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Research article

From a bat's perspective, protected riparian areas should be wider than defined by Brazilian laws



Lucas Gabriel do Amaral Pereira^{a,*}, Ubirajara Dutra Capavede Jr.^b, Valéria da Cunha Tavares^{c,d}, William E. Magnusson^b, Paulo Estefano Dineli Bobrowiec^{b,e,**}, Fabricio Beggiato Baccaro^{a,b,f,***}

^a Programa de Pós-Graduação em Diversidade Biológica, Universidade Federal do Amazonas (UFAM), 69080-900, Manaus, AM, Brazil

^b Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), 69080–971, Manaus, AM, Brazil

^c Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais (UFMG), 31270-901, Belo Horizonte, MG, Brazil

^d Departamento de Ciências Biológicas, Universidade do Estado de Minas Gerais (UEMG), 32415-250, Ibirité, MG, Brazil

e Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia (INPA), 69011-970, Manaus, AM, Brazil

^f Departamento de Biologia, Universidade Federal do Amazonas (UFAM), 69067-005, Manaus, AM, Brazil

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ABSTRACT

Riparian areas around streams are those areas in which biological communites are directly influenced by the stream. The size of protected riparian areas and their conservation has become a controversial topic after changes implemented in the Brazilian Forest Code (BFC): a set of laws that regulates the size of Permanent Protection Areas (PPA). Here, we investigate the influence of distance from water bodies on bat-species and guild composition in a lowland Amazonian rainforest. Our hypotheses were that bat assemblages would change depending on the distance to the water body and that the abundance of herbivorous bats (frugivorous and nectarivorous) would be greater in areas close to water. Bats were captured with mist-nets in 24 riparian and 25 non-riparian plots within a trail grid in an old-growth terra-firme forest, northeast of Manaus, Amazonas, Brazil. Each plot was sampled three times in a total of 7056 net-hours. We captured 1191 bats, comprising 51 species. We used model selection based on AIC (Akaike Information Criterion) to compare linear and piecewise regressions to estimate the ecological thresholds for different bat assemblages. Piecewise models with one breakpoint were more parsimonious than linear models for abundance data, and the species and guild composition of animalivorous and frugivorous bats. Animalivorous-bat abundance increased from the stream to about 181 m, and frugivorous-bat abundance decreased within 50 m of the stream. The patterns of guild abundance suggest that frugivorous bats may need greater access to streams than animalivorous bats. The most conservative model suggests that most of the variation in bat composition occurs close to the stream and extends to up 114 m from the banks. Therefore, the 30 m wide strip of riparian forest protected by Brazilian law would maintain a relatively small fraction of bat-species assemblages in Ducke Reserve, and is insufficient to represent most of the assemblage-composition variation within the riparian zone. The suggestion to reduce the width of the protected riparian zone from 30 to 15 m for streams smaller than 10 m wide, as is under discussion, would likely be prejudicial for bat assemblages.

1. Introduction

Forest ecosystems are not uniform, and consequently they are often categorized the into discrete habitats. However, the categories recognized by humans may not be relevant to other organisms and, even when they are, the boundaries among categories may be indistinct and vary among species. One of the habitats that have been found to be most critically distinct for a variety of organisms within central-Amazonian forests are the riparian zones, the stripe of forested areas located around watercourses. Riparian areas have been defined as extending from the highest level of a water body to the furthest part of the land under the influence of water (Naiman et al., 1993; Naiman and Décamps, 1997). Riparian zones shelter and provide essential resources for many species (Sabo et al., 2005), contributing to the maintenance of

**** Corresponding author. Departamento de Biologia, Universidade Federal do Amazonas (UFAM), 69067-005, Manaus, AM, Brazil.

E-mail addresses: amaralg.lucas@gmail.com (L.G.d.A. Pereira), paulobobro@gmail.com (P.E.D. Bobrowiec), fbaccaro.ecolab@gmail.com (F.B. Baccaro).

