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RESEARCH ARTICLE

Vertical stratification of phyllostomid bats assemblage (Chiroptera, Phyllostomidae) in a forest fragment in Brazilian Southwestern Amazon

Richarlly Costa Silva[1,2], Marcos Silveira[1,3,4], Rair Sousa Verde[1,5]

1 *Postgraduate Program in Ecology and Natural Resources Management, Federal University of Acre, University Campus, BR-364, Km 04 – Industrial District, P.O.Box 500, 69920-900 Rio Branco, AC, Brazil*
2 *Federal Institute of Science and Technology of Acre, Campus Baixada do Sol, Aeroporto Velho, P.O Box 2600, 69911-030, Rio Branco, AC, Brazil*
3 *Biodiversity Research Program, Regional Nucleus of Acre, University Campus, BR-364, Km 04 – Industrial District, P.O.Box 500, 69920-900 Rio Branco, AC, Brazil*
4 *Center for Biological and Nature Sciences, University Museum, Federal University of Acre, University Campus, BR-364, Km 04 – Industrial District, P.O.Box 500, 69920-900 Rio Branco, AC, Brazil*
5 *Postgraduate Program in Health and Animal Production, Federal University of Acre (UFAC), Laércio Wanderley da Nóbrega Block – 1st floor, 69920-900, Rio Branco, AC, Brazil*

Corresponding author: Rair Sousa Verde (rair.verde@gmail.com)

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Abstract

Bats represent a key group in tropical forest dynamics, given their participation in ecological interactions that lead the regulation of these forests. They are also sensitive to the heterogeneous vertical gradient in the forest, called stratification. In this study we evaluated the influence of two different forest strata on species composition and bat guild structure. The samplings were carried out over eight nights in a forest fragment located in the southwest of the Amazon; we used mist nets installed in the understory and sub-canopy. A total of 197 captures were distributed in 19 genera and 25 species; they were all representatives of the family Phyllostomidae. In the sub-canopy, 54 individuals and 15 species were captured, with four exclusive species. In the understory, 143 individuals of 21 species were recorded, of which 10 were exclusive of this stratum. The sub-canopy presented a diversity index greater than the understory, with differences between species composition of the two assemblies, due to the presence or absence of some species. We also found a variation in the presence of frugivorous, insectivorous and omnivorous species, which is the result of differences in the foraging methods of these species and also of the habitat preference. Differences were verified in the assemblies studied, demonstrating the effects of vertical stratification on the bats in the studied fragment. Studies that consider more than one vertical stratum in tropical forests are more representative than sampling with only understory mist nets, given the capture of exclusive species.

Keywords
Chiroptera, diversity, feeding guilds, habitat use, species composition

Introduction

Bats are one of the most diverse groups of animals in the world, with 18 families, 202 genera and more than 1,300 species and, except for Antarctica, they are found on all continents (Nowak 1994; Simmons 2005; Fenton and Simmons 2014). In Brazil, the members of the Order Chiroptera are distributed in nine families, 68 genera and 183 species. Among the families registered in Brazil, the most common species is the family Phyllostomidae, consisting of 92 species distributed in 43 genera (Paglia et al. 2012; Nogueira et al. 2014; Feijó et al. 2015; Moratelli and Dias 2015; Gregorin et al. 2016; Rocha et al. 2016). According to Charles-Dominique (1991), due to the high richness, abundance, broad geographical distribution and diversity of guilds, bats are an important component in the structure and dynamics of the environments in which they live, since they act in diverse ecosystem services, as in the population control of arthropods and vertebrates, the seed dispersal and pollination of a wide variety of plant species (Kunz et al. 2010).

