0	3.2	<b>29.4</b>	6.8	7.6	1.8
	5	0.56	<b>45.9(-)</b>	3.2	6.6	1.7	11.1	20.9	6.7	4.0
<i>Artibeus planirostris</i>	1	0.58	<b>66.9(-)</b>	6.3	3.9	3.4	1.8	0.8	5.4	11.5
	3	0.42	<b>60.4(-)</b>	2.6	2.7	6.2	5.9	3.7	5.8	12.7
	5	0.46	<b>46.5(-)</b>	12.9	5.8	21.5	7.0	1.5	3.7	1.1
<i>Mesophylla macconelli</i>	1	0.72	<b>33.4(-)</b>	11.3	7.5	5.0	17.0	12.5	4.9	8.4
	3	0.61	31.5	14.2	12.4	7.8	13.6	2.1	15.6	2.9
	5	0.41	<b>52.5(-)</b>	12.5	6.5	8.0	5.2	6.6	1.8	6.8
<i>Rhinophylla fischeriae</i>	1	0.49	0.0	18.0	20.3	8.7	10.3	5.3	32.3	5.0
	3	0.29	18.9	38.5	16.2	11.5	3.2	5.8	2.3	3.8
	5	0.66	7.0	8.6	15.0	9.3	13.2	<b>31.4(-)</b>	5.1	10.4
<i>Rhinophylla pumilio</i>	1	0.48	13.5	4.4	9.4	5.2	22.1	30.8	8.0	6.7
	3	0.90	8.2	11.9	12.9	5.0	11.7	14.1	<b>28.0(-)</b>	8.2
	5	0.71	8.1	3.6	6.1	3.6	14.4	29.3	23.7	11.2
<i>Sturnira lilium</i>	1	0.54	<b>54.1(-)</b>	8.7	7.2	2.1	20.3	4.5	1.6	1.4
	3	0.72	<b>52.5(-)</b>	4.4	8.5	14.7	3.8	6.1	1.3	8.8
	5	0.75	<b>43.7(-)</b>	3.9	18.9	5.2	14.8	3.8	3.4	6.3
<i>Sturnira magna</i>	1	0.63	9.7	11.4	7.7	8.1	<b>41.7</b>	7.2	8.9	5.3
	3	0.53	15.0	6.0	10.1	33.4	12.3	1.8	9.3	12.0
	5	0.54	19.5	6.6	20.6	25.1	15.9	4.0	4.0	4.3
<i>Sturnira tildae</i>	1	0.76	13.9	14.7	8.9	8.5	<b>36.3</b>	7.4	2.7	7.6
	3	0.32	43.6	1.9	2.6	2.7	29.0	2.0	17.0	1.1
	5	0.42	41.7	1.7	2.6	1.3	14.4	30.2	5.6	2.4
<i>Uroderma bilobatum</i>	1	0.35	56.0	11.7	7.6	2.3	5.6	9.2	2.1	5.4
	3	0.54	<b>58.3(-)</b>	4.1	4.0	2.8	11.3	12.4	3.2	3.8
	5	0.57	<b>48.2(-)</b>	4.5	3.9	2.2	14.4	2.6	11.7	12.5
<i>Vampyressa bidens</i>	1	0.81	14.4	13.6	22.8	23.2	7.8	4.8	10.2	3.2
	3	0.76	<b>36.1(-)</b>	8.5	15.2	8.5	6.7	5.3	4.2	15.6
	5	0.86	<b>49.0(-)</b>	3.8	9.9	3.1	2.4	2.9	1.6	<b>27.4(-)</b>
<i>Vampyressa thuyone</i>	1	0.75	11.1	<b>33.7(-)</b>	15.8	5.4	15.1	6.5	8.9	3.6
	3	0.85	6.5	<b>30.4(-)</b>	21.7	2.5	11.0	21.7	4.0	2.4
	5	0.84	0.1	<b>33.5(-)</b>	<b>27.4</b>	7.4	7.3	7.5	12.6	4.0
<b>Nectarivores</b>										
<i>Glossophaga soricina</i>	1	0.79	<b>41.7(-)</b>	<b>27.7</b>	11.6	4.8	5.5	1.6	3.4	3.8
	3	0.73	<b>55.1(-)</b>	19.6	9.3	6.8	2.3	3.8	0.8	2.3
	5	0.51	<b>69.4(-)</b>	8.0	2.3	2.7	4.2	2.4	2.7	8.3
<i>Lonchophylla thomasi</i>	1	0.47	10.1	9.5	15.0	12.4	31.0	10.7	4.7	6.7
	3	0.76	23.3	17.0	9.2	8.3	16.0	11.6	10.1	4.5
	5	0.98	13.6	14.1	8.9	11.7	21.1	13.1	16.2	1.4

Table 2. Continued.

