

# Effects of different secondary vegetation types on bat community composition in Central Amazonia, Brazil

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## Keywords

bat community structure; Chiroptera; landscape characteristic; habitat use; secondary forest.

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## Abstract

The process of secondary succession on degraded lands in the Amazon depends on their land-use histories. In this scenario, little is known about how animal communities respond to different types of secondary vegetation in the region. We examined the effects of abandoned cattle pasture, *Vismia*- and *Cecropia*-dominated regrowth on the abundance of bat species and community composition in the Central Amazon, Brazil, based on 11 netting sites and on landscape characteristics. We captured 1444 bats, representing 26 species and two families (Phyllostomidae and Mormoopidae). Among the six most-captured Phyllostomidae bats, *Sturnira lilium* and *Sturnira tildae* had significantly higher capture rates in abandoned pasture, while *Rhinophylla pumilio* predominated in both *Vismia*- and *Cecropia*-dominated regrowth. An hybrid multidimensional scaling ordination revealed significant differences in the bat community among the three types of secondary vegetation. Phyllostominae bats were more common and richer in the less-disturbed areas of *Cecropia*-dominated regrowth, while Stenodermatinae species were more captured in abandoned pastures. Our results suggest that the type of secondary vegetation, together with its land-use history, affects bat community composition in the Central Amazon. The Phyllostominae subfamily (gleaning animalivores) was habitat selective and disappeared from areas experiencing constant disturbances. On the other hand, Stenodermatinae frugivorous bats often used and foraged in altered areas. We suggest that secondary vegetations in more-advanced successional stages can be used to augment the total area protected by forest conservation units.

## Introduction

The Brazilian Amazon has been undergoing a process of ever-increasing deforestation, with rates reaching 2.4 million ha between 2002 and 2003 (Laurance *et al.*, 2004). New analyses of high-resolution satellite images capable of detecting areas of selective logging reveal that the total deforested area may be 60–123% larger than previously estimated (Asner *et al.*, 2005). After logging, previously forested areas are commonly used for slash-and-burn agriculture, principally short-rotation crops and cattle pastures. Many of these farms are maintained for 5–10 years and then abandoned when productivity, as well as government support, declines (Uhl, Buschbacher & Serrão, 1988; Nepstad *et al.*, 1996). Recently, the Brazilian government has launched new infrastructure projects, such as new highways, hydroelectric dams and gas lines, which contribute to the forest replacement by an anthropogenically disturbed habitat in the Amazon (Killeen, 2007).

Depending on the land-use history, secondary succession in anthropogenically degraded areas of the Central Amazon may follow different trajectories. In abandoned deforested areas, where the forest has been cut only for timber extraction, the regeneration is dominated by *Cecropia* species, while in deforested areas that have been converted to cattle pasture, followed by periodic burns, secondary succession is dominated by species of *Vismia* (Uhl *et al.*, 1988; Mesquita *et al.*, 2001). In the Biological Dynamics of Forest Fragments Project (BDFFP), near Manaus, Brazil, the secondary forests now dominated by *Cecropia* were clear-cut in 1983, with no other disturbances over the past 20 years (1983–2003). On the other hand, *Vismia*-dominated regrowth suffered from two to nine burns with <10 years of recovery. The regeneration under *Cecropia*-dominated regrowth in these areas results in a more diverse and heterogeneous forest composed of 300 plant species, twice that found under *Vismia*-dominated regrowth, and can return to

the structural complexity found in primary forest faster than *Vismia*-dominated regrowth (Mesquita *et al.*, 2001). However, the low species similarity among these secondary regrowth forests suggests different successional pathways (Mesquita *et al.*, 2001).

In terms of conservation, areas of secondary forest may be important for the dynamics of the fauna inhabiting nearby forest fragments (Malcolm, 1995; Gascon *et al.*, 1999). Depending on its similarity to primary forest, secondary forest can function as a powerful filter of species, affecting the composition and dynamics of the vertebrate community (Offerman *et al.*, 1995; Stouffer & Borges, 2002; Tocher, Gascon & Meyer, 2002). The capacity of species to survive deforestation depends on their ability to disperse between fragments or exploit secondary forest (Laurance & Laurance, 1999; Estrada & Coates-Estrada, 2001).

The use of degraded habitats also depends on the biological characteristics of the species and their use of existing resources. Bats can be less sensitive to the effects of fragmentation due to their capacity to fly, which allows their dispersal across long distances between fragments (Fleming, Hooper & Wilson, 1972; Heithaus & Fleming, 1978; Bernard & Fenton, 2003). For frugivorous bats, secondary vegetation plays an important role as a food source, because many pioneer plants provide abundant zoochorous fruits (Fleming & Heithaus, 1981; Galindo-González, Guevara & Sosa, 2000). Various studies have demonstrated the vulnerability of bats to fragmentation and selective logging in the Neotropics (Brosset *et al.*, 1996; Cosson, Pons & Masson, 1999; Medellín, Equihura & Amin, 2000; Schulze, Seavy & Whitacre, 2000; Clarke, Pio & Racey, 2005; Peters, Malcolm & Zimmerman, 2006). However, few studies show how the bat community responds to habitats experiencing different anthropogenic influences and in various stages of regeneration (Medellín *et al.*, 2000; Estrada & Coates-Estrada, 2001; Numa, Verdu & Sanchez-Palomino, 2005; Faria, 2006; Castro-Luna, Sosa & Castillo-Campos, 2007). In general, fragments, secondary forests and man-made habitats such as plantations and pastures are rich in species and have equally great abundances of some bats as in continuous forest (Estrada & Coates-Estrada, 2002; Numa *et al.*, 2005; Pineda *et al.*, 2005; Faria, 2006; Willig *et al.*, 2007). The use of different disturbed habitats for foraging and roosting by bats depends on the proportion and distribution of primary forest in the landscape (Lindenmayer & Hobbs, 2004).

In the present study, we evaluated differences in the abundance and composition of the bat community in three different stages of secondary succession: abandoned pastures (initial stage of succession), *Vismia*-dominated regrowth and *Cecropia*-dominated regrowth over 18 years. Specifically, we asked how the composition of the bat community is affected by the land-use history and the type of secondary vegetation, and whether these vegetation types contribute to the conservation of bat biodiversity in the Amazon. We also examined the effect of landscape characteristics (distance from primary continuous forest and the relative proportion of the primary and secondary vegetation types) on bat populations and species composition. We

expected that vegetation types with more structural heterogeneity (*Cecropia*- and/or *Vismia*-dominated regrowth) will exhibit higher abundance and richness of gleaning species, whereas in abandoned pastures, we expected higher abundance of frugivores due to the dominance of pioneer plants.