Spatial heterogeneity is an important factor promoting the diversity of animals and plants, especially in tropical forests (Tews et al. 2004), where the vertical structuring of the habitat sometimes generates a gradient called vertical stratification, in which the strata formed from the soil can be used in different ways by different types of organisms (Bernard 2001; Morato 2001; Walther 2002; Pereira et al. 2010; Pos and Sleegers 2010). The vertical heterogeneity can affect the diversity and composition of bat species, in various types of forests and the abundance and richness of bats vary along strata (Estrada and Coates-Estrada 2001; Estrada and Coates-Estrada 2002; Presley et al. 2008). According to their feeding characteristics and foraging strategies, bats may exhibit preferences for different habitats along the vertical strata (Francis 1994; Bernard 2001; Hodgkison et al. 2004; Pereira et al. 2010). In addition, they can use different strata as a foraging route to avoid predators and cluttered environments (Rex et al. 2011). Due to the difficulty of accessing the highest strata of the forest, studies on the composition and abundance of species among the forest strata in the Amazon are still scarce, compared to those that only cover the understory (Bernard 2001; Kalko and Handley 2001; Lim and Engstrom 2001; Pereira et al. 2010; Müller et al. 2013).

In Central Amazon, Bernard (2001), Sampaio et al. (2003) and Pereira et al. (2010) found a greater species richness in the understory, but they observed the existence of exclusive species in each stratum. Differences between the abundance and the richness of the guilds between the different strata are also visible; moreover, still in the Central Amazon, Pereira et al. (2010) recorded more animalivorous species in the understory and a predominance of frugivorous species in the canopy. The present study aimed to examine, preliminarily, the vertical stratification of bat assemblages in a forest fragment in the southwest of the Amazon from two perspectives: i) to verify if the richness, relative abundance and diversity of the bat assembly differs between sub-canopy and understory strata of a forest fragment in the Southwest of the Amazon and ii) to evaluate if the composition of species and the structure of the guilds varies between the two strata.

Materials and methods

Study area

The study was conducted at the Catuaba Experimental Farm, Senador Guiomard, Acre, Brazil, a forest remnant of 1,166 ha (10°04'53"S, 67°37'19"W) located near the intersection of the BR-364 and BR-317 highways, 23 km from the capital, Rio Branco (Fig. 1).

Although the study area is located in an area dominated by Dense Ombrophylous Forest, the vegetation cover of the area is characterized by the predominance of Open Ombrophylous Forest with Bamboo and Open Ombrophylous Forest with Palm, and its surroundings by secondary forests in different successional stages and pastures (Medeiros et al. 2013). Canopy height is between 20 and 40 m, with emergent trees up to 45 m (Silveira 2005). The climate in the region is Am (Köppen), with a rainy season between November and March and a drought season between July and September (Duarte 2006). Between 2010–2013 the annual average temperature was 27 °C and the average annual rainfall was 2,124 mm (± 566 mm), January being the wettest month, with an average of 340 mm, and July, the least rainy, with a mean of 30 mm; a well-defined drought season, with less than 60 consecutive days without rain, it occurs between May and October (INMET 2015).

Sample design

This study used as sample units four plots of uniform distribution of the RAPELD system (Magnusson et al. 2005). The plots, equidistant 1000m, were demarcated along one five-kilometer transect, 250m long and subdivided into 25 segments with 10-meters length, whose distribution follows the same topographic level (isocline) along its length.

Data collection

Between May 2014 and January 2015, each plot was sampled twice, one between May and September and one between October and January, and for that purpose, mist nets (12 × 3m, 19mm mesh, Ecotone), eight at ground level for understory