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^{*} Corresponding author. Programa de Pós-Graduação em Diversidade Biológica, Universidade Federal do Amazonas (UFAM), 69080-900, Manaus, AM, Brazil. ** Corresponding author. Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia (INPA), 69011-970, Manaus, AM, Brazil.

biodiversity and ecosystem processes (Naiman et al., 1993; Lawrence et al., 2014). The degradation of riparian forests may affect water supply, promote changes in hydrological dynamics, temperature and humidity, and alter forest productivity (Naiman et al., 1993; Silva et al., 2011; Soares-Filho et al., 2014).

The Amazon is the largest hydrographic basin covered by continuous tropical forest in the world. Such a large and "pristine" area is hard to maintain under traditional economic-development models (Fearnside, 2005). Habitat loss and fragmentation in combination with other human-related threats, has pervasive consequences in Brazilian forests. Riparian forests cover strips of riparian ecosystems and are declared Permanent Preservation Areas (PPAs, or APPs, the official abbreviation in Portuguese), which must be fully protected to preserve water resources, landscape, geological stability and biodiversity, facilitate gene flow, protect the soil and ensure the well-being of human populations (BRASIL, 2012). Definitions as taken from from the recently revised Brazilian Forest Code (hereafter BFC) state that riparian protected zones cover areas within 30 m of stream banks for watercourses less than 10 m wide, and 500 m around watercourses greater than 600 m wide (BRASIL, 2012). The width of riparian protected areas defined in the BFC was based only on forest strata, disregarding the spatial distribution of other groups, such as animals (Metzger, 2010; Nazareno, 2012; Soares-Filho et al., 2014). This highlights the need for conservation-related studies to understand the biodiversity associated with watercourses in tropical areas. Smaller riparian areas prescribed by the BFC may not be suitable for the effective conservation of several animal taxa, including bats.

The forest around small streams in terra-firme non-flooded forests often contains plant and animal assemblages that are distinct from the surrounding forest. In Central Amazonia, 90% of the variation in treeand palm-species composition occurs in the first 200 m from stream channels less than 10 m wide (Schietti et al., 2013). Riparian understory-herb composition differs from better-drained areas up to100 m from the stream channel (Drucker et al., 2008). Riparian zones also influence the distribution of several animal taxa that depend on vegetation for food and shelter (Lees and Peres, 2008; Marques et al., 2012; Ribeiro et al., 2012). Snake-species composition shows a marked change 100 m from the stream course (Fraga et al., 2011), while most variation in understory-bird-assemblage composition occurs within 200 m of the stream (Bueno et al., 2012). The composition of animal species is probably related to structural characteristics of the vegetation and climatic conditions in riparian and non-riparian forests. Higher soil and air humidity associated with the relatively open vegetation of riparian zones may influence the distribution of other animal species, such as ants (Oliveira et al., 2008), cockroaches (Tarli et al., 2014), harvestman (Tourinho et al., 2014) and frugivorous bats (Zarazúa-Carbajal et al., 2017). The integrity of riparian zones, characterized by the intrusion of external disturbances such as logging, overgrazing of domesticated livestosk, exotic plants, and the proportion of surrounding degraded forest, also influence the composition of species that use these forests (Lees and Peres, 2008; Zimbres et al., 2017; Mitchell et al., in press).

Among tropical mammals, bat assemblages have the highest species diversity and the greatest variety of guilds co-occurring in single localities (Tavares et al., 2017). The Neotropical family Phyllostomidae is a highly diverse clade of bats, both in number of species and ecological interactions (Kalko et al., 1996; Adams and Pedersen, 2013). Phylostomids include frugivorous, nectarivorous, insectivorous, carnivorous, and sanguivorous species with different foraging strategies in relation to topography, vegetation clutter, and food distribution (Marciente et al., 2015; Bobrowiec and Tavares, 2017; Capaverde et al., 2018). Frugivores and nectarivores fly long distances inside the forest to consume fruits and nectar from patchily-distributed shrubs and trees (Bonaccorso and Gush, 1987; Lobova et al., 2009), and insectivores and carnivores forage over smaller distances hunting for arthropods and/or small vertebrates on the surrounding vegetation and soil (Arlettaz et al.,