	Scale	$R_{\text{dev}}^2$	Compositional characteristics				Configurational characteristics			
			Cover	Density	Size	Diversity	Edge	Shape	Nearest	Proximity
Gleaning Animalivores										
<i>Lophostoma silvicolom</i>	1	0.23	12.2	5.7	7.3	13.1	15.3	3.2	30.2	12.9
	3	0.70	4.5	13.6	18.3	21.4	3.0	23.2	6.6	9.3
	5	0.80	7.1	22.2	11.4	<b>29.5(-)</b>	10.8	5.4	10.1	3.5
<i>Mimon crenulatum</i>	1	0.50	0.6	6.4	5.3	7.9	<b>62.8</b>	6.5	6.4	4.1
	3	0.54	0.1	6.5	7.6	2.3	<b>47.0</b>	7.3	14.2	15.0
	5	0.54	0.3	11.6	6.5	2.6	<b>52.8</b>	6.6	13.0	6.5
<i>Phyllostomus elongatus</i>	1	0.43	0.4	19.6	15.8	8.8	2.9	5.0	17.8	29.6
	3	0.47	0.7	4.9	6.7	3.3	8.3	4.6	<b>61.1</b>	10.4
	5	0.83	0.0	17.6	7.4	4.5	7.5	15.8	<b>42.6</b>	4.5
<i>Phyllostomus hastatus</i>	1	0.46	14.6	7.0	8.6	4.7	<b>33.3</b>	16.6	10.4	5.0
	3	0.67	1.2	8.9	9.0	4.3	<b>60.4</b>	7.1	4.5	4.6
	5	0.29	8.5	4.9	7.5	17.3	8.8	22.6	18.6	11.9
<i>Tonatia saurophila</i>	1	0.76	25.3	7.4	5.7	6.2	22.9	4.2	17.9	10.3
	3	0.80	16.8	12.0	16.4	12.3	24.0	2.5	10.0	6.0
	5	0.73	9.2	15.5	14.8	7.5	29.5	4.6	8.3	10.7
Assemblage-level										
Richness	1	0.51	29.5	11.4	12.9	10.4	15.4	4.5	2.3	13.6
	3	0.49	12.1	21.9	14.2	2.4	30.3	10.3	4.1	4.6
	5	0.40	7.6	30.6	8.9	5.1	15.6	3.8	6.3	22.1
Evenness	1	0.35	5.1	5.0	4.4	7.8	13.9	4.5	51.3	7.9
	3	0.85	1.9	9.3	11.1	8.1	14.1	23.1	<b>26.7(-)</b>	5.7
	5	0.82	3.8	4.8	7.2	5.1	23.9	9.8	<b>40.2(-)</b>	5.1
Diversity	1	0.50	2.0	5.5	8.5	5.7	7.1	32.5	29.4	9.2
	3	0.47	1.0	27.7	13.9	16.1	17.0	6.3	14.4	3.6
	5	0.61	0.0	23.0	5.2	6.7	25.1	19.7	14.9	5.4
Dominance	1	0.24	0.1	3.7	4.0	8.1	41.9	11.8	24.0	6.3
	3	0.80	0.4	8.8	14.1	5.0	22.3	18.9	25.4	5.1
	5	0.78	1.0	6.2	10.6	3.8	<b>32.2</b>	7.3	<b>37.7(-)</b>	1.3
Rarity	1	0.47	11.6	9.9	13.2	9.5	18.6	4.3	4.7	28.2
	3	0.45	3.4	15.2	19.3	2.8	37.5	11.8	2.9	7.1
	5	0.38	0.8	23.6	12.7	6.0	24.0	5.8	8.7	18.4

each focal scale. Forest cover and edge density were associated most frequently with patterns of species abundance and were the only significant predictors of patterns at the ensemble level (Fig. 2). Abundances of 10 species were associated significantly and negatively with forest cover, and abundances of six species were associated significantly and positively with edge density at one or more spatial scales (Table 2). The abundances of three species (*Lonchophylla thomasi*, *Tonatia saurophila*, and *Artibeus anderseni*) were not related significantly to any landscape characteristic at any focal scale.

