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Artículo

DIVERSITY AND SEASONALITY OF A PHYLLOSTOMID ASSEMBLAGE FROM THE ATLANTIC FOREST OF SOUTHEASTERN BRAZIL

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ABSTRACT. Phyllostomids are locally abundant, ecologically diverse, and form rich assemblages. They also provide essential ecosystem services, which may change along the year in response to changes in bat abundances. Here we report on a phyllostomid assemblage studied at Reserva Biológica União (RBU), an Atlantic Forest area with outstanding diversity in southeastern Brazil. We assessed seasonal variation in diversity profiles for alpha and beta components, as well as in the abundance of the most common species. Spatial variation in phyllostomid diversity profiles and components was also assessed, using published information from three nearby sites. Based on a sample of 786 mist net captures and records from monitored roosts, the phyllostomid assemblage at RBU was found to include at least 19 species, two of which recognized as endangered at the national level (*Lonchorhina aurita* and *Lonchophylla peracchii*). The diversity profile for RBU was heavily influenced by common species and was one of the richest but less diverse in the region due to its uneven distribution. The diversity profiles suggested no seasonal differences in alpha diversity. Beta diversity profiles for spatial and seasonal analyses showed that samples behaved as subsets of a single assemblage, suggesting a relative homogeneity of resources in these dimensions. At the population level, however, some expected seasonal variation in abundance was confirmed (e.g., in *Artibeus* spp. and in *Carollia perspicillata*). The high relative frequency of *Sturnira tildae* at RBU differentiated this site, thus reinforcing its conservation importance.

RESUMO. **Diversidade e sazonalidade de uma assembleia de filostomídeos da Floresta Atlântica do sudeste do Brazil.** Morcegos filostomídeos são localmente abundantes, ecologicamente diversos, e formam ricas assembleias. Eles fornecem serviços ecossistêmicos essenciais, cuja disponibilidade pode mudar ao longo do ano por flutuações na sua abundância. Nos reportamos aqui a uma assembleia de filostomídeos estudada na Reserva Biológica União (RBU), uma área com grande diversidade no sudeste do Brasil. Apresentamos uma avaliação da variação sazonal de perfis de diversidade para os componentes alfa e beta, assim como da abundância das espécies mais comuns. Variação espacial na riqueza e diversidade de filostomídeos também foi investigada a partir de dados publicados de três sítios próximos. Baseado em uma amostra de 786 capturas em redes de neblina e registros a partir do monitoramento de abrigos, a assembleia de filostomídeos da RBU inclui pelo menos 19 espécies, duas das quais reconhecidas nacionalmente como ameaçadas de extinção (*Lonchorhina aurita* e *Lonchophylla peracchii*). O perfil de diversidade da RBU mostrou-se fortemente influenciado pelas espécies mais comuns, sendo um dos mais ricos da região mas pouco diverso em função da distribuição pouco equitativa. Os perfis de diversidade alfa indicaram a ausência de diferenças sazonais. Os perfis de diversidade beta para análises espaciais e sazonais mostraram que as assembleias locais se comportam como subconjuntos de uma única assembleia, sugerindo uma relativa homogeneidade de recursos nessas dimensões. Em nível populacional, entretanto, variações sazonais já esperadas foram confirmadas (e.g., *Artibeus* spp. e *C. perspicillata*).

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A frequência elevada de *Sturnira tildae* na RBU diferencia esse site dos demais aqui analisados, reforçando sua importância para a conservação.

Key words: diversity partition, diversity profiles, Reserva Biológica União, Rio de Janeiro, *Sturnira tildae*.

Palavras chave: partição de diversidade, perfis de diversidade, Reserva Biológica União, Rio de Janeiro, *Sturnira tildae*.

INTRODUCTION

The Neotropical region harbors the most diverse mammalian fauna in the world although its area ranks 4th among major biogeographic regions (Ojeda 2013). At least 1550 species inhabit this region, corresponding to 30% of the extant mammal fauna (Solari et al. 2012). The proportion of endemic species is also remarkable: nearly 70%, considering only the land forms (Solari et al. 2012). An examination of the literature concerning mammalian conservation, however, revealed that this region, although presenting high levels of endemism and threats, has received relatively little attention (Amori & Gippoliti 2000). In order to improve both the quantity and quality of the conservation actions directed to Neotropical mammals, it is important to understand patterns and processes that may account for their extraordinary diversity. Spatial patterns, like those related to latitude and elevation gradients, have long been investigated (e.g., Voss & Emmons 1996; Maestri & Patterson 2016), and an increasing effort has been made to understand temporal variation, particularly when related to climatic changes (Davies et al. 2011).

Essential to the understanding of large scale macroecological patterns, is the availability of consistent local surveys (Bergallo et al. 2003). If we consider the Atlantic Forest, one of the world's most threatened biomes, results from bat surveys conducted with mist nets have accumulated since the 1980's, allowing important generalizations, such as the relatively high influence of temperature seasonality on species richness (see Stevens 2013). This conclusion was based on an analysis of phyllostomid bats, which are easy to catch with ordinary ground-level mist nets and are highly diverse, both taxonomically and ecologically (Simmons & Voss 1998).