2001; Schnitzler and Kalko, 2001). Bats are the most species-rich mammalian assemblages in the Amazonian forest, but few studies examined the influence of streams on Neotropical bats assemblage structure (Galindo-González and Sosa, 2003; Medina et al., 2007; Avila-Cabadilla et al., 2012; de la Peña-Cuéllar et al., 2015; Bobrowiec and Tavares, 2017; Zarazúa-Carbajal et al., 2017). Most of those studies focused on the species composition associated with riparian zones and and showed greater abundance of frugivorous bat species near riparian vegetation. However, none have examined the width of the riparian zone needed to conserve bat assemblages. In this study, we evaluated the influence of distance to streams on bat assemblages in a 25-km² area of continuous terra-firme forest in central Brazilian Amazonia. Our hypothesis was that the bat assemblages would change with distance from the stream. We predicted that the abundance and the number of species, especially of animalivorous, frugivorous and nectarivorous phyllostomids would be higher in areas close to streams. We also predicted that the species composition would be related to the distance from the water, which in turn influences guild composition. This information may be important for conservation decisions, especially in relation to Brazilian legislation, which specifically protects riparian zones.

2. Materials and methods

2.1. Study area

Our study site was in Reserva Ducke (hereafter Ducke Reserve, $02^{\circ}55' \cdot 03^{\circ}01'$ S, $59^{\circ}53' \cdot 59^{\circ}59'$ W), situated northeast of the city of Manaus, Amazonas State, Brazil (Fig. S1). The Ducke Reserve covers 10,000 ha of terra-firme non-flooded forest. The climate of Ducke Reserve is tropical monsoon (Peel et al., 2007), with average annual temperature of 24.9 °C in 2013 (data from the Ducke Reserve Climatological Station). The rainy season generally occurs from November to May, and the dry season from June to October, with annual rainfall of 3385 mm in 2013 (data from the Ducke Reserve Climatological Station). The forest covering the Ducke Reserve has a dimly-lit understory with prevalence of stemless palms. The canopy is continuous, with emergent trees reaching 45–60 m (Oliveira et al., 2008).

In 2001, a RAPELD (Rapid Assessment Program/Long Term Ecological Research) trail system was installed in Ducke Reserve. The RAPELD system at Ducke Reserve, consists of a grid formed by 9 northsouth and 9 east-west oriented trails spaced at 1 km intervals (Magnusson et al., 2013), covering an area of 64 km². Each of the eastwest trails of the grid have eight permanent plots spaced 1 km apart (Fig. S1). We used a subset of the grid covering 25 km², comprising 30 plots (Fig. S1). Additional to the regularly-spaced plot system, within our 25 km² study area, we also sampled 19 riparian plots oriented parallel to streams (250-m long plots consisting of 10 m straight-line segments each with a minimum distance of 1.5 m from stream margins). Five of the 30 regularly-spaced plots fell close to streams, resulting in 24 riparian plots and 25 non-riparian plots. All plots were 250 m long, and the regularly-spaced plots followed terrain contours to minimize within-plot soil, topographic, and vegetation variation (Costa and Magnusson, 2010; Magnusson et al., 2005, 2013).

Our sampling area is situated in the western basin of the Ducke Reserve, formed by the Acará and Bolivia stream basins that flow into the Negro River (Ribeiro et al., 1999). We sampled plots associated with first (n = 15), second (n = 6), and third (n = 3) order streams with mean width of the 3.05 m (SD \pm 1.20, min = 1.26, max = 5.33) and mean depth of 0.40 m (\pm 0.16, min = 0.18, max = 0.65). The distances between riparian and non-riparian plots varied from 100 m to 1 km.