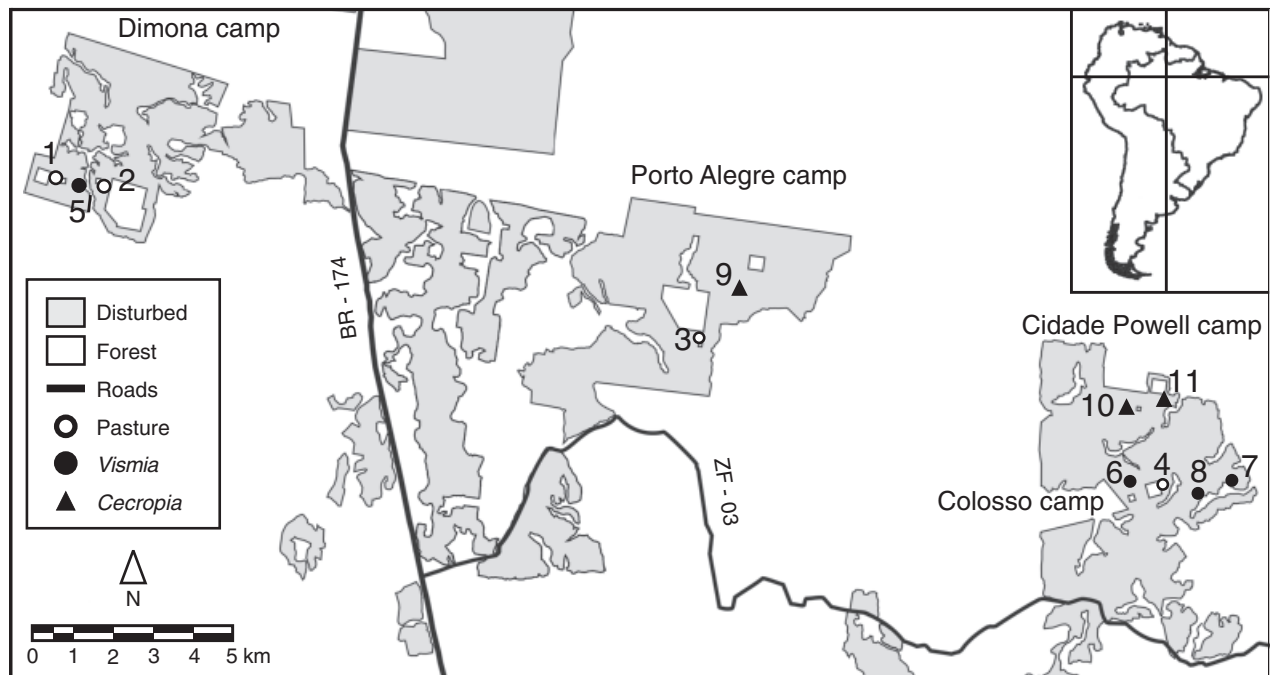
## Materials and methods

### Study area

This study was conducted at the BDFFP, about 80 km north of Manaus, Amazonas state, Brazil (2°25'S, 59°50'W) (Fig. 1). The area covers *c.* 40 × 10 km of *terra firme* forest within the farms Dimona, Porto Alegre and Esteio, lies 30–125 m a.s.l. and is made up of primary continuous forest, experimental forest fragments created by BDFFP (10, 100 and 1000 ha), secondary forest and abandoned pastures. The area of the disturbed landscape in each farm varied from 1731 to 3060 ha of secondary forests and from 80 to 592 ha of abandoned pastures. Canopy height is between 15 and 20 m, with emergent trees that reach 25 m (Mesquita *et al.*, 2001). The dominant families are different between the two secondary forests, with Clusiaceae, Piperaceae, Melastomataceae, Myrtaceae and Fabaceae dominant in *Vismia*-dominated regrowth and Fabaceae, Burseraceae, Arecaceae, Annonaceae and Moraceae in *Cecropia*-dominated regrowth (Mesquita *et al.*, 2001). The abandoned pastures are composed by a layer of Poaceae and Cyperaceae with scattered shrubs of *Vismia*, *Solanum*, *Cecropia*, *Trema* and *Goupia*. Annual rainfall varies between 1900 and 3500 mm year<sup>-1</sup>, with a rainy season from October to May (Laurance, 2001).

### Sampling sites

We sampled bats monthly between October 2001 and September 2002, in four camps within the BDFFP area: Colosso, Dimona, Cidade Powell and Porto Alegre (Fig. 1). All camps had part of their primary forest cover clear-cut in 1983, creating a mixture of open areas and forest fragments in the middle of a large continuous forest. Colosso and Dimona camps were burned and used as cattle pasture for 4 years before being abandoned. In these areas, the canopy species and understorey recruits were dominated by three species of *Vismia* (Clusiaceae: *Vismia guianensis*, *Vismia japurensis* and *Vismia cayennensis*) (Mesquita *et al.*, 2001). Cidade Powell and Porto Alegre camps were abandoned after the first cut of primary forest in 1983, and because then, have never been burned; they were dominated by *Cecropia sciadophylla*, *Cecropia purpurascens*, *Bellucia* spp., *Laetia procera* and *Byrsonima stipulacea* (Mesquita *et al.*, 2001). Periodically, during the years 1983–2001, the forest fragments of these areas (Colosso, Dimona and Porto Alegre) were re-isolated by the planned cutting and burning of a 100 m swath of vegetation surrounding the fragments, emulating a commonly used practice for maintaining pasture throughout the Amazon. Over the years, these areas were often used as cattle pasture. Here, abandoned pasture



**Figure 1** Map of the study area in the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazonia, Brazil. Disturbed areas are shaded in grey and primary forest in white. Open circles indicate abandoned pasture sample sites (1–4), full circles indicate *Vismia*-dominated regrowth sites (5–8) and triangles indicate *Cecropia*-dominated regrowth sites (9–11).

vegetation reached a maximum height of 3 m during the study period and was dominated by grasses and a mix of pioneer shrubs. We selected 11 sampling sites distributed across the three types of secondary vegetation: four sampling sites in abandoned pasture (two in Dimona, one in Colosso and one in Porto Alegre), four in *Vismia*-dominated regrowth (three in Colosso and one in Dimona) and three in *Cecropia*-dominated regrowth (two in Cidade Powell and one in Porto Alegre) (Fig. 1). The distance between the sites of the same secondary vegetation varied from 0.70 to 28.7 km.