Although the Atlantic Forest in the state of Rio de Janeiro is comparatively well-sampled for bats (Bergallo et al. 2003; Stevens 2013), few studies have been conducted in the north of the state, where Reserva Biológica União (RBU) and other important reserves are located (Jenkins et al. 2011). This area is of great zoogeographical importance, given that several bat species in the Emballonuridae and Phyllostomidae reach the southernmost limit on record of their distribution in northern Rio de Janeiro (*Rhynchonycteris naso* and *Gardnerycteris crenulatum*) or in the neighboring state of Espírito Santo (*Centronycteris maximiliani*, *Trinycteris nicefori*, *Rhinophylla pumilio*, *Dryadonycteris capixaba* and *Dermanura gnoma;* Gardner 2008; Peracchi & Nogueira 2010). Here we present results of a phyllostomid survey at RBU, focusing on diversity, assemblage composition, and seasonal abundance patterns of these bats. Temporal heterogeneity of resources such as food may result in different assemblage compositions along the year (Tschapka 2004; Rex et al. 2008; Pereira et al. 2010). The occurrence of seasonal changes is a reasonable expectation at least for frugivorous phyllostomids (Mello 2009), because their food seems to be more abundant in the wet season, a pattern confirmed for our study region (Mello et al. 2004; Lapenta 2007). The opposite is probably true for hematophagous species (Zortéa & Alho 2008), whose food (vertebrate blood) availability is not expected to change seasonally (Freitas et al. 2006). We also performed diversity comparisons including three other sites from the same region (São João river basin), to gain insight into bat diversity at the regional spatial scale. The various phyllostomid assemblages at São João river basin were suggested to present marked differences (Mello & Schittini 2005), and a comparative approach incorporating diversity profiles and the partition into alpha and beta components (Jost 2007; Marcon et al. 2012) may shed light into possible differences of assemblage composition at the basin scale.

MATERIAL AND METHODS

Study site

Reserva Biológica União (RBU; 22º27′30″ S and 42º02′15″ W) is a 2547 ha conservation unit (recently increased to 7756 ha) composed of Atlantic Forest fragments located in the municipality of Rio das Ostras, state of Rio de Janeiro, southeastern Brazil (**Fig. 1**). Most of its area is covered by submontane ombrophilous forest (47%) and lowland ombrophilous forest (29%), with the rest of the Reserve covered by secondary shrubby vegetation (capoeira) and *Eucaliptus* plantations (ICMBIO 2008). Climate in the region is hot and humid, with an average annual rainfall varying between 1500 and 2000 mm (Primo & Völker 2003). The less rainy months, from May to August (average monthly rainfall 59 mm), are also those with lower temperatures and are here recognized as a dry season. The wet season, from September to April presents an average monthly rainfall of 177 mm. The average daily temperatures are high throughout the year, ranging between 22 °C in the dry season to 26 °C in the wet season (ICMBIO 2008).

The three other sites close to RBU, and for which there is published information on phyllostomid captures used in our analyses (see below), are Morro de São João (MSJ; Esbérard et al. 2013), Reserva Biológica de Poço das Antas (RBPA; Baptista & Mello 2001), and Reserva Particular do Patrimônio Natural Fazenda Bom Retiro (FBR; Menezes-Jr et al. 2015a). These sites are separated from RBU at distances of, respectively, 8, 20, and 25 km (**Fig. 1**), and their sizes are, respectively, 2000 ha, 5052 ha, and 494 ha. FBR is the farthest site from RBU and presents the smallest area in our samples, but it is located north to the BR101 federal road, in a patch of fragments that is more connected (via small forest corridors) to this latter site than to RBPA and MSJ. The most isolated site is MSJ, which is surrounded by pastures (**Fig. 1**).

Bat sampling

Sampling points were chosen along trails and roads (possible routes of bats' flights) in the reserve interior,

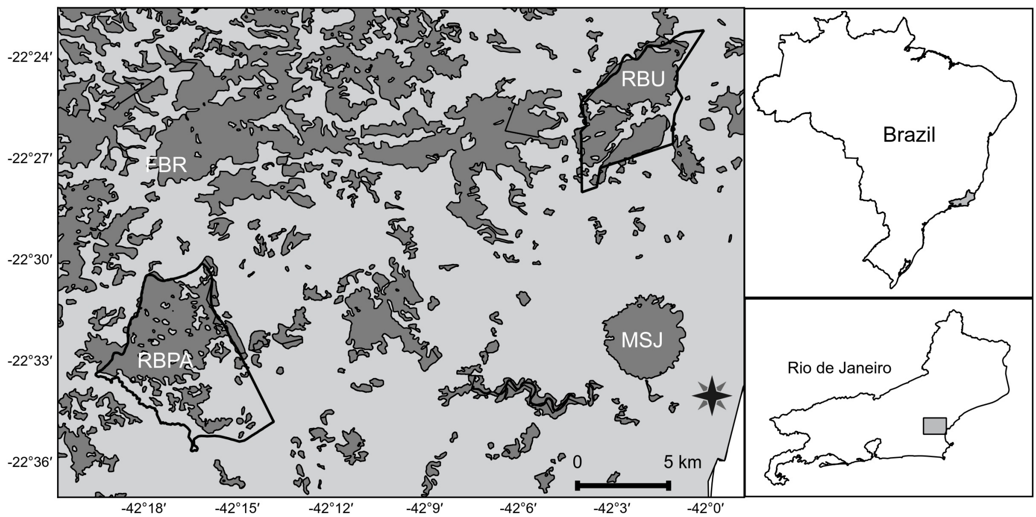

Fig. 1. Map showing the location of Reserva Biológica União (RBU) and other forest remnants in the São João river basin used for comparison: Morro de São João (MSJ), Reserva Biológica de Poço das Antas (RBPA), and RPPN Fazenda Bom Retiro (FBR). Thick black lines indicate Federal Reserve Contours (RBU and RBPA). Shapefile for forest remnant areas obtained from SOS Mata Atlântica (http://mapas.sosma.org.br/).