2.2. Stream-distance estimation

We used a drainage map based on SRTM (90 m spatial resolution)

using a 30-pixel minimum contribution area (= 0.41 km^2) to estimate the distances of each plot to nearest water body. This drainage map was validated along the trail system in the field in several points (more details in Schietti et al., 2013). SRTM data for Ducke Reserva was obtained from http://www2.jpl.nasa.gov/srtm/, with a horizontal resolution of 3 arc-seconds (90 m near the equator) and a vertical resolution of 1 m. To minimize the possible effect of 90 m pixel resolution, the Euclidean distance between plots and nearest drainages was calculated based on the average of bilinear interpolation values for 25 locations along each permanent-plot centre line. The distance of the center line of each plot from the nearest watercourse varied between 1.5 and 429 m (mean \pm SD = 209 \pm 161 m). The distance between riparian plots and the streams was set to zero in all analysis.

2.3. Bat sampling

We captured bats between October 2013 and February 2014, at the end of the dry season and the beginning of the rainy season. Each plot was visited three times, with an interval of about 30 days between each visit. In each plot, we erected eight mist nets (Ecotone^{*} 12 m \times 3 m, 19 mm mesh, six shelves) arranged sequentially, and set at ground-level. The net lines started 20 m from the beginning of the center line of each plot to avoid interference from grid trails. Nets remained opened from 18:00 to 00:00 and were checked every 15 min. We use net*hours as the unit of sampling effort (one net*hour = one net open*1 h).

All captured bats were marked with a numbered ball-chain necklace and released. We recaptured 42 bats (3.5% of captures) from seven species. Recapture-data were not used in analyses. Identifications of bat species were based on dichotomous keys and descriptions found in Simmons and Voss (1998), Charles-Dominique et al. (2001), Lim and Engstrom (2001), Gardner (2007), Miranda et al. (2011), and literature sources specific for each taxa. Taxonomy followed Gardner (2007), with modifications as implemented by the updated list of Brazilian bats (Nogueira et al., 2014). The data and metadata on the species captured are deposited in the public repository of the Programa de Pesquisa em Biodiversidade (http://ppbio.inpa.gov.br/repositorio/dados). The data can be accessed by the title in Portuguese "Morcegos, altitude, frutos e insetos em 49 parcelas da Reserva Florestal Adolpho Ducke".

2.4. Data analysis

We restricted the analysis to bats of the family Phyllostomidae and the aerial insectivorous mormoopid *Pteronotus parnelli* (family Mormoopidae), because bats of other families are not commonly captured in ground-level mist nets (Bobrowiec et al., 2014; Rocha et al., 2017). We allocated captured bats to a particular trophic guild (frugivore, nectivore, animalivore, sanguivore, and aerial insectivore) based on the feeding habitat and foraging mode as reported by Kalko (1998).

We use the overall abundance and number of bat species, the abundance and number of animalivorous, frugivorous and nectarivorous species, and the abundance and presence/absence composition of species and guilds as response variables, and the distance to the nearest stream of each plot as the predictor variable. The total abundance of bats and the number of species of frugivores was log transformed (log + 1) to normalize model residuals.

We used one-dimensional Non-metric Multidimensional Scaling (NMDS) ordinations to represent species and guild composition based on relative abundance of species and guilds, and species presence/absence data. The species-abundance data were standardized by the total abundance of bats in each plot, in order to make the ordination sensitive to composition rather than total abundance. NMDS was calculated using the Bray-Curtis index for the abundance data and the Sørensen index for presence/absence data.

We used linear and piecewise regression models (Toms and Lesperance, 2003) to evaluate relationships between the response variables and the distances to streams. Piecewise regressions are robust

analyses that have been used to determine ecological thresholds between continuous variables and evaluate the break points of two or more regression lines (Bacon andWatts, 1971; Toms and Lesperance, 2003; Ficetola and Denoel, 2009). A significant break point of a piecewise regression represents major changes in the distribution of the response variable deviations in relation to the predictor variable. We tested spatial autocorrelation using Moran's I index with equal numbers of connections and 9999 randomisations in SAM V.4 software (Rangel et al., 2010). The significance test indicated that no spatial correction of the data was necessary.

