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Vertical stratification in bat assemblages of the Atlantic Forest of south-eastern Brazil

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Abstract: Tropical forests are three-dimensional spaces with species and resources heterogeneously distributed. The vertical stratification of tropical forest biotas has been observed for several organisms and regions, but, surprisingly, the vertical structuring of large areas of important tropical forests, such as Brazil's Atlantic Forest, remains poorly studied. Here, we addressed the use of different Atlantic Forest strata by bats, comparing ensemble composition and relative abundance between the understorey and the canopy. A total of 618 bats belonging to 31 species and four families were recorded, including 11 species of frugivores and seven species of gleaning insectivores, the two trophic guilds predominantly represented in our sampling. Fifteen species were captured exclusively in the canopy, and six exclusively in the understorey, and many of those species were represented by a low number of captures (< 5). The bat species composition, richness and relative abundance between canopy and understorey strata varied. *Chiroderma villosum* was exclusively captured in the canopy, *Artibeus lituratus* was netted predominantly in the canopy and *Carollia perspicillata* and *Desmodus rotundus* were mostly captured in the understorey. Although processes such as resource partitioning between species and ecomorphological constraints may explain the differential use of forest strata, this remains little understood because of the scarcity of data for the Atlantic forest canopies.

Key Words: canopy diversity, Chiroptera, Mata Atlântica, Rio Doce State Park

INTRODUCTION

Spatial heterogeneity has been considered determinant in shaping species richness and diversity in megadiverse, highly heterogeneous tropical forests (Condit *et al.* 2002, Erwin 1988, Givnish 1999, Ozanne *et al.* 2003, Pennington & Dick 2010, Sedio *et al.* 2012, Wright 2002). Such heterogeneity may be expressed both horizontally and vertically, considering that tree canopies may reach well above 50–70 m high in tropical forests, and contributes to the high diversity found in tropical forests (Barker & Pinard 2001, Erwin 1988, Lowman & Nadkarni 1995, Lowman & Wittman 1996, Ozanne *et al.* 2003).

Canopies have unique conditions compared with other forest strata, including variation in temperature, light incidence and humidity (Nakamura *et al.* 2017, Ozanne *et al.* 2003) and faunal composition. Vertical stratification in tropical forests has been observed for insects (Basset *et al.* 2012, Schulze *et al.* 2001, Yanoviak & Kaspari 2000), birds (Pearson 1971, Walther 2002) and small mammals (Bernard 2001, Kalko & Handley 2001, Vieira & Monteiro-Filho 2003, Voss *et al.* 2001).

Nonetheless, studies on the vertical distribution of the fauna in tropical communities are still scarce for many groups (Kays & Allison 2001, Ozanne *et al.* 2003) and often limited (Lowman & Wittman 1996). There are a few exceptions for rodents and marsupials in the Atlantic Forest (Grelle 2003, Passamani 1995, Vieira & Monteiro-Filho 2003) and some preliminary insights from studies of bats (Carvalho & Fabián 2011, Pires & Fabián 2013). Bats are relatively easy to sample, and are key components of tropical community dynamics because of their high species richness, high abundance and functional diversity (Kalko *et al.* 1996, Voss & Emmons 1996, Willig 1986). Constraints related to the body size (mass can vary from

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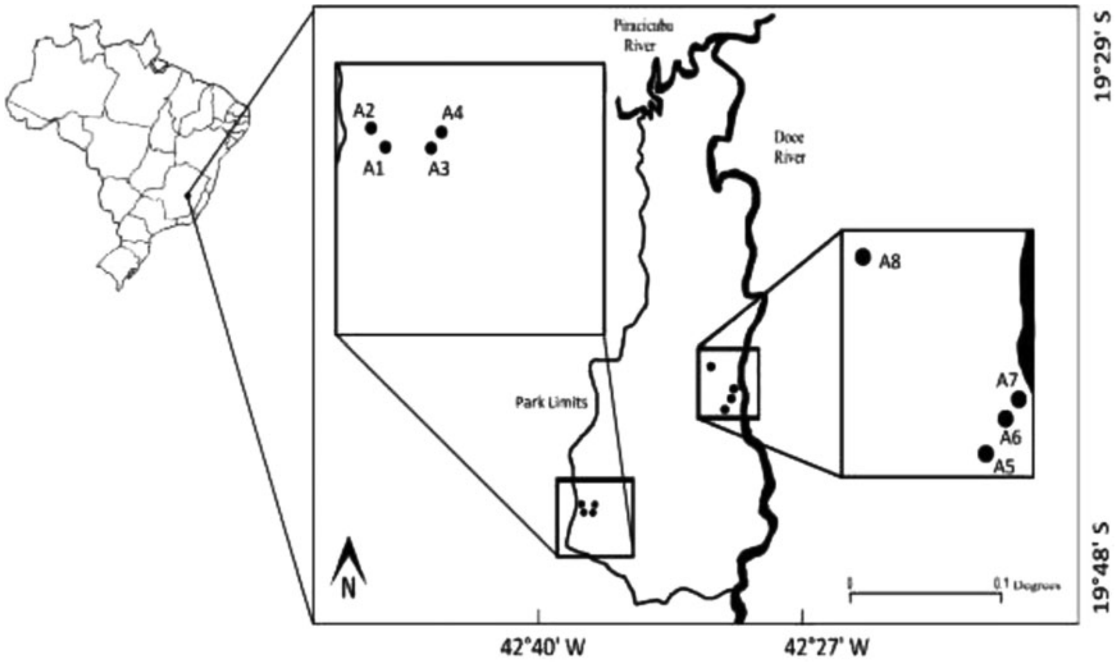