Only characteristics of landscape configuration (mean nearest neighbour distance and edge density) had significant independent effects on assemblage-level indices (evenness and dominance) and only at the medium and large focal scales. Richness, species diversity and rarity were not related to any landscape characteristic at any focal scale.

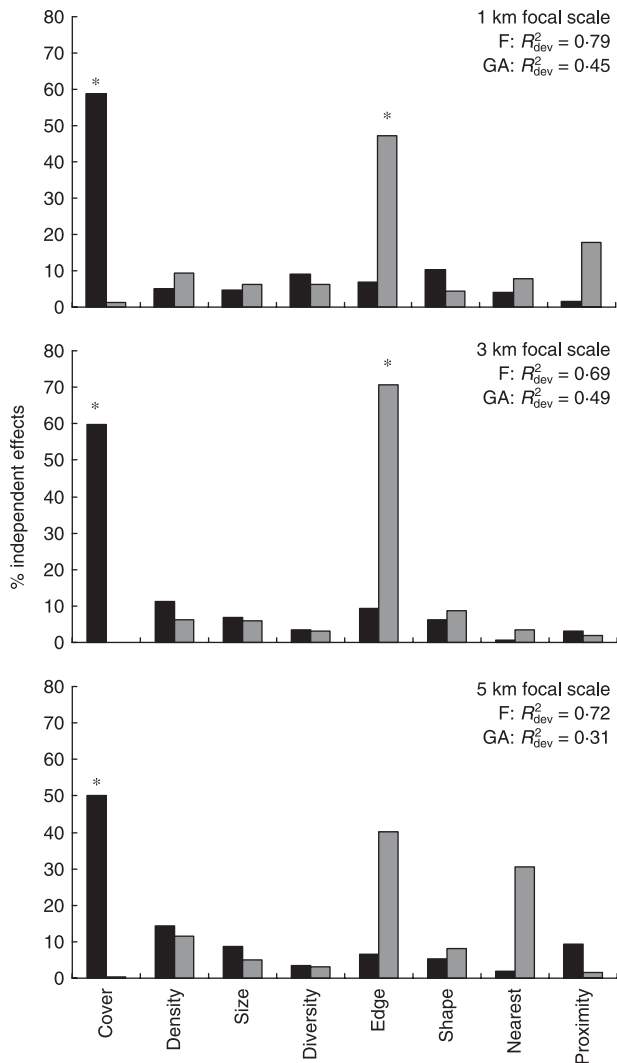
## Discussion

The associations between population- or assemblage-level aspects of biodiversity and landscape characteristics were scale-dependent (Table 2). Many empirical studies of frag-

mentation have evaluated the response of particular species to the spatial structure of habitat at a single, patch-based scale (McGarigal & Cushman 2002; Fahrig 2003). However, as evidenced by this study, the effects of fragmentation operate at multiple spatial scales, probably depending on species-specific behavioural or life-history characteristics (Kareiva 1990).

## ENSEMBLE-SPECIFIC DIFFERENCES IN POPULATION-LEVEL RESPONSES

For a variety of taxa in a number of habitats, landscape composition rather than spatial configuration has a greater impact on the abundance of species in habitat mosaics (e.g. McGarigal & McComb 1995; Villard *et al.* 1999; Gorresen & Willig 2004). This held true for frugivorous bats in fragmented Amazonian rainforest as well (Table 2). In contrast, characteristics of landscape configuration had the strongest independent effects on abundances of gleaning animalivores (Table 2). These two observations suggest that modes of foraging and characteristics of prey may mould the landscape-level response of bats to fragmentation. Although frugivores generally responded to aspects of composition, the particular