### Bat captures

We captured bats using six mist nets ( $12.0 \times 2.5$  m) in abandoned pasture and eight nets in both older secondary forest types, set at ground level on existing trails. Each site was sampled on average five nights with an interval of at least 30 days between samplings. Nets were opened between 19:00 and 00:00 h and checked at intervals of 15 min. Captured bats were placed in individual cotton bags, identified, measured, marked with a numbered ball-chain necklace and released. Nights with rain and full moon were not sampled. Our analyses are restricted to the families Phyllostomidae and Mormoopidae, the bats most commonly captured using ground-level nets in the region, in order to avoid errors that may occur in adding in the data of species with extremely different capture probabilities, such as Vespertilionids, Molossids and Emballonurids that forage over the canopy. We follow the taxonomic nomenclature of Sim-

mons (2005). *Artibeus planirostris* is used in place of *Artibeus jamaicensis*, as proposed by Lim & Wilson (1993) for the Central Amazon.

### Landscape analyses

To explain the response of bat community to habitat features, it is important to recognize that bats interact with the landscape in a broad spatial scale. The landscape characteristics of the BDFFP study area were categorized with minimum distance supervised classification using ENVI 4.2 (ENvironment for Visualizing Imagery), based on 2001 LandSat TM satellite images with pixels of  $30 \times 30$  m resolution. The classified map produced four land-cover classes: primary forest, *Vismia*-dominated forest, *Cecropia*-dominated forest and non-forest (exposed soil and pastures). The area of land-cover classes was quantified using ArcView 3.2. Land-cover classes were estimated for a circle of 300 m radius (32.1 ha) centred in each of the 11 netting sites (Table 1). We used the 300 m radius because the abundance of small bats ( $< 40$  g) responds better to small-scale variation of the forest cover (Pinto & Keitt, 2008). Our results showed that small bats represented 85% of the species ( $n = 22$ ) and 98% of all captures ( $n = 1416$ ).

### Statistical analyses

We used analysis of variance (ANOVA) to identify possible differences in the capture frequency of the most abundant bat species among the three types of secondary vegetation,

**Table 1** Area of land-cover classes (ha) and distance (m) from the primary forest of > 1000 ha in three types of secondary vegetation at the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazonia, Brazil

Site	Vegetation type	Area of land-cover classes (ha)			Primary forest cover	Distance from the forest (m)
		Pasture cover	<i>Vismia</i> forest cover	<i>Cecropia</i> forest cover		
1	Abandoned pasture	1.1	24.8	0	6.3	34
2	Abandoned pasture	7.7	10.3	0	14.1	48
3	Abandoned pasture	0.72	0	30.7	0.7	258
4	Abandoned pasture	3.9	18.6	0	9.6	22
5	<i>Vismia</i> forest	0.1	28.4	0	3.7	106
6	<i>Vismia</i> forest	0	28.1	0	4.1	160
7	<i>Vismia</i> forest	0	23.9	0	8.2	81
8	<i>Vismia</i> forest	2.1	21.4	0	8.6	50
9	<i>Cecropia</i> forest	0	0	31.2	0.9	471
10	<i>Cecropia</i> forest	0	0	20.7	11.4	47
11	<i>Cecropia</i> forest	0	0	19.0	13.1	30

The sites represent the sample sites as numbered in Fig. 1.

followed by a *post hoc* Tukey test. A hybrid multidimensional scaling (HMDS) ordination was used to reduce the bat community composition data into two dimensions (two axes). We performed two ordinations: one using abundance data and another using presence-absence data of captured individuals. In each one of the 11 sampling sites, the capture frequency was standardized by capture effort (net-hours), measured in net-hours that corresponds to the number of nets opened per night multiplied by hours of netting.

For the ordination analysis, we used the Bray-Curtis index to measure the similarity among the bat communities of the 11 sampling sites, using the abundance data. This index is considered robust when large differences in species composition are possible between distinct locations (Faith, Minchin & Belbin, 1987). The Jaccard index was applied to estimate the similarity among sites, using data of species occurrence. We compared the three types of secondary vegetation using a multiple analysis of variance (MANOVA), with the two first axes of the HMDS as the response variables and the three secondary vegetation types as the explanatory variables. To understand whether bat composition was a function of the spatial distribution of sampled sites, we used the three farms (Dimona, Porto Alegre and Esteio-Colosso and Cidade Powell camps together) as the explanatory variables in the MANOVA.

The relationships of the landscape characteristics with response variables (abundance of the six most-captured bat species, abundance and richness of frugivore and gleaning animalivore bats and more explanatory HMDS axis) were assessed by performing a multiple linear regression. Explanatory variables used in regressions included distance from the continuous primary forest with > 1000 ha and the relative proportion of abandoned pasture, *Vismia*-dominated forest, *Cecropia*-dominated forest and primary forest (Table 1). The relative proportions with each site of primary and secondary vegetation types were expressed as hectares (Table 1). The forward stepwise method was used to select the explanatory variables that maximize the explanation of

the dependent variable. The best-fitting model was selected using the Akaike information criterion (Diniz-Filho, Bini & Hawkins, 2003). A Pearson correlation matrix was used to evaluate the multi-collinearity among explanatory variables. A significance correlation was found between *Vismia*- and *Cecropia*-dominated regrowth ( $r = -0.884$ ; Bonferroni corrected,  $P = 0.003$ ); therefore, *Vismia*-dominated regrowth was excluded from the regression model.

The lack of spatial independence of the capture frequency of bats between pairs of netting sites can result in Type I errors when testing statistical hypotheses using ANOVAs and regressions (Legendre, 1993). The possible spatial autocorrelation in data was tested using Moran's *I* coefficients for the residuals of the multiple regressions models at five distance classes with upper limits of 0.77, 6.24, 13.31, 21.48 and 28.08 km. An equal number of pairs of sampling sites between distance classes for each Moran's *I* coefficients was used in the correlograms to maximize the similarity in the number of connections between distance classes and to avoid much smaller number of connections that can affect the results of Moran's *I* coefficients (van Rensburg, Chown & Gaston, 2002). The values of Moran's *I* coefficients range from  $-1$  to  $+1$ , with positive values indicating that the capture frequency in sampling sites within a distance classes are more similar than expected for a random spatial pattern (Diniz-Filho *et al.*, 2003). Each Moran's *I* value was tested for significance by 1000 Monte Carlo randomizations.