We used the Akaike Information Criterion (AIC) to compare linear and piecewise models. Models were selected *a posteriori* based on an assessment of the maximum-likelihood fit between the adjusted model and the original data (Akaike, 1998; Richards, 2005). Models with lower AIC values have better fit, controlling for the effect of model complexity (more complex models, such as piecewise regression, are less parsimonious). Values of Δ AIC < 2, which is a simple cut-off rule widely used for comparing models, and high values of Akaike weights (w_i) (i.e. closest to 1) (Burnham and Anderson, 2001) were used to identify the models that received the strongest support and that most likely best represent the relationships between the response variables and the distance to the stream.

We conducted all analyses using version 3.1.2 of the R program (R Core Team, 2017). We used *metaMDS* and *vegdist* functions from the 'vegan' package (Oksanen et al., 2015) to obtain NMDS axes, the *davies.test* function to run piecewise regressions, and segmented functions from the 'segmented' package (Muggeo, 2015). AIC models were selected *usingmodel.sel* function from the 'MuMIn' package (Bartón, 2015).

3. Results

We captured 1191 bats of 51 species from five families over 147 nights (7056 net*hours) (Table S1). Phyllostomids were the most commonly captured bats (n = 1115, 93.6%), and contributed the largest number of species (n = 38; 74.5%). Frugivores were most frequently captured (n = 771 captures; 72.6%), followed by animalivores (n = 180; 16.9%), and nectarivores (n = 163; 13.7%). Frugivore and animalivore guilds had the highest number of species (16 species each). The ten most-captured Phyllostomidspecies represented 83.8% of the total; *Carollia perspicillata* was the most common (n = 453; 42.7% of phyllostomids captured), followed by *C. brevicauda* (n = 138; 13%), *Hsunycteris thomasi* (n = 76; 7.2%), *Rhinophylla pumilio*(n = 66; 6.2%), and *Phyllostomus elongatus* (n = 58; 5.5%). The fruit bat *C. perspicillata* was captured in all 49 plots, while 29 species (74.4%) occurred in ≤ 10 plots.

Linear and piecewise models were equally parsimonious for the abundance of animalivorous species (Table 1), but the piecewise model had a higher weight ($w_i = 0.69$) and explained more variance $(r^2 = 0.23)$ than the linear model $(w_i = 0.31; r^2 = 0.16)$. The breakpoint of the regression line was 181 m (\pm 70.2 m; SD) from the stream (Fig. 1). For frugivore abundance (Table 1), the piecewise regression was the best model ($w_i = 0.77$) with a breakpoint in the regression line at 50 \pm 27.7 m from the stream (Fig. 1). Abundance of frugivores in sites below the breakpoint was 2.4 times higher than at sites above the break point. This difference was caused mainly by the frugivores C. perspicillata, C. brevicauda, C. benkeithi, Artibeus gnomus, and Vampyriscus bidens, which were more frequently captured near streams (Fig. 2). In contrast, linear models of total abundance, abundance and number of nectarivorous species, and number of frugivorous species had better fits than the piecewise models (Table 1). However, the explained variance for these relationships was weak ($r^2 \le 0.03$). We were unable to use AIC model selection with the total number of species and number of animalivorous species because the break points of the regression lines of piecewise models exceeded the variation of the sampled gradient, suggesting that no break point exists (Table 1).

Table 1

Results of the linear and piecewise regression models of number of species, abundance, and species and guild composition of bats captured in the Ducke Reserve, Manaus, Amazonas State, Brazil. ΔAIC : Akaike criterion differences; w_i: Akaike weights; lim: estimated regression line break points in meters, SD: standard deviation of estimated regression lines break points for piecewise models, β : regression line slope, -: unable to perform AIC model selection.