trying to cover both lowland and submontane forest areas. Following the map of internal roads of the reserve management plan, the four sampling points we selected were Estrada do Buracão, Trilha Interpretativa do Pilão, Estrada do Lava Pé and Estrada das Três Pontes (ICMBIO 2008). Bat sampling was conducted every two months between August 2012 and September 2015, with at least three capture sessions in each visit to the reserve. Sporadic net sessions were made from 2006 to 2011 during field courses promoted by the Graduate Program in Ecology and Natural Resources, Universidade Estadual do Norte Fluminense. These samples, and data from roosts, were not included in the statistical analyses, but they were used to complement our species list.

In each capture session we used 3 to 6 ground-level mist nets of 6, 9 or 12 m long and 3 m high. In addition to exploring trails and roads, we also placed these nets over water bodies and close to roosts. In general, nets were set before sunset and remained open for at least 5 hours. Nets were monitored every 20 minutes, to preserve physical integrity of individuals and prevent net damage. We restricted the sampling to the first half of the night, when phyllostomid bats are expected to be more active (Fleming et al. 1972; Fleming 1988; Aguiar & Marinho-Filho 2004). We avoided repeating sampling points in consecutive days and sampling in full-moon periods; reportedly, both situations reduce capture success (Bergallo et al. 2003; Esbérard 2006; Saldaña Vázquez & Munguía-Rosas 2013). Net effort was calculated according to Straube & Bianconi (2002), with a unit effort corresponding to one square meter of net exposed for one hour ($h.m^2$). Vouchers were prepared as skin and skull or as fluid-preserved specimens with skull removed; all specimens were deposited in the Coleção de Mamíferos da Universidade Estadual do Norte Fluminense and at Coleção Adriano Lúcio Peracchi (Laboratório de Mastozoologia, Universidade Federal Rural do Rio de Janeiro). Classification follows Baker et al. (2016) at subfamily level; below subfamily, nomenclature follows Nogueira et al. (2014).

Data analysis

Intersite comparisons - The phyllostomid assemblage from RBU was compared to those sampled by other authors in the same region using diversity profiles decomposed into alpha, beta and gamma components (Marcon et al. 2014). The general function for diversity as effective numbers of species (Jost 2007) is:

$$^{q}D = \left(\sum p_s^q\right)^{\frac{1}{1-q}},$$

where p_s is the probability in the given assemblage that a sampled individual belongs to species *s*, and the exponent *q* is the order of the diversity index. Known indices are related to specific orders, such as species richness ($q=0$), Shannon entropy ($q=1$) and Simpson ($q=2$). The function is actually undefined at $q=1$, but its limit is equal to the exponential of Shannon entropy (Jost 2006). Larger values of *q* are more sensitive to most common species, whereas smaller values of *q* are more sensitive to rare species (Jost 2007). Considering a number of sites forming a meta-assemblage in a region (Marcon et al. 2014), the gamma diversity $^{q}D_g$, based on all individuals sampled, irrespective of collection site, can be decomposed into the components of alpha and beta diversities, as $^{q}D_g = {}^{q}D_a * {}^{q}D_b$. The alpha diversity is a within-site component, calculated as a weighted average diversity over all sites, and the beta diversity is a between site component (Marcon et al. 2012). Confidence intervals for the profiles were estimated with 1000 replicates sampled from the original distribution of the species (Marcon & Hérault 2015). The effective number of species, or elements, has slightly different interpretations depending on the component. For alpha and gamma diversities, they are effective numbers of species (Jost 2006), the diversity equivalent to an assemblage with the same number of equally abundant species. In the case of beta diversity, the effective number of elements ranges from 1 (the meta-assemblage behaves as a single set) to the maximum number of assemblages being compared (if each one has a completely different species composition from the others).

Diversity profiles were calculated for each site's alpha and for the partition into a combined alpha, beta and gamma (Marcon et al. 2014). Profiles plot estimated diversity against the order (*q*) of the estimate. Because the changing orders give different weights to rare or common species, the profile of an assemblage can be compared and ranked against other assemblages with a more complete assessment of species distribution and the influence of dominant species. All diversity estimates were corrected for bias due to undersampling (Marcon & Hérault 2015), using an estimate of sample coverage (C) calculated from the number of singletons (species captured only once) in sample I, denoted S^1_i, and sample size n_i as $C_i = 1 - S^1_i/n_i$. The sample coverage multiplies the species frequencies in the calculation of entropies and diversities, as presented in the correction formula in Marcon et al. (2014). Because the number of specimens captured was different among areas, we weighted the calculation of combined (total) alpha diversity using the proportion of their sample contribution to the meta-assemblage sample (n_i/N).