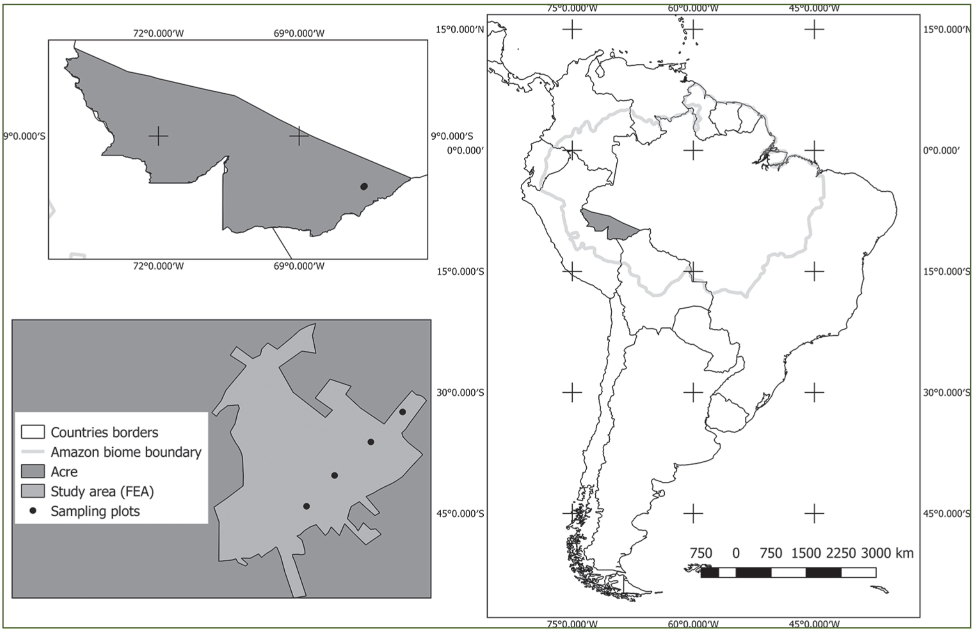

Figure 1. Location of the study area (Fazenda Experimental Catuaba), Senador Guiomard, Acre, Brazil. Points represent the sample plots.

sampling and two at sub-canopy sampling. The last two were installed according to Carvalho and Fábian (2011), vertically and sequentially, starting from three meters high and forming a "wall" of 9 × 12 m. The collections were not performed during periods of full moon, to avoid the phenomenon of the lunar phobia (Morrison 1978; Prugh and Golden 2013; Mello et al. 2013). The captures began at sunset, surveys occurred at 15-minute intervals, nets were closed six hours after their opening, and the capture effort was calculated according to Straube and Bianconi (2002).

Bats captured under SISBIO license N° 44089-1 were placed in individual cotton bags for weighing, checking of body measurements and identification, remaining in them until the nets closed, thus avoiding the capture of the same individual at the same night or in more than one stratum.

In the field, bats were identified based on the keys proposed by Emmons and Feer (1997), Simmons and Voss (1998), Eisenberg and Redford (1999), Lim and Engstrom (2001) and Gardner (2007), and through gender-specific keys (Velazco 2005; Velazco et al. 2010). Due to the difficulty embedded in the identification of individuals of *Carollia* Gray, 1838, the individuals of this genus were treated as *Carollia* spp. For the formation of a collection of voucher specimens material, the bats were euthanized according to resolution N° 301 of the Federal Council of Biology, and the samples deposited in the Zoological Collection of Mammals at the University Museum at the Federal University of Acre.

According to Kalko (1997) and Schnitzler and Kalko (1998), the species were categorized into seven guilds that include dietary habits and foraging strategies of Neotropical bats: frugivorous, canopy frugivorous, understory frugivorous, hematophagous, insectivorous, nectarivorous and omnivores.

Data analyses

In order to compare the abundance and number of species among the strata, a rarefaction curve was constructed and, since the sampling effort in the strata was distinct, for any comparisons we used the relative abundance of the species, calculated from the number division of species records by the sampling effort of the treatment. Assembly ordering was performed by using the non-metric multidimensional scaling (NMDS), using the Bray-Curtis distance and the minimum *stress* value of 0.20, as the *stress* values above 0.20 mean that the ordering performed is not sufficiently explanatory. In addition to the NMDS, in order to test the patterns of the community structure, a non-parametric permutational multivariate (PERMANOVA) analysis was performed, with 9999 permutations. All analyzes were performed with the "*vegan*" package of the R 3.0.3 software (Oksanen et al. 2013; R Development Core Team 2015).

Results

With a total effort of 8,640 m^2.h for the sub-canopy nets and 13,824 m^2.h for understory nets, 197 captures were taken from at least 25 species distributed in 19 genera. In the sub-canopy, 54 captures were taken from at least 15 species and 143 captures from at least 21 species were recorded in the understory (Table 1).

The rarefaction curve by individuals showed that the richness of bats at the point of intersection of 54 individuals was of 15 species for the sub-canopy and 14 species in the understory (Fig. 2), so there was no difference between the richness of species between the two strata.