Response variable	Model	ΔAIC	$\mathbf{w}_{\mathbf{i}}$	r^2	lim	SD	β
Abundance data							
Total	Linear	0	0.5	0.03			-0.0007
	Piecewise	0.02	0.5	0.09	106.3	77.8	
Animalivores	Linear	1.59	0.31	0.16			0.007
	Piecewise	0	0.69	0.23	181	70.2	
Frugivores	Linear	2.44	0.22	0.1			-0.001
	Piecewise	0	0.77	0.19	50.6	27.7	
Nectivores	Linear	0	0.75	0.01			-0.002
	Piecewise	2.19	0.25	0.02	159.2	108.8	
Richness data							
Total	Linear	-	-	0.003			0.002
	Piecewise	-	-	-	-	-	
Animalivores	Linear	-	-	0.18			0.004
	Piecewise	-	-	-	-	-	
Frugivores	Linear	0	0.7	0.01			-0.002
	Piecewise	1.7	0.3	0.03	159.2	99.8	
Nectivores	Linear	0	0.69	0.02			-0.0003
	Piecewise	1.56	0.31	0.008	296.7	98.9	
Species composition data							
Abundance data	Linear	1.55	0.32	0.17			-0.001
	Piecewise	0	0.68	0.24	43.9	26.6	
Presence/absence	Linear	4.93	0.08	0.11			0.0006
data	Piecewise	0	0.92	0.24	114.3	60.4	
Guilds	Linear	2.94	0.19	0.18			0.001
(abundance data)	Piecewise	0	0.81	0.28	46.2	25.2	

The NMDS ordination axis for the species-abundance and the presence/absence data explained 34.6% and 30.6% of the variation of the original species-composition distances between plots, respectively, while the NMDS axis for guilds explained 27.8%. The piecewise models for species (abundance and presence/absence data) and guild composition were more parsimonious with higher explained variance ($r^2 > 0.24$) than the linear models (Table 1). We estimated that strong changes in the bat assemblages (abundance data) and guild composition start at around 45 m (\pm 26.6 m) from the nearest stream (Fig. 3). For the presence/absence data (Fig. 3), the breakpoint was at 114 m (\pm 60.4 m).

4. Discussion

Variations of the bat-assemblage in relation to the distances from the streams depend on the assemblages and on the guilds considered. The selection of piecewise models indicates that there is a nonlinear structure of the bat assemblages correlated to the distances from the streams, particularly in the case of frugivore and animalivore species relative abundances and species and guild composition. The number of individuals and species of animalivorous bats tended to increase with distance from the stream, and the number of individuals and species of phytophagous bats (frugivores and nectarivores) captured tended to decrease with distance from the stream. The differences in number of individuals and species reflected differences in species assemblages and guild structure, which showed clear changes at distances that varied between from approximately 50 m-160 m, depending on the guild. The concurrent distances and conspicuous changes for bat assemblages are similar to those that have been reported for assemblages of other animal and plant taxa investigated in the same area (trees and palms, Schietti et al., 2013; herbs, Drucker et al., 2008; snakes, Fraga et al., 2011; understorey birds, Bueno et al., 2012, Mitchell et al., in press).

All seven phytophagous bats (six frugivores, and the nectarivore Anoura caudifer), representing nearly a half of Phyllostomid captures (n = 564) were concentrated at close distances of less than 174 m away from the streams. Frugivorous-bat distributions are generally expected to associated to the spatial distribution of food resources (August 1983; Fenton, 1990; Arlettaz et al., 2001; Patterson et al., 2003). Studies conducted in the same plots at Ducke reserve by Capaverde et al. (2018) revealed that the composition of fruit trees consumed by bats was associated with the fruit bat species distribution and it was distinct between areas near the streams and better-drained plateaus. The bats A. gnomus and R. fischerae were more abundant in plots near streams that contained the bat chiropterochorous genus Peperomia, while the three large Artibeus (A. lituratus, A. obscurus, and A. planirostris) were more frequent on the plateaus with a higher abundance of Bactris, Oenocarpus, and Philodendron (Capaverde et al., 2018). Bat species from the genus Artibeus and Rhinophylla are known to consume the fruits of Peperomia, Bactris, Oenocarpus and Philodendron (LoGiudice and Ostfeld, 2002; Bredt et al., 2012; Marques et al., 2012). Vegetation structure may also play an important role in structuring the bat assemblages (Marciente et al., 2015). Understory frugivores fly long distances into the forest in search of trees and shrubs with ripe fruits that are usually irregularly distributed (Capaverde et al., 2018). Oliveira et al. (2015) also studying the same plots at Ducke Reserve, reported that the vegetation close to streams was relatively more open than that on plateus.