Intrasite (seasonal) comparisons – We based our seasonal analyses on dry vs. wet season comparisons within RBU only (the other sites did not have seasonal data). We used capture rates (captures per unit effort—see net effort calculation above), and the partition of diversity profiles (described above) into alpha (within season) and beta (between season) components. For the following analyses, each capture session was treated as a sample unit, and bias related to differences in net effort was avoided by using capture rates, instead of raw capture numbers. Capture rates for the whole assemblage in different seasons were analyzed via a graphical comparison using box plots, where notches in the boxes provide a 95% confidence interval for the median (McGill et al. 1978) The proportion of captures of the most common species in the wet season was compared to a random expectation (the proportion of effort allocated to the same period) using 95% confidence intervals. Finally, we used distance-based redundancy analysis to assess seasonal differences in assemblage composition (Legendre & Anderson 1999). This ordination technique based on distances was chosen because we found a high proportion of zeros (80%) in the abundance matrices for species per sample (Zuur et al. 2007). Also, because we detected an over-dispersed distribution of abundances, we chose to transform the species abundances into presence/absence data and use the Jaccard similarity index (more precisely, its distance counterpart: Distance = 1 – Similarity) because it is asymmetric (only presences are considered evidence of similarity) and metric (Legendre & Legendre 2012).

Software - Statistical analyses and graphics were performed using the R environment (R Development Core Team 2015). We calculated the diversity profiles with the R package entropart (Marcon & Hérault 2015). The redundancy analysis was performed in R package vegan (Oksanen et al. 2015).

RESULTS

Diversity at RBU and intersite comparisons

With a total effort of 15 069 h.m², we captured 786 individuals belonging to 15 genera and 18 species of Phyllostomidae, grouped in 5 ensembles (**Table 1**). Frugivores corresponded to 93% of all captures, mainly due to the wide dominance of *Carollia perspicillata* in the assemblage (73%). The second most common species (9%), *Artibeus lituratus*, was also a fruit-eating bat. Except for *Trachops cirrhosus,* which raised our total richness to 19, all species were captured in mist nets away from known roosts. Most species (60%) were recorded in the beginning of our samplings (within the first 100 captures), but *Gardnerycteris crenulatum* was recorded only after more than 700 individuals were captured. *Chrotopterus auritus* was sampled in our first capture session and never recorded again.

Diversity profiles comparing RBU with other forest remnants in the São João river basin indicated that the order of diversity (the exponent *q*) strongly influenced the estimates, with a pattern of decreasing diversity when the most dominant species were given larger weights (**Fig. 2**). The alpha diversity within sites was non-comparable because the profiles intersect (**Fig. 2**, upper right panel), showing that ranking of diversity depended on *q*. Considering $q = 0$ (species abundance is disregarded, equivalent to richness), the diversity of RBU was the largest. On the other hand, as *q* approached 1 (diversity based on Shannon entropy), the hyperabundance of *C. perspicillata* greatly decreased RBU diversity and it fell to a second-to-last position in the site ranking. The profiles of MSJ and FBR were less steep than RBU and RBPA, indicating a more even distribution of species abundances. These results suggested that the influence of *C. perspicillata* in the estimated richness and diversity measurements were larger for RBU than for other sites in the same region. The beta diversity was higher for smaller values of *q*, suggesting that the most relevant species composition differences among assemblages were due to rare species (**Fig. 2**, lower left panel). The 95% confidence interval ranged from approximately 1.3 to 1.7 when $q = 0$, showing uncertainty due to sampling of rare species. The most common species were basically the same in all assemblages and the profile of beta diversity approached 1 as *q* approached 2. The regional diversity (gamma) was, therefore, mostly a function of the combined alpha diversity for local assemblages, as shown by the profile similarities (**Fig. 2**, upper left and lower right panels).

Table 1

List of phyllostomid bats from Reserva Biológica União, municipality of Rio das Ostras, state of Rio de Janeiro, southeastern Brazil, including number of individuals by season, relative abundances, and ensemble classification. Individuals obtained from roosts are treated separately and were not used in statistical analysis.

Species	Season		Total	Relative Abundance (%)	Roost sample	Ensemble*
	Wet	Dry				
Subfamily Micronycterinae						
Micronycteris microtis Miller, 1898	1	0	1	0.13	3	Ga
Subfamily Desmodontinae						
Desmodus rotundus (É. Geoffroy, 1810)	12	17	29	3.69		S
Subfamily Lonchorhininae						
Lonchorhina aurita Tomes, 1863	1	2	3	0.64	3	Ga
Subfamily Phyllostominae						
Chrotopterus auritus (Peters, 1856)	0	1	1	0.13		Ga
Gardnerycteris crenulatum (É. Geoffroy, 1803)	1	0	1	0.13		Ga
Phyllostomus hastatus (Pallas, 1767)	1	4	5	0.64		O
Trachops cirrhosus (Spix, 1823)	-	-	-	-	3	Ga
Subfamily Glossophaginae						
Anoura caudifer (É. Geoffroy, 1818)	0	1	1	0.13		N
Glossophaga soricina (Pallas, 1766)	3	7	10	1.27	19	N
Subfamily Lonchophyllinae						
Lonchophylla peracchii Dias, Esbérard & Moratelli, 2013	3	1	4	0.51		N
Subfamily Carolliinae						
Carollia perspicillata (Linnaeus, 1758)	230	346	576	73.28	1170	F
Subfamily Stenodermatinae						
Dermanura cinerea Gervais, 1856	7	0	7	0.89		F
Artibeus lituratus (Olfers, 1818)	65	8	73	9.29		F
Artibeus obscurus (Schinz, 1821)	21	7	28	3.56		F

(Table 1 cont.)