The most abundant taxa were *Carollia* spp. with 119 records, representing 60.40% of total catches, with a greater abundance in the understory (78%) than in the sub-canopy (22%). *Artibeus planirostris* (Spix, 1823), *Phyllostomus hastatus* (Pallas, 1767), *Tonatia saurophila* Koopman & Williams, 1951 and *Lophostoma silvicolum* d'Orbigny, 1836, with six records each, representing 12.20% of the captures; 16 species had less than six catches and five were caught only once (Table 1).

Fifteen species were captured in the sub-canopy, among them, *Artibeus obscurus*, *Dermanura* cf. *glauca*, *Platyrrhinus brachycephalus* and *Uroderma bilobatum* were exclusive and represent 37.5% of the richness of this stratum. Among the 21 species found in the understory, 10 (47.6% of the species) were exclusive: *Dermanura cinerea*, *Glyphonycteris sylvestris*, *Lophostoma brasiliense*, *Mesophylla macconnelli*, *Micronycteris hirsuta*, *Sturnira lilium*, *Sturnira tildae*, *Trachops cirrhosus*, *Vampyressa thyone* and *Vampyriscus bidens*.

Table 1. List of bat species captured in the study area (Fazenda Experimental Catuaba), Senador Guiomard, Acre, Brazil. Values represent the number of captures and capture rate in each strata and total captures.

Taxon	Sub-canopy	Understory	Total captures (%)
Carolliinae			
Carollia spp.	26 (0.752)	93 (0.673)	119 (60.40)
Desmodontinae			
Desmodus rotundus (E. Geoffroy, 1810)	2 (0.057)	1 (0.007)	3 (1.52)
Gardnerycterinae			
Gardnerycteris crenulatum (E. Geoffroy, 1810)	2 (0.057)	1 (0.007)	3 (1.52)
Glossophaginae			
Glossophaga soricina (Pallas, 1766)	1 (0.028)	4 (0.029)	5 (2.54)
Glyphonycterinae			
Glyphonycteris sylvestris (Thomas, 1896)	–	2 (0.014)	2 (1.02)
Micronycterinae			
Lampronycteris brachyotis (Dobson, 1879)	1 (0.028)	4 (0.029)	5 (2.54)
Micronycteris hirsuta (Peters, 1869)	–	3 (0.022)	3 (1.52)
Phyllostominae			
Lophostoma brasiliense (Peters, 1866)	–	1 (0.007)	1 (0.51)
Lophostoma silvicolum (d'Orbigny, 1836)	1 (0.028)	5 (0.036)	6 (3.05)
Phyllostomus elongatus (E. Geoffroy, 1810)	2 (0.057)	3 (0.022)	5 (2.54)
Phyllostomus hastatus (Pallas, 1767)	5 (0.144)	1 (0.007)	6 (3.05)
Tonatia saurophila Koopman &Williams, 1951	3 (0.035)	3 (0.022)	6 (3.05)
Trachops cirrhosus (Spix, 1823)	–	2 (0.014)	2 (1.02)
Stenodermatinae			
Artibeus lituratus (Olfers, 1818)	1 (0.028)	4 (0.029)	5 (2.54)
Artibeus obscurus Schinz, 1821	1 (0.028)	–	1 (0.51)
Artibeus planirostris (Spix, 1823)	2 (0.057)	4 (0.029)	6 (3.05)
Dermanura cinerea Gervais, 1856	–	2 (0.014)	2 (1.02)
Dermanura cf. *glauca* Thomas, 1893	5 (0.144)	–	5 (2.54)
Mesophylla macconnelli Thomas, 1901	–	2 (0.014)	2 (1.01)
Platyrrhinus brachycephalus (Rouk & Carter, 1972)	1 (0.028)	–	1 (0.51)
Sturnira lilium (E. Geoffroy, 1810)	–	1 (0.007)	1 (0.51)
Sturnira tildae de la Torre, 1959	–	4 (0.029)	4 (2.03)
Uroderma bilobatum Peters, 1866	1 (0.028)	–	1 (0.51)
Vampyressa thyone Thomas, 1909	–	1 (0.007)	1 (0.51)
Vampyriscus bidens Dobson, 1878	–	2 (0.014)	2 (1.02)
Number of captures	54 (0.015)	143 (0.010)	197
Richness	15	21	25
Exclusive species	4	10	–
Effort (m^2h)	3456	13824	22464