The HMDS ordinations were performed on a PATN computer program (Belbin, 1992). For ANOVAs, MANOVAs, regressions and the Pearson's correlation test, we used statistical package SYSTAT version 8. Spatial autocorrelation analyses were carried out using SAM software version 3 (Rangel, Diniz-Filho & Bini, 2006).

## Results

In 54 nights (1449 net-hours), we captured 1444 bats, representing 26 species, 18 genera and two families

**Table 2** Phyllostomid and mormoopid bats captured and sampling effort in three types of secondary vegetation at the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazonia, Brazil

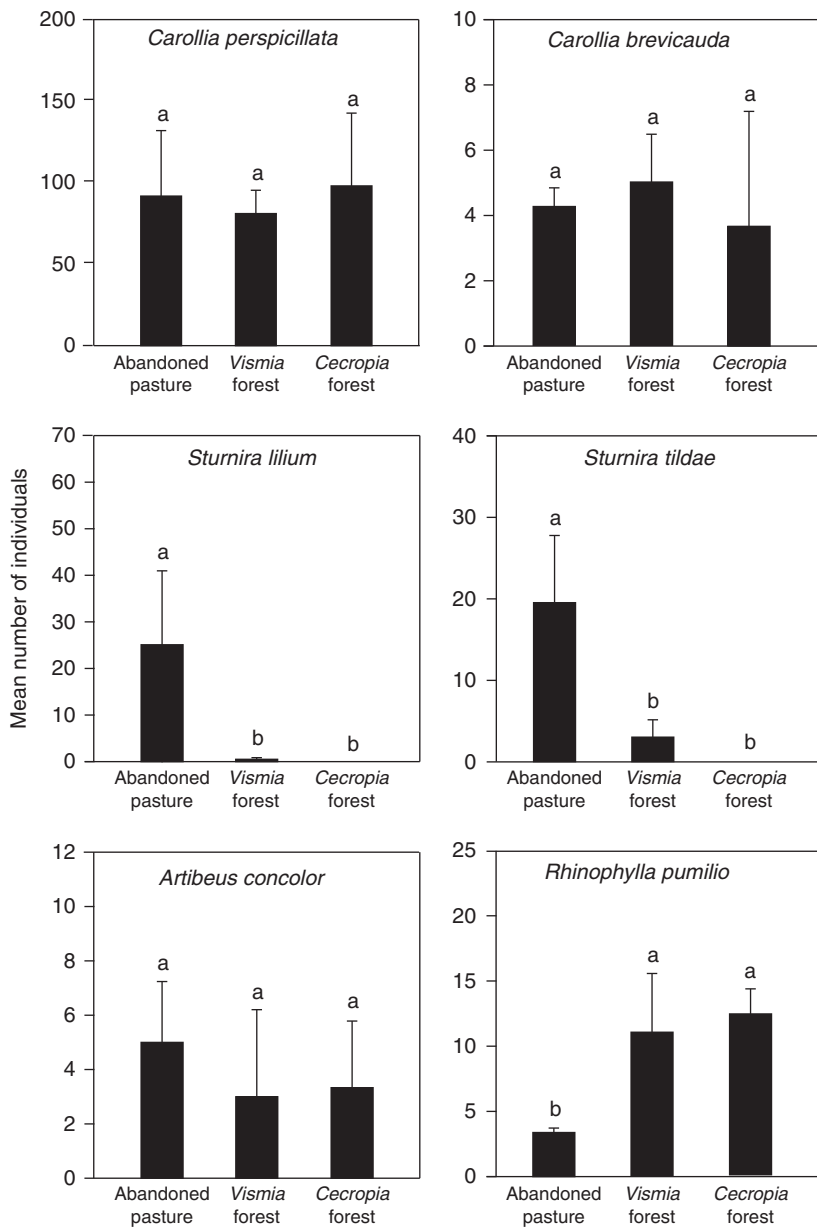
Bat species	Abandoned pasture	<i>Vismia</i> forest	<i>Cecropia</i> forest	Total	Weight (g)
Phyllostomidae					
Carollinae					
<i>Carollia perspicillata</i>	367	324	294	985	17.3 ± 0.8
<i>Carollia brevicauda</i>	17	20	11	48	13.0 ± 1.5
<i>Rhinophylla pumilio</i>	14	44	37	95	10.5 ± 1.2
Stenodermatinae					
<i>Sturnira lilium</i>	101	2	0	103	22.5 ± 2.7
<i>Sturnira tildae</i>	78	12	0	90	25.7 ± 3.6
<i>Artibeus concolor</i>	20	12	10	42	20.7 ± 2.8
<i>Artibeus cinereus</i>	6	1	1	8	10.5 ± 1.6
<i>Artibeus gnomus</i>	0	0	2	2	14.0
<i>Artibeus obscurus</i>	5	9	1	15	41.2 ± 1.2
<i>Artibeus planirostris</i>	0	1	0	1	47.5
<i>Artibeus lituratus</i>	6	2	2	10	66.3 ± 4.5
<i>Uroderma bilobatum</i>	5	0	0	5	20.0 ± 3.6
<i>Mesophylla macconnelli</i>	2	0	1	3	7.3 ± 1.2
<i>Ametrida centurio</i>	2	0	0	2	10.0 ± 2.8
<i>Platyrrhinus helleri</i>	2	0	0	2	14.5 ± 0.7
<i>Vampyressa bidens</i>	2	0	0	2	10.5 ± 0.7
Phyllostominae					
<i>Phylloderma stenops</i>	0	0	1	1	47.0
<i>Phyllostomus elongatus</i>	0	0	5	5	34.4 ± 4.3
<i>Tonatia saurophila</i>	2	0	5	7	28.3 ± 3.4
<i>Lophostoma silvicolium</i>	0	0	2	2	33.5 ± 4.9
<i>Trachops cirrhosus</i>	0	0	1	1	37.0
<i>Micronycteris megalotis</i>	0	1	2	3	6.3 ± 0.6
<i>Mimon crenulatum</i>	0	0	2	2	12.0
Glossophaginae					
<i>Glossophaga soricina</i>	0	2	2	4	7.2 ± 1
Desmodontinae					
<i>Desmodus rotundus</i>	0	1	0	1	33.0
Mormoopidae					
<i>Pteronotus parnellii</i>	0	4	1	5	24.0 ± 2.3
Captures	629	435	380	1444	
Species	15	14	18	26	
Net-hours	589	469	391	1449	
Nights	24	16	14	54	