Species	Season		Total	Relative Abundance (%)	Roost sample	Ensemble*
	Wet	Dry				
Platyrrhinus recifinus (Thomas, 1901)	12	6	18	2.29		F
Pygoderma bilabiatum (Wagner, 1843)	0	3	3	0.38		F
Sturnira lilium (É. Geoffroy, 1810)	2	2	4	0.51		F
Sturnira tildae de la Torre, 1959	4	16	20	2.54		F
Vampyressa pusilla (Wagner, 1843)	2	0	2	0.25		F
Total	365	421	786	100		
Sampling effort (h.m^2)	8333	7398				

* F = frugivore (see text for a refine classification in some species), N = nectarivore, Ga = gleaning animalivore, O = omnivore, S = sanguivore

Seasonal variation in abundance and diversity at RBU

Capture rates for the whole phyllostomid assemblage in RBU did not differ between seasons (**Fig. 3**), as the boxplot comparison indicated an overlap of median confidence intervals. When the most common species were considered separately, groundstory frugivores (*C. perspicillata* and *S. tildae*) were more frequent than expected in the dry season and some fig specialists sensu Dumont (2003; specifically, *Artibeus lituratus* and *A. obscurus*) were more frequent than expected in the wet season (**Fig. 4**). The confidence intervals of wet season capture proportions of sanguivorous *Desmodus rotundus* and the fig specialist *Platyrrhinus recifinus*, included the expected proportion of 53%, indicating no seasonal changes in capture.

When diversity profiles of different seasons were compared for RBU, the wet season presented a slightly higher diversity regardless of q, but the difference is contained in the confidence interval for the combined total alpha diversity (**Fig. 5**, upper right and left panels). Uncertainty regarding alpha and beta diversities was higher for lower values of q, probably due to the resampling of rare species, as can be seen in the larger confidence intervals (**Fig. 5**, upper and lower left panels). The multi-season diversity in RBU (gamma) had a large alpha component, as the between seasons (beta) profile showed small diversity, approaching 1 when more weight was given to common species (larger q). These results suggested that a single assemblage, instead of two (one for each season) seemed to be present in the area along the whole year.

The distance-based redundancy analysis showed significant (permuted $P = 0.0239$) but weak (only c. 5% of similarity explained) seasonality in species composition between capture events. The association between species and seasons was due to higher relative abundances of *C. perspicillata* in the dry season and *A. lituratus* in the wet season, a tendency also detected in the capture rate data.

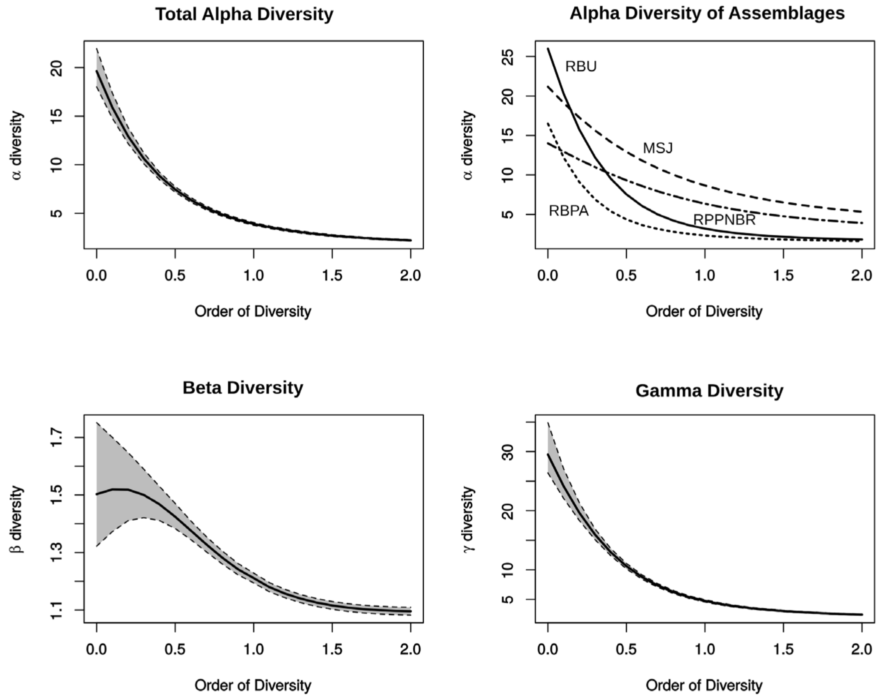

Fig. 2. Diversity profiles of assemblages at different locations within the São João River Basin. The diversity components (in number of effective elements) are plotted against order of diversity (the exponent *q*); 95% confidence intervals are shown as grey areas. Profiles for different sites are identified by acronyms and line type. RBU: solid line; RBPA: dotted line; MSJ: dashed line; FBR: dot and dashed line.