Figure 1. Sampling sites in the Atlantic Forest of Rio Doce State Park, eastern state of Minas Gerais, Brazil. In each site nets were set at ground and canopy level to access the vertical stratification of local bat faunas.

3 to 250 g – Bernard 2001) and ecomorphology of bats affect the ways that they use the vertical space (Marinello & Bernard 2014) with direct implications for their ecology, and to the processes they are involved in, such as seed dispersal and forest regeneration (Melo *et al*. 2006, Mendes *et al*. 2016, Santo-Silva *et al*. 2013, 2015; Tabarelli *et al*. 2010). Clearly, studies to account for the diversity of tropical bat communities relying solely on captures using ground-level mist nets provide incomplete pictures of the structure of bat assemblages (Meyer *et al*. 2011, Rex *et al*. 2011, Tavares *et al*. 2017). Studies in different strata of the Amazon forest indicated that some bat species might follow sharp vertical distributions (Bernard 2001, Handley 1967, Kalko & Handley 2001, Marques *et al*. 2015, Pereira *et al*. 2010, Sampaio *et al*. 2003, Simmons & Voss 1998). General patterns include the prevalence of selected species of insect-feeding emballonurid bats and small fruit-eating stenodermatine bats in the canopy, while the *Piper*-feeding *Carollia perspicillata*, and the common blood-feeding *Desmodus rotundus* are understorey users in the Amazon.

Here we provide the first test of vertical stratification for Atlantic Forest bat communities based on a comprehensive inventory in south-eastern Brazil. We hypothesize that bat abundance, species richness and composition are distinct between canopy and understorey strata of Atlantic forests even for forests not as tall as Amazonian sites. We expected to find different bat ensembles and distinct patterns of relative abundance in different strata due the bat ecological requirements (e.g. food and roosts), and ecomorphological constraints to flight. We also hypothesize that trophic guilds of bats are probably not distinct between forest strata, but are driven by specific intra-guild competition, which can displace competing species to occupy different strata.

METHODS

Study area and sampling

The study site is located in the Rio Doce State Park (PERD), eastern state of Minas Gerais (19°48′18″–19°29′24″S, 42°38′30″–42°28′18″W; Nunes *et al*. 2007). Altitude varies between 230 and 515 m asl (Lopes *et al*. 2002) and climate is Aw (hot and wet – Lopes *et al*. 2002), with well-defined rainy and dry seasons. With a total area of 35 974 ha, PERD harbours a complex of 44 natural lakes (Bovini *et al*. 2001) and is one of the largest strictly preserved remnants of semi-deciduous Atlantic Forest in Brazil, bordered to the north by Piracicaba river and to the east by Doce river.

We captured bat in eight sites selected according to their vegetation structure and level of disturbance: four sites in secondary forest with different levels of succession (A1–A4), and four sites in a primary forest area (A5–A8 – Figure 1), and repeating some of the sites sampled in the late 1990s as reported by Tavares *et al*. (2007). In each of the eight sampling sites two Ecotone©

Table 1. Bat species, strata of capture and assigned guild for bat assemblages of eight Atlantic Forest sampling sites at Rio Doce State Park, eastern state of Minas Gerais, Brazil. Species marked with (^{S}) were used in an Indicator Value test. Guilds are (following Kalko *et al.* 1996): uncluttered space/aerial Insectivores (USAI), background cluttered space/aerial insectivores (BSAI), highly cluttered space/gleaning insectivores (HSGI), highly cluttered space/gleaning carnivores (HSGC), highly cluttered space/gleaning sanguinivores (HSGS), highly cluttered space/gleaning frugivores (HSGF), highly cluttered space/gleaning omnivores (HSGO) and highly cluttered space/gleaning nectarivores (HSGN).