**Fig. 2.** Percentage of independent effects of landscape characteristics on frugivores (F, black bars) and gleaning animalivores (GA, grey bars) at each of three focal scales. Asterisks indicate significant effects ( $P < 0.05$ ). The relationship between frugivores abundance and percentage cover is negative and the relationship between gleaning animalivores abundance and edge density is positive.  $R_{dev}^2$  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.

characteristic to which they responded and the behavioural mechanism underlying those responses differed among species. Abundances of frugivores were associated primarily with changes in forest cover (Fig. 2) and probably responded to variation in fruit availability, capitalizing on the higher density of successional fruits in more open areas while exploiting dispersed patches of fruit in closed canopy forest. Frugivores (e.g. *Artibeus*) that specialize on canopy fruits can travel long distances in search of ripe fruits, minimizing the influence of landscape configuration on abundance, whereas understorey frugivores (e.g. *Carollia* and *Rhinophylla*) often roost close to multiple feeding areas (Heithaus & Fleming

1978) and exploit resources in closed canopy forest as well as in other habitats (i.e. secondary forest and abandoned fields). Consequently, the identity and proportion of nonforest matrix habitats in the landscape may influence the abundance of frugivores more than the spatial arrangement of forest patches.

Gleaning animalivores are highly edge-sensitive, and respond negatively to disturbance and forest fragmentation (Fenton *et al.* 1992; Medellín *et al.* 2000; Meyer *et al.* 2008). In contrast to these generalities, the abundance of gleaning animalivores was associated positively and significantly with edge density in Iquitos (Figure 2). This may be a response to higher abundances or catchability of prey (insect or small vertebrate species) along forest edges or to the presence of prey species that are adapted to edge habitat (Laurance *et al.* 2002). The magnitude and direction of an edge-effect can be influenced by the degree of contrast between forest fragments and the matrix. Landscapes characterized by high-contrast edges (e.g. forest vs. water) elicit the strongest negative responses (Laurance *et al.* 2002; Ewers & Didham 2006). The low contrast between forest and nonforest habitats in the current study area (e.g. forest vs. secondary forest) may enable some species of gleaning animalivore to exploit edge habitat for hunting and feeding, or for use as flyways that connect resource patches. The notion that species sensitivity to forest edges is variable, depending on the degree of fragment-matrix contrast, is supported by studies of bats in other Neotropical landscapes (Bernard & Fenton 2003, 2007; Meyer *et al.* 2008). The association of ensembles with particular characteristics of landscape structure remains a fertile area for further consideration. Moreover, examination of the relationship of matrix identity or degree of forest-matrix contrast with species abundances is relatively recent, but provides valuable information regarding responses to fragmentation by groups of species that exploit similar resources with different strategies.

#### HIGH- VS. LOW-INTENSITY DEFORESTATION

In general, the abundances and richness of species was higher in fragmented forest than in continuous forest. These results are more consistent with studies concerning the response of bats to selective logging (e.g. Clarke, Pio & Racey 2005a; Clarke, Rostant & Racey 2005b; Peters, Malcolm & Zimmerman 2006) than to the response of bats to deforestation (e.g. Fenton *et al.* 1992; Cosson *et al.* 1999). Forest exploitation in the vicinity of Iquitos is not as extensive or intensive as in many areas of the Neotropics. Percentage of closed canopy forest for sites at the smallest focal scale (27–99%) was more variable than at the largest focal scale (47–92%), corroborating the contention that deforestation occurs at a small scale (i.e. 1- to 4-ha patches) in this region. Visual inspection of the region surrounding the study sites revealed expansive closed canopy forest (Fig. 1). Such small-scale forest conversion and the absence of extensively deforested areas may predispose anthropogenic activities to manifest primarily as changes in abundance (e.g. *C. perspicillata*, *C. brevicauda*, *A. obscurus*,

and *R. pumilio*) or behaviour, rather than as alterations in the presence of species (Gorresen & Willig 2004; Clarke *et al.* 2005a, b; Willig *et al.* 2007; Presley *et al.* 2009).