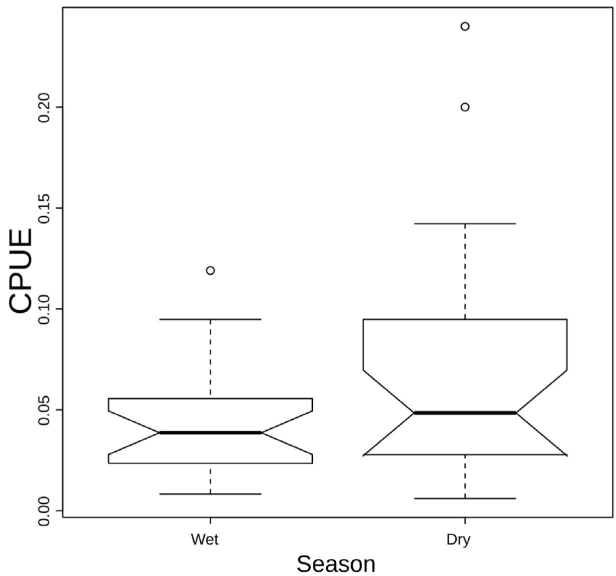

Fig. 3. Boxplot comparing bat captures per unit effort (individuals/h.m^2) in sampling nights during different seasons at Reserva Biológica União. The notch indicates a 95% confidence interval for the median (thick horizontal line).

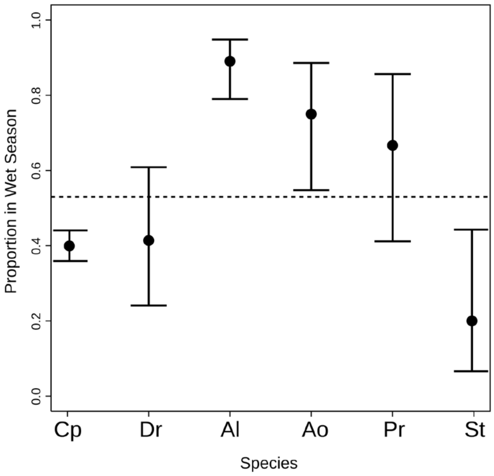

Fig. 4. Proportion of captures in the wet season with 95% confidence intervals for different species at Reserva Biológica União. Dotted line corresponds to proportion of capture effort in the wet season (0.53), considered as a null expectation of no difference in captures between seasons. Species acronyms are: Cp = *Carollia perspicillata*, Dr = *Desmodus rotundus*, Al = *Artibeus lituratus*, Ao = *Artibeus obscurus*, Pr = *Platyrrhinus recifinus*, St = *Sturnira tildae*.

DISCUSSION

Diversity at RBU and intersite comparisons

Phyllostomid assemblages have been extensively sampled along the Atlantic Forest, with richness values ranging between 4 and 30 species, and averaging 14 ($N = 60$ sites; Stevens 2013). With at least 19 phyllostomid species, RBU is slightly above the average for the biome, with an assemblage similar to those sampled in the three other localities in the same region. These areas can be viewed as subsamples of a single general assemblage anteriorly spread over the São João river basin (Grativol et al. 2008). Given the heterogeneity of the regional landscape (e.g., MSJ is more isolated from other forests and RBPA is more fragmented), this similarity in species composition deserves further consideration. Although a pattern of species abundance distribution with a few very abundant species and many rare species characterizes all areas (McGill et al. 2007), the abundance distributions

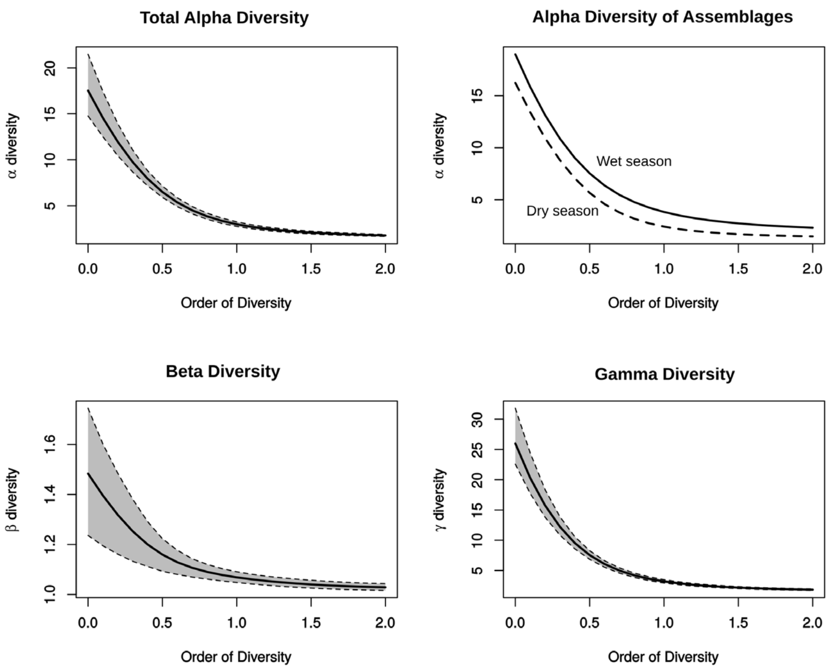

Fig. 5: Diversity profiles of assemblages in different seasons at Reserva Biológica União. The diversity components (in number of effective elements) are plotted against order of diversity (the exponent q); 95% confidence intervals are shown as grey areas. Profiles for different seasons are identified by names and line type. Wet season: solid line; Dry season: dashed line.