(Mormoopidae and Phyllostomidae) (Table 2). The average capture rates did not differ between the three types of secondary vegetation (1.07 bat/net-hour in abandoned pasture sites, 0.93 and 0.97 in *Vismia*- and *Cecropia*-dominated regrowth sites; ANOVA,  $F_{2,8} = 0.01$ ,  $P = 0.99$ ). The family Mormoopidae was represented by only one species, *Pteronotus parnellii*. Among the Phyllostomidae, we captured 13 species of the subfamily Stenodermatinae, followed by seven Phyllostominae species, three Carollinae and one Desmodontinae. The subfamily Carollinae made up 78.1% of all captures (1128 captures), followed by Stenodermatinae with 19.7% (285 captures).

The six most frequently captured species represent 94.4% of the total captures. *Carollia perspicillata* was the most abundant species, making up 68.2% of the captures, followed by *Sturnira lilium* (7.1%), *Rhinophylla pumilio*

(6.6%), *Sturnira tildae* (6.2%), *Carollia brevicauda* (3.3%) and *Artibeus concolor* (2.9%) (Table 2). Phyllostomidae bats with < 10 individuals made up 65.4% of the total species (17 species), but represented only 3.54% of the individuals (51 captures) (Table 2).

The correlograms of the regression residuals of the response variables as functions of landscape characteristics show no significant spatial autocorrelation (see supporting information Appendix S1). This indicates independence between netting sites, a condition required to proceed with the standard methods of statistical analysis. The capture rates of three Phyllostomidae bats varied across secondary vegetation types (Fig. 2). *Sturnira lilium* and *S. tildae* were significantly more abundant in abandoned pasture (ANOVA, *S. lilium*:  $F_{2,8} = 5.91$ ,  $P = 0.03$ ; *S. tildae*:  $F_{2,8} = 9.79$ ,  $P = 0.007$ ) (Fig. 2). The rate of *R. pumilio* capture was

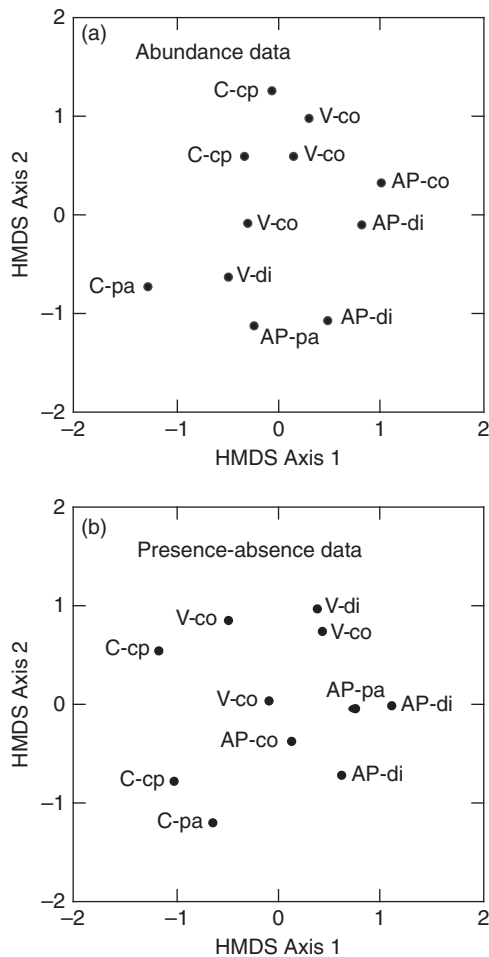


**Figure 2** Mean number of individuals captured of the six most abundant bat species in three secondary forests at the Biological Dynamics of Forest Fragments Project, Central Amazonia, Brazil. Different letters indicate significant differences among habitats in a *posteriori* Tukey's test. Vertical lines on the bars represent  $\pm 1$  SE.

higher in secondary forests (85.3%) than in abandoned pasture (14.7%) (ANOVA,  $F_{2,8} = 6.73$ ,  $P = 0.019$ , Tukey's tests pasture vs. *Vismia*:  $P = 0.03$ , pasture vs. *Cecropia*:  $P = 0.04$ ), with similar capture rates in both *Vismia*- and *Cecropia*-dominated regrowth (Tukey's test,  $P = 0.88$ ) (Fig. 2). *Carollia perspicillata*, *C. brevicauda* and *Ar. concolor* exhibited no significant difference in capture rates among the three types of secondary vegetation (ANOVA,  $F_{2,8} = 0.34$ ,  $P = 0.72$ ;  $F_{2,8} = 0.61$ ,  $P = 0.57$ ;  $F_{2,8} = 0.17$ ,  $P = 0.84$ , respectively) (Fig. 2), although *Ar. concolor* appeared most frequently in abandoned pasture (Table 2).

The number of species sampled was similar between secondary vegetation types, varying from 14 in *Vismia*-dominated regrowth to 18 in *Cecropia*-dominated regrowth

(Table 2). However, the community composition of bats in the BDFFP area was different among types of secondary vegetation. According to the HMDS ordination of the abundance data, *Vismia*- and *Cecropia*-dominated regrowth were more similar than abandoned pasture (Fig. 3a). On the other hand, the presence-absence data revealed that abandoned pasture and *Vismia*-dominated regrowth were more similar to each other, as can be observed along Axis 1 (Fig. 3). MANOVA tests on the HMDS axes revealed a significant difference in the community composition among types of secondary vegetation, using capture abundances (Pillai trace = 0.95,  $P = 0.027$ ) (Fig. 3a) and presence-absence data (Pillai trace = 1.26,  $P = 0.002$ ) (Fig. 3b). Combining the capture data from the *Vismia*- and *Cecropia*-dominated



**Figure 3** Hybrid multidimensional scaling (HMDS) ordinations of the bat community captured in three types of secondary vegetation at the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazonia, Brazil, based on (a) abundance data and (b) presence–absence data. Secondary forests: AP, abandoned pasture; V, *Vismia*-dominated regrowth; C, *Cecropia*-dominated regrowth; camps: co, Colosso; di, Dimona; pa, Porto Alegre; cp, Cidade Powell.

forests – both structurally similar with tall trees and dense vegetation – we found that the bat community differed significantly from that caught in the abandoned pasture in terms of abundance (Pillai trace = 0.84,  $P = 0.001$ ) and presence–absence of species (Pillai trace = 0.63,  $P = 0.019$ ). The MANOVA test performed to compare bat species composition among the three farms showed a significant difference using abundance data (Pillai trace = 1.04,  $P = 0.015$ ), but occurrence data resulted in no difference (Pillai trace = 0.63,  $P = 0.169$ ).