Contrary to results from the Atlantic Forest of Paraguay involving similar landscape characteristics, the majority of phyllostomids (e.g. *C. perspicillata*, *A. lituratus*, *S. lilium*) captured in Iquitos responded negatively to forest cover and positively to characteristics indicative of fragmentation (e.g. edge density). Although a number of species had higher abundances in moderately fragmented Atlantic Forest, species responded positively to forest cover and patch density, and negatively to edge density. In Iquitos, 10 species responded negatively to forest cover and four species responded positively to edge density at a range of scales (Table 2). These observations are consistent with a number of interpretations. Many of the species captured in Paraguay are at the edge of their geographical ranges, and population dynamics often are regulated by different factors at edges (e.g. climatic, decreased food and roost availability) than at centres (e.g. competition, predator-prey interactions) of ranges (Brown, Stevens & Kaufman 1996). This may explain why the abundances of species that are present in Atlantic Forest and Amazonian forest were disparate (e.g. *C. perspicillata*: 163 of 7725 captures in Paraguay, and 1022 of 3034 captures in Iquitos; Gorresen & Willig 2004, Table 1), especially considering that the sampling effort in Paraguay (140 sampling nights) was much greater than that of the current study (84 sampling nights). Furthermore, forest conversion occurs at a relatively small scale in Iquitos, and openings caused by anthropogenic disturbances may mimic characteristics of natural disturbances, which often increase the abundances of some species in fragmented areas (Willig *et al.* 2007). In contrast, eastern Paraguay has experienced deforestation rates twice that of the Amazon basin and has less than 20% of its forest remaining (Keel, Gentry & Spinzi 1993), causing species to show responses typical of those associated with large-scale anthropogenic disturbance rather than with small-scale natural disturbances (Gorresen & Willig 2004; Gorresen *et al.* 2005). Finally, methodological differences between studies may account for these observations in that nets were deployed in multiple-habitat types in Paraguay but only in the focal habitat (forest) in Peru.

#### TROPHIC DYNAMICS

For birds and forest-interior bats, insectivores are especially vulnerable to fragmentation, whereas many frugivores and nectarivores remain stable or increase in abundance in fragments (Kalko 1998; Gorresen & Willig 2004; Wunderle, Willig & Henriques 2005; Peters *et al.* 2006; Willig *et al.* 2007). The eight most abundant species in the study area were frugivores (Table 1) and probably account for the positive relationship between dominance and edge density, and the negative relationship of nearest neighbour distance with dominance and evenness at the medium and large focal scales. This pattern of response by bat populations to anthropogenic disturbance may be related to species-specific aspects of their

foraging ecology (Charles-Dominique 1991; Thies & Kalko 2004; Henry, Pons & Cosson 2007). The most common frugivores (i.e. *Carollia*, *Artibeus*, and *Sturnira*) and nectarivores (i.e., *G. soricina* and *L. thomasi*) have higher abundances in moderately fragmented sites than in sites characterized by continuous closed canopy forest. Many fruit-bearing plants (e.g. *Cecropia*, *Piper*, and *Solanum*) on which bats feed are early- or mid-successional species (Fleming 1988; Gorchov *et al.* 1993). As a result, frugivores and nectarivores often exploit elevated densities of food resources after forest conversion to agriculture and during subsequent succession. Consequently, a matrix of mature forest with patches of secondary forest and agriculture may provide a more profitable landscape for some frugivores and nectarivores compared to extensive, intact forests (Clarke *et al.* 2005a; Willig *et al.* 2007), at least when deforestation and fragmentation represent a small proportion of the regional landscape.

Even moderate amounts of fragmentation, associated with conversion of forest habitat, can affect local populations of more specialized bat species and may alter the structure of assemblages. For Neotropical bats, roosting habitat is most abundant in forests because many bat species roost in trees, dense vegetation, termite nests, or understorey palms to avoid predation and exposure to microclimatic factors, as well as to be close to food sources (Kunz & Lumsden 2003). Nonetheless, gleaning animalivores often are affected disproportionately by fragmentation, whereas abundances of frugivores remain stable or increase. Indeed, all 14 species of gleaning animalivores were rare, suggesting that diet and foraging strategy may more strongly affect sensitivity to forest fragmentation than do roosting requirements. Gleaning animalivores consume arthropods and occasionally small vertebrates from vegetative surfaces (Gardner 1977; Bonaccorso 1978). This foraging strategy requires continuous, slow flight in highly cluttered environments, as well as perching and waiting for prey, making areas of dense vegetation and closed canopy forest ideal for protection from predators while foraging. The short, broad wings of gleaning bats provide high manoeuvrability in obstacle-rich environments (edges), but constrain continuous flight over long distances (open areas; Norberg & Rayner 1987). This may discourage gleaning species from traversing large open areas, but facilitate use of edge habitats.