do not follow similar models and can be said to be non-comparable (Tóthmérész 1995). This happens because it is possible to find diversity indices that rank the assemblages in different ways (depending on *q*). The diversity profiles for RBU and RBPQ indicated a strong sensitivity to dominant species, whereas for MSJ and FBR, the abundance distributions were more equitable and the diversity profiles were less influenced by the most common species. This pattern was observed because a strong dominance of *C. perspicillata* is shared only between RBU (73% of all phyllostomids) and RBPA (78%). The lower abundance of *C. perspicillata* at MSJ (37%) and FBR (46%) may be related to local plant assemblages, more specifically to a reduced availability of *Piper* fruits (Esbérard et al. 2013), which form the core of the diet of this species (Fleming 1986). This association can be viewed as a more general pattern for frugivorous phyllostomids (Rex et al. 2008).

The high abundance of *C. perspicillata* is determinant for the strong dominance of the frugivore ensemble at RBU, but this pattern seems to be widespread in Neotropical bat assemblages, and not only when just phyllostomids are considered (Lim & Engstrom 2001). Several authors have emphasized possible methodological biases leading to this pattern (Simmons & Voss 1998), but as predicted by energy availability (Robinson & Redford 1986), phytophagous (frugivorous and nectarivorous) bats are expected to be more abundant at a particular site than those in higher trophic levels, such as insectivorous and carnivorous (Arita 1993). At our study site, phyllostomid nectarivores did not constitute an abundant ensemble (just 1.9% of all captures in this family), and the same was observed in RBPA and in FBR (0.7%). A relatively higher abundance of nectarivores was recorded at MSJ (4.7%); in this respect, this site, departs from the regional tendency, but this may be an artifact of sampling bats close to banana plantations (Esbérard et al. 2013).

The diversity profile for MSJ indicated a more even distribution of abundances and higher diversity when common species were given greater weight. This was a surprising result, considering that some detrimental aspects to bat diversity, such as isolation from other forested areas and insertion in a harsh matrix (Meyer et al. 2016), are particularly noticeable at this site. It can be argued, however, that MSJ presents a more favorable shape to maintain bat diversity, because it is more compact and rounded than the other sites, reducing potential negative effects of habitat edges (Meyer et al. 2016).This argument is also congruent with our finding that RBPA, which is composed of a more fragmented landscape (Brito et al. 2004; Figueiredo & Fernandez 2004), presented the lowest phyllostomid diversity.

The presences at RBU of *Lonchorhina aurita* and *Lonchophylla peracchii*, species categorized as endangered at the national level (MMA 2014), are noteworthy and reinforce the importance of this natural reserve for conservation. Maybe even more remarkable is the unusual abundance pattern we recorded for *Sturnira lilium* and *S. tildae*. These species are widely distributed in eastern Brazil (Velazco & Patterson 2013), but the former is usually much more common in local inventories than the latter (Esbérard 2006; Luz et al. 2013). The reverse trend recorded at RBU—*S. tildae* four times more abundant than *S. lilium*—should be investigated under a macroecological approach, but it might be the case that factors such as dependence of lowland humid forests with low fragmentation levels contributed to this pattern (Brosset & Charles-Dominique 1990; Simmons & Voss 1998). Support to this hypothesis comes also from the absence of this species at RBPA, a more fragmented area (Baptista & Mello 2001) and from the more isolated MSJ (Esbérard et al. 2013). In fact, *S. tildae* is currently recorded in only a few localities in the state of Rio de Janeiro, and in all of them few individuals were captured (Esbérard et al. 2006; Luz et al. 2011, 2013; Menezes-Jr et al. 2015b; Souza et al. 2015). In states like Rio de Janeiro, where most lowland forests were removed and conservation units of integral protection are largely circumscribed to mountain areas (Tanizaki-Fonseca & Moulton 2000), *S. tildae* populations may be facing a substantial decline.

From a zoogeographic standpoint, a remarkable species in our phyllostomid list was

Gardnerycteris crenulatum. This bat ranges from Mexico to southeastern Brazil (Williams & Genoways 2008), and its southernmost known records came from localities near our study site (Mello & Pol 2006). Capture data obtained at RBU are in agreement with those summarized by Mello & Pol (2006), including the association of *G. crenulatum* with water bodies (small dam) and its occurrence in low abundances. In Mexico, this species presents a restricted distribution and is rare, leading Ceballos (2014) to classify it as endangered. In Rio de Janeiro, *G. crenulatum* is classified as vulnerable, due to the small size of its populations and destruction of its habitat (Bergallo et al. 2000). Our record, nearly 17 years after the captures reported by Mello & Pol (2006), add a third locality for this species in Rio de Janeiro and reinforces the importance of forests at São João river basin to protect its apparently meridional edge populations in eastern Brazil—this species has never been captured in more southern and intensively sampled regions of Rio de Janeiro and São Paulo states (e.g., Esberard 2003; Bolzan et al. 2010; Garbino 2016).