The differences in bat community composition among the types of secondary vegetation can be explained by the abundances of the most captured subfamilies. Stenodermatinae bats were significantly more abundant in abandoned pasture (ANOVA,  $F_{2,8} = 5.83$ ,  $P = 0.014$ ). The subfamily Phyllostominae, all gleaning animalivores, had captures

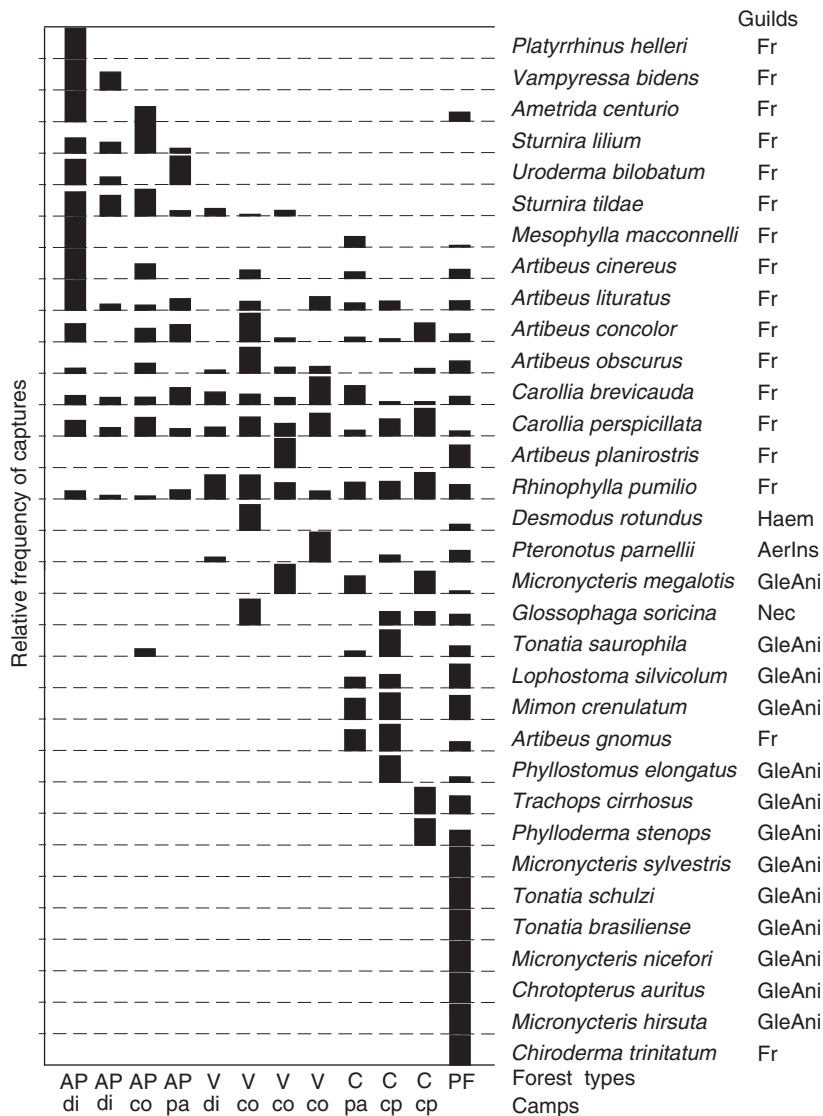
(ANOVA,  $F_{2,8} = 7.72$ ,  $P = 0.014$ ) and species (ANOVA,  $F_{2,8} = 47.02$ ,  $P = 0.000$ ) associated with *Cecropia*-dominated regrowth (Table 2; Fig. 4). Among the seven species of Phyllostominae captured, only *Tonatia saurophila* and *Micronycteris megalotis* were not exclusively captured in *Cecropia*-dominated regrowth (Table 2; Fig. 4). *Artibeus concolor*, *Artibeus lituratus*, *Artibeus obscurus* and *Mesophylla macconnelli* were the only Stenodermatinae species captured in *Cecropia*-dominated regrowth; however, these four species were most abundant in abandoned pasture and *Vismia*-dominated regrowth (Fig. 4). Four bat species from the family Stenodermatinae, *Vampyressa bidens*, *Platyrrhinus helleri*, *Ametrida centurio* and *Uroderma bilobatum* were captured only in abandoned pasture (Table 2).

The results of regressions showed a relationship between abundances of most-captured species, gleaning animalivores and HMDS Axis 1 with the primary forest, *Cecropia*-dominated regrowth and abandoned pasture, supporting the results found in ANOVA tests (Table 3). The most captured bat, *C. perspicillata*, was positively associated with forest and negatively with abandoned pastures (Table 3). Abandoned pasture was positively associated with the capture frequency of *S. tildae* and *S. lilium*, with higher abundances grouped into pasture sites (Table 3). The capture frequency of *R. pumilio* responded negatively with abandoned pasture (Table 3). Gleaning animalivores richness was positively associated with *Cecropia*-dominated regrowth (Table 3). The abundance and occurrence data of the HMDS Axis 1 were associated with *Cecropia*-dominated regrowth, with an evident separation between the *Cecropia*- and the *Vismia*-dominated regrowth sites.