List of vouchers:
Vampyressa thyone CZM–0934
Vampyriscus bidens CZM–0376
Lophostoma brasiliense CZM–0575
Micronycteris hirsuta CZM– 0907
Phyllostomus elongatus CZM–0535
Sturnira tildae CZM–0520
Tonatia saurophila CZM–0904
Dermanura cinerea CZM–0564
Dermanura cf. glauca CZM–0510
Glyphonycteris sylvestris CZM–0524
Lampronycteris brachyotis CZM–0521
Mesophylla macconnelli CZM–0523
Artibeus lituratus CZM–0632

The assembly ordering in two dimensions (*stress* = 0.07) revealed a clear separation between understory and sub-canopy (Fig. 3), while PERMANOVA detected a significant difference between the two assemblies (*pseudo* F= 2.26, P = 0.01), which shows that the difference between the two assemblies was greater than expected at random.

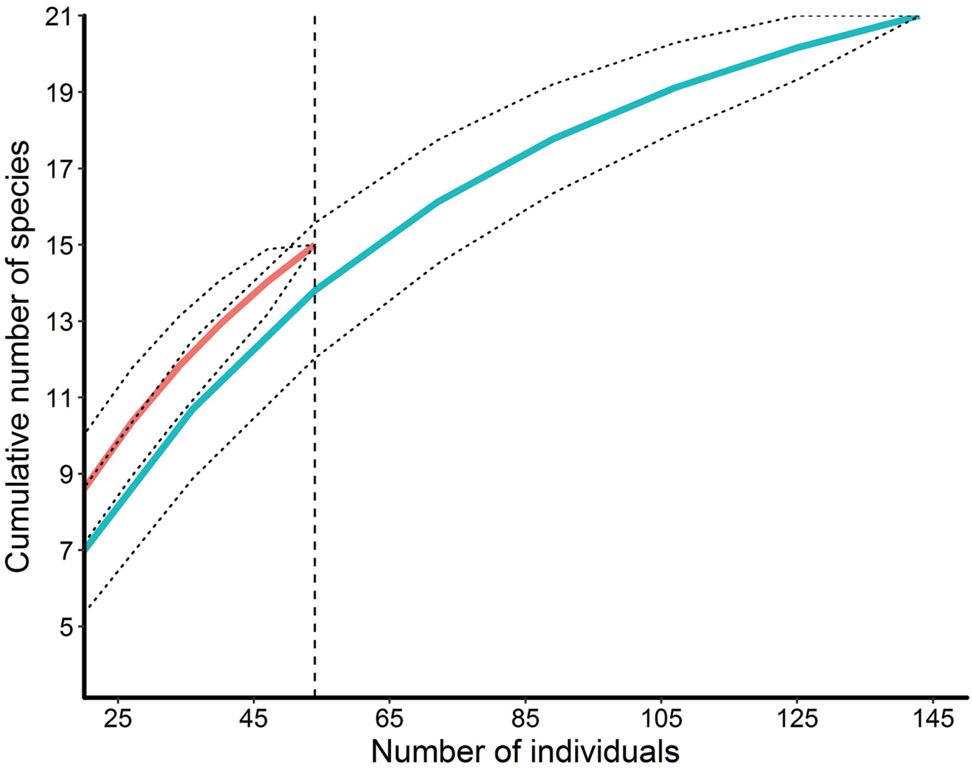

Figure 2. Individuals-based species accumulation curves for captures in in the study area. The gray line represent captures in sub-canopy and the black line represent captures in understory strata, dashed lines represent 95% CI. The vertical dashed line highlights the intersection point of 54 individuals.