Seasonal variation in abundance patterns

The phyllostomid assemblage did not present significant changes in composition throughout the year at RBU, but behind the similar general capture rates at both seasons, consistent evidences of seasonal shifts in a few species were detected, corroborating previous studies in the Atlantic Forest (Mello 2009). The most conspicuous pattern was the higher capture rate of *C. perspicillata* and *S. tildae* in drier months, contrasting with the trend of *Artibeus* spp. to be more frequent in the wet season. Fruit availability seems to be a main driver of general abundance patterns in frugivorous species (Rex et al. 2008), and seasonal changes are also likely to respond to this factor (Fleming 1988; Giannini 1999; Mello 2009). In the case of *Artibeus* spp., there is local evidence that some seasonality exists in their core fruit plants (sensu Fleming 1986). Lapenta (2007), for example, found that more species of *Cecropia* bear ripe fruits during the wet season in RBU.

The higher capture rates of groundstory bats in the drier season is contrary to our expectation, mainly in the case of *C. perspicillata*, whose core food plants (*Piper* spp.; Fleming 1986) produce fruit more abundantly in the wet season (Mello et al. 2004). As a possible explanation, one could argue that this bat needs to travel less between roosts and feeding areas during this season, which could reduce its chance of being captured in mist nets spread over the study area. In Costa Rica, *C. perspicillata* travels greater distances in the dry season, when resources are less abundant and more heterogeneously distributed (Fleming 1988). Also important to support this hypothesis is the high site fidelity previously recorded for *C. perspicillata* (Bianconi et al. 2006), since species that forage over large areas, like *Artibeus* spp. (Morrison 1978), probably go beyond our sampling stations or move to different forest fragments during the dry season. For *S. tildae*, whose core food plants are species of *Solanum* (Lobova et al. 2009), variation in capture rates are difficult to interpret given the lack of local phenological data.

The lack of seasonality in capture rates of *D. rotundus* was in accordance with our expectation and literature records (Young 1971; Freitas et al. 2006; Zortéa & Alho 2008), and is probably explained by the continuous availability of mammals as blood source for this species at RBU and its immediate surroundings. Not only cattle is available in the area; the reserve also harbors abundant populations of collared peccary (*Tayassu pecari*) and capybaras (*Hydrochoerus hydrochaeris;* L. R. Monteiro, unpublished data), both of which can be considered potential targets for this bat (Bobrowiec et al. 2015). The other aseasonal species in our sample, *Platyrrhinus recifinus,* is a canopy fruit-eating bat, which departed from results obtained for other Moraceae specialists, *Artibeus* spp. *Ficus* and *Cecropia* are used frequently by these bats (Lobova et al. 2009), but *P. recifinus* is a much smaller species, which may be a limiting factor for moving to other foraging areas in periods of food scarcity (Kalko et al. 1996; but see also Albrecht et al. 2007 and Villalobos-Chaves et al. 2017).

The seasonal diversity profiles at RBU were largely affected by the most common species, but the assemblages in the two seasons presented a similar pattern of dependence of diversity on *q*. These results can be viewed as evidence of the potential of the dry season at RBU to support a rich phyllostomid assemblage. This is in agreement with results from other assemblage-level analyses performed here, such as the redundancy analysis, which showed small effects or no difference related to season. Investigating phyllostomids in an Atlantic Forest site in Rio de Janeiro, Gomes et al. (2015) found no seasonal differences in species richness or assemblage composition, but higher general abundance in the wet season. Although these authors did not analyze species separately, it can be derived from their data that this abundance pattern was largely determined by the same species that are dominant at RBU (*A. lituratus* and *C. perspicillata*). While the ecological role of these species, mainly seed dispersal, might be more intense depending on the season (Mello 2009), the year-round maintenance of similar assemblages, including their ensemble composition, might also prove important for ecosystem functioning and regeneration (Silveira et al. 2011).

CONCLUDING REMARKS

Analyses of local assemblages are essential tools for the description of world's biodiversity, establishing the basic knowledge for its conservation (Balmford & Gaston 1999). Here we highlighted the importance of RBU for the conservation of Phyllostomidae, the most ecologically diverse bat family, analyzing our data set both qualitatively and quantitatively, and including both spatial (inter-site) and temporal (seasonal) components of variation. Although at a regional scale, results presented here pointed to low among-site diversity, singularities, as revealed by species such as *S. tildae,* show that RBU may conceal ecological opportunities that are masked when assemblage metrics are considered alone. The metric richness, and alpha and beta diversity, are also insensitive to differences in functional diversity, and further analyses in the same region should formally incorporate this aspect. Our qualitative data in this respect showed that nearly all the same five ensembles (see **Table 1**) are widely distributed, being gleaning animalivorous the only absence from FBR. This similarity is surprising, considering the level of fragmentation in the landscape, and suggest some resilience of this bat family, which is important for the maintenance of its ecological function.

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