Fig. 1. Piecewise model of relative abundance of (a) gleaning-animalivorous and (b) frugivorous bats in relation to distance to the nearest stream in 49 plots in Ducke Reserve, Manaus, Amazonas State, Brazil. The triangle on the x-axis shows the estimated breakpoint, and the line delimits the 95% confidence interval.



Fig. 2. Relationships between the relative abundances of each species of bat grouped according to their trophic guild, and the distance to the nearest stream. The dashed line represents a threshold in species composition as a function of distance from the nearest stream. We used the largest breakpoint of 114 m estimated for presence/absence species-composition data.

Streams often constitute flying corridors and facilitate long-distance commuting by bats between feeding areas and may explain the greater abundance of some frugivorous taxa, such as *Carollia*, in areas close to streams.

Frugivorous bats may cover huge areas in a single night while foraging (Bonaccorso and Gush, 1987; Lobova et al., 2009), but in dense forest they often travel along streams that they use as fly ways (Bonaccorso and Gush, 1987; Cosson et al., 1999). Our results are congruent with these observations, as more individuals and species of herbivorous bats were captured near streams (as well as in Medina et al., 2007; Avila-Cabadilla et al., 2012; Bobrowiec and Tavares, 2017; Zarazúa-Carbajal et al., 2017), suggesting that this guild may be more resilient to changes in riparian-forest protection areas. However, current legislation protects only 30 m on either side of small streams, and edge effects may reduce the effective area of such corridors in areas where the surrounding forest is replaced by crops or pasture. Although some frugivorous and nectarivorous bats are commonly found in fragmented environments, the excessive reduction of PPAs as proposed by the BFC may not maintain viable populations in riparian zones and compromise ecosystem functions. The reduction in the abundance of frugivores can be harmful to important ecological functions, such as plant gene flow via seed dispersal and pollination (Gorchov et al., 1993; Law and Chidel, 2002; Fleming et al., 2009). Rare species of frugivores are likely to be the first to disappear from small strips of riparian areas with the consequence of compromising the seed dispersal of their associated chiropterochorous plant species.

Our results are somewhat surprising, as riparian areas are thought to be preferred foraging areas for many species of insectivorous bats (Fukui et al., 2006; Hagen and Sabo, 2014). Most of the insectivorous bats in our sample, with the possible exception of foliage gleaning insectivore *Trinycteris nicefori*, were more frequently captured at larger distances from the streams. This possibly occurs because terra-firme



Distance to the nearest stream (m)

Fig. 3. Piecewise regression models for species composition based on (a) presence/absence data, (b) abundance data, and (c) guilds of bats in relation to the distance to the nearest stream for 49 plots in DuckeReserve, Manaus, Amazonas State, Brazil. The triangle on the x-axis shows the estimated breakpoint and line delimits the 95% confidence interval.

streams in central Amazonia tend to be acid, and to have low primary productivity, which may reduce the biomass of insects associated with them. The biomass and the size of the insects increases relative to the distance from the stream (Oliveira et al., 2015), suggesting that foraging areas for insectivores may not be located close to streams. However, the change in abundance of animalivores in relation to the distance from the stream revealed to be gradual as indicated by the large value of the breakpoint confidence interval. In deforested areas, eutrophication could increase the production of insects associated to the streams, but it is likely that narrower protected riparian zones will not be sufficient to support most species of insectivorous bats now present in the region.