#### CONSERVATION IMPLICATIONS

This study represents the first attempt to identify the responses of phyllostomids to spatially explicit landscape characteristics measured at multiple focal scales in fragmented, lowland Amazonia. Because organisms are cognizant of resources and habitat features at a number of scales (Kotliar & Wiens 1990), they may respond to both local and regional characteristics. Additionally, conservation decisions based on associations of biodiversity metrics (e.g. richness, diversity, and rarity) with landscape structure may be problematic. No landscape characteristic had a significant independent effect on richness, diversity, or rarity at any scale despite multiple species-specific and ensemble-specific responses at all scales.

Biodiversity metrics do not respond to changes in landscape structure, *per se*, but are a sum of all species responses. Therefore, assemblages characterized by high taxonomic or functional diversity may contain multifarious responses to landscape pattern that cancel or reflect only the response of a dominant functional group. Consequently, multi-scale approaches conducted at the level of species and ensembles are critical to the success of management and conservation strategies, and for the mechanistic interpretation of variation in assemblage-level characteristics.

Disturbed habitats may provide resources at greater density and in higher quality for some taxa (e.g. *G. soricina*, *C. perspicillata*, and *S. lilium*) that feed on fruits or flowers of early successional plants (Fleming 1988; Gorchov *et al.* 1993) or for particular phyllostomids (e.g. *Phyllostomus hastatus*) that opportunistically supplement their animalivorous diet with fruit (Simmons & Voss 1998). In the current study, the species richness and abundances of phyllostomids were greater in moderately fragmented forest, demonstrating that maintenance of large areas of continuous forest with a mix of successional habitats and human land uses may sustain bat diversity with little negative consequence. This has been documented previously for bats in Trinidad (Clarke *et al.* 2005a, b), Paraguay (Gorresen & Willig 2004), and in the context of a non-manipulative experiment (closed canopy forest, early secondary forest, vs. agriculture) in Peru (Willig *et al.* 2007).

Small-scale deforestation may not diminish the tendency for bats to traverse open or disturbed areas (Gorchov *et al.* 1993; Bernard & Fenton 2003). For example, large species in the genus *Artibeus* (e.g. *A. lituratus*, *A. planirostris*, and *A. obscurus*) probably travel farther than 2–5 km in a night and may visit multiple forest fragments in search of fruiting trees (Morrison 1980). However, as the size, frequency and intensity of deforested areas increase, connectivity of remaining forest patches will decrease and fewer frugivorous species may be able to traverse these large open areas. Understorey frugivores (e.g. *Carollia* and *Rhinophylla*) that feed on scattered fruits, produced in small amounts, for extended periods of time, will probably be affected most severely by reduced connectivity because these bats employ a foraging strategy that relies more on short search flights devoted to finding food items within foraging areas, rather than on commuting flights that employ longer, more energetically costly flights among several foraging areas (Thies & Kalko 2004; Henry *et al.* 2007). Indeed, abundance of *Rhinophylla pumilio* decreased along a gradient of decreasing landscape connectivity even when food availability remained stable or increased (Henry *et al.* 2007). Consequently, reduced connectivity of forest fragments may appreciably alter patterns of seed dispersal. This could adversely affect tropical ecosystem functioning and regeneration of forest, because bats play a critical role in dispersing seeds of successional plants.

Bat biodiversity can be maintained in fragmented tropical forests as long as deforestation occurs at small scales (relative to the organism) and areas of unfragmented forest at the regional scale are pervasive. However, long-term research

that employs multiple sampling methods (i.e. mist netting, roost searching, and acoustic monitoring) in areas such as Iquitos is necessary to adequately understand and forecast the responses of bat species, ensembles, or assemblages to forest fragmentation. Such knowledge is critical for designing sustainable tropical landscapes that preserve biodiversity and promote revegetation of disturbed areas.

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