## Discussion

Our results indicate that successional pathways of deforested areas in Central Amazonia affect the bat community composition. This impact is more noticeable in the species composition than in the species richness. The number of bat species did not differ markedly between the three types of secondary vegetation (Table 2), but the bat assemblages did so. The earlier stage of secondary succession represented by abandoned pastures showed more species of Stenodermatinae frugivorous bats and a greater abundance of two *Sturnira* species, whereas *Cecropia*-dominated regrowth supported more species of the Phyllostominae (Fig. 4). A similar response was documented in south-eastern Mexico, where a young secondary forest was abundant in frugivorous bats, while a majority of rare species and Phyllostominae prevailed in older secondary forest (Castro-Luna *et al.*, 2007). The abundance of the most common bat species, the richness of Phyllostominae and the bat community composition seem to be significantly influenced by the type of vegetation cover, whereas the distance to the nearest continuous primary forest has a negligible effect on these response variables. Even so, the proximity of all the sampling points with the undisturbed continuous forest and fragments (Table 1) was an important driver of the bat community composition and species abundance. Some





**Figure 4** Distribution of captured bats in secondary forests and primary forest at the Biological Dynamics of Forest Fragments Project (BDFFP) study sites in Central Amazonia, Brazil. Solid bars represent the number of individuals captured divided by the sampling effort (net-hours) at the given site. Because the Y-axis of the abundance of each species is on a different scale, it is not possible to make a direct comparison among the species. Vegetation types: PF, primary forest; C, *Cecropia*-dominated regrowth; V, *Vismia*-dominated regrowth; AP, abandoned pasture; camps: co, Colosso; di, Dimona; pa, Porto Alegre; cp, Cidade Powell. Guilds: Fr, frugivore; Hem, hematophagous; AerIns, aerial insectivore; GleAni, gleaning animalivore; Nec, nectarivore. Primary forest understory data are from Bernard (2001).

frugivorous and gleaning animalivore species can make several trips between the primary forest and the altered areas to feed (Bernard & Fenton, 2003; Loayza & Loiselle, 2008), which would increase the species diversity in disturbed vegetation.

The pattern of use of secondary vegetation by bats is associated with foraging strategies of frugivorous bats (Galindo-González *et al.*, 2000). Secondary vegetation has abundant production of fleshy fruits of successional plants, and occur here distributed over large areas (2200 ha in both Porto Alegre and Colosso farms) such that it minimizes the competition for food (Marinho-Filho, 1991). The populations of the frugivorous bats can be favoured in areas with several types of altered vegetation. The high complexity of the mosaic of floristic composition in abandoned pasture, *Vismia*- and *Cecropia*-dominated regrowth at Esteio farm (Mesquita *et al.*, 2001) explains the largest abundance of the

common frugivorous species (Fig. 4) and its separation from the other farms (Dimona and Porto Alegre) in the abundance data. In the study area, fruit-bearing plants such as *Vismia* spp. and *Solanum* spp. were highly consumed by the six most common frugivorous bats (Bobrowiec, 2003).

Frugivorous bats attained higher abundances in abandoned pastures compared with other successional forests. However, abandoned pastures may be hostile places for bats because they lack a corridor of arboreal vegetation for flight between fragments and habitats for roosting, which increases the predation risks. Our sample sites in abandoned pastures were located 20–250 m from the edge of the fragments (Table 1), allowing capture of species that forage in open areas of abandoned pasture close to fragments. The positive association of *C. perspicillata* with the forest cover (Table 3) suggests that this species requires patches of forest near the disturbed areas used for foraging. On a small scale



**Table 3** Results of the multiple linear regressions of the landscape characteristics on abundance of bat species, trophic guild and ordination axis. Explanatory variables that maximize  $R^2$  were selected by the forward stepwise method. Symbols of plus or minus denotes the sign of regression coefficients associated with a particular landscape characteristic

	<i>P</i>	Sign
<i>Carollia perspicillata</i>		
Model $R^2 = 0.77$		
Forest cover	0.002*	+
Pasture cover	0.014*	-
<i>Carollia brevicauda</i>		
Model $R^2 = 0.28$		
Forest cover	0.094	-
<i>Stunira lilium</i>		
Model $R^2 = 0.32$		
Pasture cover	0.070	+
<i>Stunira tildae</i>		
Model $R^2 = 0.44$		
Pasture cover	0.026*	+
<i>Rhinophylla pumilio</i>		
Model $R^2 = 0.32$		
Pasture cover	0.070	-
Stenodermatinae abundance		
Model $R^2 = 0.27$		
Pasture cover	0.100	+
Gleaning animalivore richness		
Model $R^2 = 0.43$		
<i>Cecropia</i> forest cover	0.029*	+
Gleaning animalivore abundance		
Model $R^2 = 0.66$		
Distance from the forest	0.104	+
<i>Cecropia</i> forest cover	0.106	+
Frugivore richness		
Model $R^2 = 0.22$		
<i>Cecropia</i> forest cover	0.148	+
Frugivore abundance		
Model $R^2 = 0.33$		
Forest cover	0.063	+
HMDS Axis 1 abundance data		
Model $R^2 = 0.42$		
<i>Cecropia</i> forest cover	0.030*	-
HMDS Axis 1 richness data		
Model $R^2 = 0.67$		
Distance from the forest	0.013*	-
<i>Cecropia</i> forest cover	0.033*	-

\*Significant effects at  $P < 0.05$ .

of disturbance, some frugivorous bat may travel distances of 0.5 km or more for foraging in open areas (Bernard & Fenton, 2003; Albrecht, Meyer & Kalko, 2007; Loayza & Loiselle, 2008).

In relation to Phyllostominae bats, a previous study found 15 and 13 species in undisturbed continuous forest and fragments at the BDFFP, respectively (Sampaio, 2000), vs. seven species of this family found in *Cecropia*-dominated regrowth studied here (Table 2). Continuous

forest and fragments shared in common all seven species found in *Cecropia*-dominated regrowth (Table 2), yielding a Jaccard similarity index of 0.47 and 0.60 with continuous forest and fragments, respectively, based on occurrence data. This association indicated that *Cecropia*-dominated regrowth can maintain a significant proportion of the Phyllostominae diversity, but that patches of undisturbed forest are essential for the conservation of the entire subfamily. In disturbed landscapes, small patches of different types and ages of altered habitats may have a higher conservation value than homogenous altered habitats (Pardini *et al.*, 2009).

Many authors have shown that Phyllostominae bats, especially species such as *Micronycteris* spp., *Lophostoma silvicolum*, *Phyllostomus elongatus*, *Phylloderma stenops* and carnivorous bats, are sensitive to loss of primary forest and fragmentation (Fenton *et al.*, 1992; Wilson, Ascorra & Solari, 1996; Medellín *et al.*, 2000). In the BDFFP, the higher abundance and the richness of Phyllostominae bats were associated with *Cecropia*-dominated regrowth. However, 20 years of recovery was still not enough to attract the full complement of Phyllostominae bats as observed in the pristine forest.