Discussion

Our results indicate that species composition are different between understory and sub-canopy, indicating differences on forage pattern and vertical stratification; ten species were exclusive in understory and four were captured only in sub-canopy. Most of the studies involving bats and vertical stratification carried out in Amazon compare understory and canopy (Bernard 2001; Kalko and Handley Jr. 2001; Pereira et al. 2010). Our study compares the understory and sub-canopy nets, between six and nine meters, a stratum studied only in the Atlantic Forest (Carvalho et al. 2013; Gregorin et al. 2017). The species richness sampled in our study was similar in the two strata, when analyzed through the rarefaction curve, and differs from the results found by Carvalho et al. (2013) and Gregorin et al.(2017) in the Atlantic Forest, where the richness in the canopy is greater than in the sub-canopy and understory. Although the composition of bat species in our study was similar between strata, a greater richness was observed in high strata, an effect possibly caused by the stratified distribution of food resources (e.g. fruits and insects) used by bats (Rex et al. 2011), as well as their shelter needs (Bernard 2001; Kalko and Handley Jr. 2001;

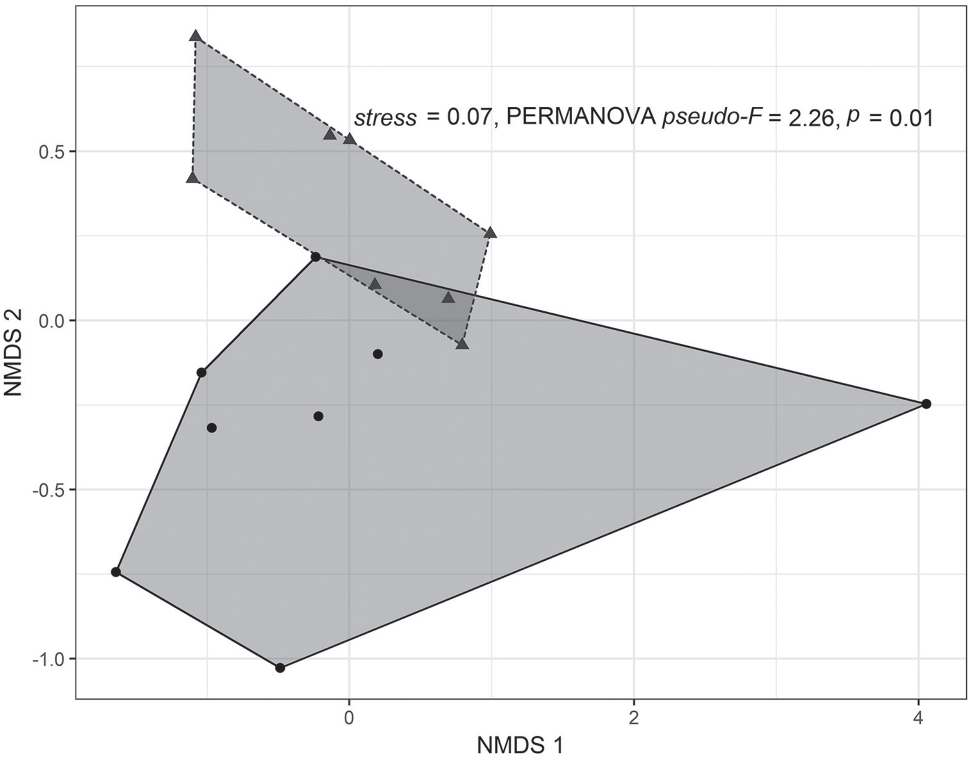

Figure 3. NMDS plot of assemblage structure of bats in two strata in the study area. Black triangles represent sub-canopy assemblage and black circles represent understory assemblage.

Pereira et al. 2010).The species composition of the studied assembly differs among the strata, since 10 species were found exclusively in the understory and only four in the sub-canopy.

All categories of guilds proposed by Kalko (1997) and Schnitzler and Kalko (1998), except for carnivores were represented in both strata. *Trachops cirrhosus* is considered a carnivore specialist of understory, given that its diet is mainly composed of anurans. In this study, *T. cirrhosus* was captured exclusively in the understory, as it was also recorded in the studies by Kalko et al. (1999), Bernard (2001), Sampaio et al. (2003) and Pereira et al. (2010). Insectivorous richness was also higher in the understory, with seven species, compared to four in the sub-canopy, a pattern also found for the relative abundance of insectivores, which was higher in the understory than in the sub-canopy, since these animals forage in places where there is a greater density of prey. Among the insectivores, four species were captured in both strata, but *G. sylvestris*, *L. brasiliense* and *M. hirsuta*, only in the understory. A small number of records of these species in the canopy were found by Bernard (2001), probably as a result of the foraging strategy of these animals, which is more effective in the understory, since they capture insects on the substrate or vegetation (Kalko 1997).