Irrespectively of the differences found between large assemblages of bats throughout the Amazon (Marciente et al., 2015; Martins et al., 2017; Rocha et al., 2017; Tavares et al., 2017) the regional and local scale distributions of bat assemblages and their relationships with geomorphological parameters appears to be recurrent (e.g. elevation according to Capaverde et al., 2018). Therefore, the importance of the riparian áreas, and of protecting those areas for forest bats should be very similar for most, if not all bat assemblages. Bats have been identified as useful indicators of anthropogenic disturbances and suitable as a group to assess the ecosystems health by environmental managers (Jones et al., 2009). Environmental-impact studies tend to use univariate variables, such as abundance and number of species, to characterize species assemblages. As identified here, species composition, especially when based on abundance data, is often more useful to determine ecological thresholds for assemblages (Ficetola and Denoel, 2009; Guénette and Villard, 2004; Toms and Lesperance, 2003; Bueno et al., 2012). Species composition takes into account the identity of the species and abundance, and therefore its biology, and may also reflect the importance of abundant species in the assemblage.

4.1. Conservation remarks

Preserving riparian corridors has been employed as an ad hoc conservation tool for maintaining natural processes and stream functions (Laurance and Gascon, 1997; Marczak et al., 2010). Unfortunately the data considered by BFC lawmakers for the definition of PPAs in riparian zones were based solely on trees, and considered only the influence of vegetation structure on environment temperature and humidity (Naiman et al., 1993). Nonetheless the Brazilian legislation for PPA includes the preservation of water resources, landscape, geological stability and biodiversity, which cannot be properly explained solely by tree composition and diversity. Our results show that frugivorous bats were associated with riparian zones, and clearly point to the fact that the current minimum size of riparian zones (PPAs) currently formalized in the Brazilian laws is not enough to preserve the diversity of this group. In addition the current size predicted for PPA may highly selective for a reduced amount of bats species in the riparian zones. Our results also show that species composition is more appropriate to describe the ecological thresholds of riparian zones than the more traditionally used number of species and relative abundance. Therefore, technical criteria for establishing the size of riparian zones must take into account assemblage components of biodiversity (Metzger, 2010).

From a bat's perspective, riparian areas around small streams (< 10 m width) protected by Brazilian legislation should be wider than predicted by law (30 m) ensuring the conservation of animalivourous bats that were most abundant distant from the small streams, with beneficial effects for the whole communities. Our data suggests that the

appropriate width of riparian zones must be $\geq 120 \text{ m}$, the largest breakpoint estimated for presence/absence species-composition data. Since protection of riparian areas is one of main strategies of the Brazilian government to control land use, we strongly recommend a revision of riparian protected-area laws to accommodate those critical recent discoveries. A large increase in the width of riparian reserves appears to be unrealistic to restore areas that are within the limit size established by current law, because of the high cost of restoring degraded areas, and pressures from agrobusiness sectors may discourage the Brazilian government to interfere in lands modified under the parameters set by the current regulating legislation. However, our proposal, together with recent results from other taxonomic groups that converge with ours may explain better the riparian ecosystem structure and its conservation, and can be used to establish new legislation for areas not yet cleared. We encourage also studies other types of vegetation (eg. seasonally inundated forests and dry forests) and their associated communities in order to establish riparian zones suitable for other biomes, and particularly in the case of Brazil in order to preserve biodiversity by improving the legislation that rules the PPAs.

New proposals for BFC are under discussion, such as reducing the width of the riparian zone from 30 to 15 m for streams smaller than 10 m wide (Lewinsohn, 2010; Garcia, 2012). This would influence the dynamics of another regulation currently under discussion in Brazil is the modification of the term "riparian zone" to apply to the lowest level of flooding area, which previously included the entire floodable area (Lewinsohn, 2010; Garcia, 2012). Changes, such as these, could result in losses of over 60% of protected vegetation within the riparian zone, which will have profound effects on bat diversity, and all the associated plant and animal communities.

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Appendix A. Supplementary data

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