In Neotropical forests, the majority of bat species are captured in low numbers of individuals (Brosset *et al.*, 1996; Lim & Engstrom, 2001; Bernard & Fenton, 2002). In our study, the majority of Phyllostomidae species (65.4%; 17 species) were considered rare, exhibiting less than 10 captured individuals (Table 2). The low abundance of some species is not necessarily associated with the stage of secondary succession. Some bat species have small population sizes, being rare in both undisturbed and altered habitats (Estrada & Coates-Estrada, 2001; Faria, 2006). In the BDFFP, 15 species captured here were also rare in the continuous primary forest (*Artibeus cinereus*, *Artibeus gnomus*, *Ar. planirostris*, *Am. centurio*, *M. macconnelli*, *U. bilobatum*, *P. helleri*, *V. bidens*, *P. stenops*, *P. elongatus*, *Trachops cirrhosus*, *M. megalotis*, *Mimon crenulatum*, *Glossophaga soricina* and *Desmodus rotundus*) (Bernard, 2001). The response to deforestation and the degree to which they use altered habitats is difficult to evaluate, but our results suggest that secondary vegetations allow the inclusion of a proportion of the rare bat species.

The six most abundant bat species here are also the most frequently found in BDFFP primary forest (Sampaio *et al.*, 2003). Their population sizes remain stable (e.g. *R. pumilio*) or even increase in disturbed habitats. *Carollia perspicillata* and *C. brevicauda* were four and two times more abundant in secondary vegetations than in primary forest, respectively, whereas *S. lilium* and *S. tildae* were 13 times more abundant in abandoned pastures (data compared with Bernard, 2001; 1064 net-hours). The similar abundance of *R. pumilio* in primary and older secondary forest understorey (Bernard, 2001) indicates a moderate response to deforestation, but a low tolerance to open habitats. On the other hand, *Ar. concolor* was four times more abundant in primary forest understorey from BDFFP, where it was considered as a canopy species (Bernard, 2001). The use of

secondary vegetation regrowth by *Ar. concolor* was associated with its consumption of *Vismia* fruits, which represented >80% of its diet (Bernard, 2002; Bobrowiec, 2003). Although the canopy was not sampled here, the fact that *Vismia* fruits were available in the lower strata of the abandoned pastures and *Vismia*-dominated regrowth may explain the high capture rate of *Ar. concolor* in ground-level nets.

*Sturnira tildae* and *S. liliium* were virtually absent in the *Vismia*- and *Cecropia*-dominated regrowth (Table 2). As found in other studies, these bats are known to forage in open areas and plantations (Brosset *et al.*, 1996; Galindo-González *et al.*, 2000). The use of abandoned pasture by two *Sturnira* species is related to their specialization on *Solanum* fruits (Marinho-Filho, 1991; Bobrowiec, 2003), where these pioneer plants are more abundant (Bobrowiec, 2003). *Solanum* spp. fruits make up 42 and 77% of the diet of *S. tildae* and *S. liliium*, respectively (Bobrowiec, 2003). However, the captures of *S. tildae* (13.3%) in the *Vismia*-dominated regrowth may be explained by its consuming *Vismia* fruits, which make up 38% of the diet of these bats, but only 6% in *S. liliium* (Bobrowiec, 2003). Although foraging over abandoned pastures, *S. liliium* selects roosts in large-diameter trees, making the nearby primary forest a critical resource (Fenton *et al.*, 2000; Evelyn & Stiles, 2003).

Our results illustrate that old *Cecropia*-dominated regrowth close to the continuous forest seems to be more suitable to habitat-selective forest bats than *Vismia*-dominated regrowth and abandoned pastures. Mature *Cecropia* forest allows the persistence of many bat species that are found in the primary forest, such as Phyllosotminae species. Abandoned pastures close to fragments and *Vismia*-dominated regrowth may also be exploited by bats, mainly for Stenodermatinae frugivores that forage on fruits of pioneer plants. A similar pattern of abundance and richness changes has been described for other Amazonian vertebrates. In general, the use of disturbed vegetations by sensitive species depends on the type of secondary vegetation. For birds and frogs, as in bats, *Cecropia*-dominated regrowth seems to be more permeable to primary forest species and more diverse than the fire-shaped habitats such as pastures and *Vismia*-dominated regrowth (Tocher, 1998; Stouffer & Borges, 2002; Antongiovanni & Metzger, 2005). The re-colonization of forest fragments by birds is faster in fragments surrounded by *Cecropia*-dominated regrowth (Stouffer & Borges, 2002).

Our results show that the structure of the bat communities has been affected by expansion of cattle ranching in the Amazon. Livestock is becoming a major economical activity in the Amazon and it already includes 36% of the Brazilian herd (Smeraldi & May, 2008). The large-scale slash-and-burn practices have been contributing to the establishment of huge areas (>10 000 ha) of abandoned pastures and *Vismia*-dominated regrowth, especially in southern and eastern Amazonia. In such highly disturbed areas, it is likely that the bat communities are very impoverished and that the ecological processes mediated by bats, such as seed dispersal, may be disrupted.

Many existing reserves in Brazil are surrounded by secondary forests, which are frequently considered as areas of poor conservation value. Our data suggest that, wherever possible, they should be included in the conservation plans to increase the total protected area and the bat biodiversity. The structure of bat communities, and other faunas as well, depends on nearby pristine forest. A combination of continuous forest with mosaics of fragments and different stages of secondary forests maintains high bat diversity (Estrada & Coates-Estrada, 2002; Sampaio *et al.*, 2003; Faria, 2006). The *Cecropia*-dominated regrowth possesses a high conservation value, and may be used as corridors to ameliorate the negative effects of deforestation, and allow the maintenance of populations of frugivorous and gleaning bats in a fragmented landscape.

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## Supporting Information

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

**Appendix S1.** Correlograms of the regression residuals models of the response variables (six most-captured species of bats, abundance and species richness of Stenodermatinae,

gleaning animalivore, and frugivore bats) as function of the distance from the continuous primary forest, relative proportion with each site of primary forest, *Vismia*-dominated forest, *Cecropia*-dominated forest, and abandoned pasture (explanatory variables). Moran's  $I$  coefficient values were considered significant at  $P < 0.05$ .

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