In studies carried out in central Amazon, Bernard (2001), Kalko and Handley Jr. (2001) and Pereira et al. (2010) recorded *P. elongatus* mainly in the understory and *P. hastatus* mainly in the canopy. In our study, *P. hastatus* was captured mainly in the sub-canopy and *P. elongatus* was evenly distributed between the two strata. According to Rex et al. (2011) *P. hastatus* have preference for larger fruits that occur in higher strata; however, this preference may change according to the dynamics of the ripe fruits present in a given area. According to the results of Rex et al. (2011), in a study conducted in Costa Rica, *P. hastatus* can completely change its spatial niche between the periods of drought and rain. The richness of canopy frugivorous was similar in both strata; however, four of the ten species were captured only in the understory, a result that contrasts with the pattern found by other authors in the Amazon (Bernard 2001; Pereira et al. 2010). In addition, the number of catches of canopy frugivorous was higher in the understory, probably due to their feeding on fruits of *Solanum* and *Piper*, which are abundant in the understory (Mello et al. 2008; Paulino-Neto et al. 2014).

Species of the genus *Artibeus*, considered as canopy frugivorous, are more captured in the canopy than in the understory, mainly because they feed on fruits that are common in the canopy (ex. *Ficus*), using the understory during periods of drought to compensate for the low availability of fruits in the higher strata (Bernard 2001; Kalko and Handley Jr. 2001; Pereira et al. 2010). Unlike these results, however, in congruence as in the study of Carvalho et al. (2013) and Gregorin et al. (2017) in the Atlantic Forest, we recorded twice as many individuals of this genus in the understory, which may reflect a low availability of food resources in higher strata in the studied area.

Members of the genus *Sturnira*, here represented by *S. lilium* and *S. tildae*, are classified as understory specialists (Sampaio et al. 2003; Pereira et al. 2010). In fact, in our study area, both species were captured exclusively in this stratum, which may result from the distribution of food resources, especially fruits of the genus *Solanum*, found abundantly in the understory (Uieda and Vasconcelos-Neto 1985).

Bats from the genus *Carollia* have high capture rates in studies conducted in the Amazon (see Bernard 2001; Willig et al. 2007; Pereira et al. 2010; Bobrowiec 2012; Carvalho et al. 2013, Bobrowiec et al. 2014; Marciente et al. 2015), and in this study they were also abundant. In addition, they were more captured in the understory, as other authors recorded (Bernard 2001; Pereira et al. 2010). Representatives of this genus are considered foragers of understory, since they have preference for fruits of the genus *Piper*, very abundant in the understory (Fleming and Heithaus 1986; Marques et al. 2012). However, this behavior was not absolute, with some taxa captured in the sub-canopy, evidencing the ability of this small frugivorous to use other vertical strata of the forest.

The preliminary results reported here demonstrate that the vertical structure of the forest functions as an environmental filter, regulating the species richness of bats in the southwest of the Amazon, given the exclusivity of some species to the forest strata. Therefore, more studies that contemplate several vertical strata should be performed, since they allow the capture of species that are not frequently captured in the understory, allowing to generate more precise conclusions on the environmental factors that are being approached.

Even though our effort may not be enough to answer questions about vertical stratification for all species, we suggest that the main limitation in relation to our results is the uneven sampling effort between the platforms and the need for a longer sampling period to be able to record a relatively considerable number of unusual species. On the other hand, this is the first attempt to test the vertical stratification of bat assemblies in the far west of the Brazilian Amazon; in addition, we find evidence of vertical stratification patterns that are similar to those found in other studies in the Amazon (see Bernard 2001; Kalko and Handley Jr. 2001; Pereira et al. 2010). Therefore, we recognize that the sampling effort, especially in the sub-canopy, is limited, but our results are enough to show differences at the assembly level and for more abundant species.

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