Taxa	Understorey	Canopy	Total	Guild
Phyllostomidae				
Artibeus fimbriatus Gray, 1838	1	2	3	HSGF
Artibeus lituratus (Olfers, 1818)	74	77	151^{S}	HSGF
Artibeus obscurus (Schinz, 1821)	8	5	13^{S}	HSGF
Artibeus planirostris (Spix, 1823)	7	6	13^{S}	HSGF
Chiroderma doriae Thomas, 1891	0	1	1	HSGF
Chiroderma villosum Peters, 1860	0	24	24^{S}	HSGF
Platyrrhinus lineatus (Geoffroy, 1810)	1	0	1	HSGF
Platyrrhinus recifinus (Thomas, 1901)	0	4	4	HSGF
Sturnira lilium (Geoffroy, 1810)	4	4	8	HSGF
Vampyressa pusilla (Wagner, 1843)	0	1	1	HSGF
Glossophaga soricina (Pallas, 1766)	22	3	25^{S}	HSGN
Dryadonycteris capixaba (Nogueira, Lima, Peracchi & Simmons, 2012)	1	0	1	HSGN
Anoura geoffroyi Gray, 1838	0	2	2	HSGN
Lophostoma brasiliense Peters, 1866	1	0	1	HSGI
Micronycteris minuta (Gervais, 1856)	0	1	1	HSGI
Micronycteris schmidtorum Sanborn, 1935	0	1	1	HSGI
Gardnerycteris crenulatum (Geoffroy, 1803)	0	2	2	HSGF
Phyllostomus hastatus (Pallas, 1767)	0	2	2	HSGO
Trachops cirrhosus (Spix, 1823)	6	0	6	HSGC
Chrotopterus auritus (Peters, 1856)	1	0	1	HSGC
Carollia perspicillata (Linnaeus, 1758)	258	7	265^{S}	HSGF
Desmodus rotundus (Geoffroy, 1810)	35	2	37^{S}	HSGS
Diphylla ecaudata Spix, 1823	0	2	2	HSGS
Vespertilionidae				
Myotis nigricans (Schinz, 1821)	6	1	7	BSAI
Rogheesa hussoni Genoways & Baker, 1996	0	1	1	BSAI
Thyropteridae				
Thyroptera wynneae Velazco, Gregorin, Simmons & Voss, 2014	2	0	2	BSAI
Molossidae				
Molossus aztecus Saussure, 1860	1	13	14^{S}	USAI
Molossus molossus (Pallas, 1766)	0	6	6	USAI
Molossus rufus Geoffroy, 1805	0	3	3	USAI
Nyctinomops laticaudatus (Geoffroy, 1805)	0	17	17^{S}	USAI
Nyctinomops sp.	0	2	2	USAI
Total – 31 species	428	189	617	

12 × 3-m canopy nets were set forming a rectangle of 12 × 6-m with maximum heights varying from 11 to 19.5 m. Canopy nets were fixed using pulleys and supporting ropes (Humphrey *et al.* 1968). An additional eight ground-level mist-nets were erected to sample the understorey. Most canopy nets were set in natural tree fall gaps and some in man-made openings, and understorey nets were set along trails previously opened. All nets remained opened for a period of 6 h after sunset.

We conducted 10 field expeditions between April 2012 and September 2013 on a total of 80 nights of sampling and eight net-nights in each expedition. Sampling effort was calculated according to the methods described by Straube & Bianconi (2002) multiplying total area of nets (number of nets × 12 × 3 m) and total time (hours per night × number of nights). The canopy sampling effort by site was 4320 m^2 h totalling 34 560 m^2 h for that stratum, the understorey sampling effort per site was 17 280 m^2 h, totalling 13 8240 m^2 h, and the total effort for this study including both canopy and understorey stratum was 172 800 m^2 h.

We followed the guidelines for animal research as described in Sikes *et al.* (2016). Collection permits were granted by the Instituto Chico Mendes – ICMBio (18528-3) and by Instituto Estadual de Florestas de Minas Gerais (IEF COL 003/12).

Analyses

We ran non-metric multidimensional scaling (NMDS – Clarke 1993) for the ordination of bat assemblages along

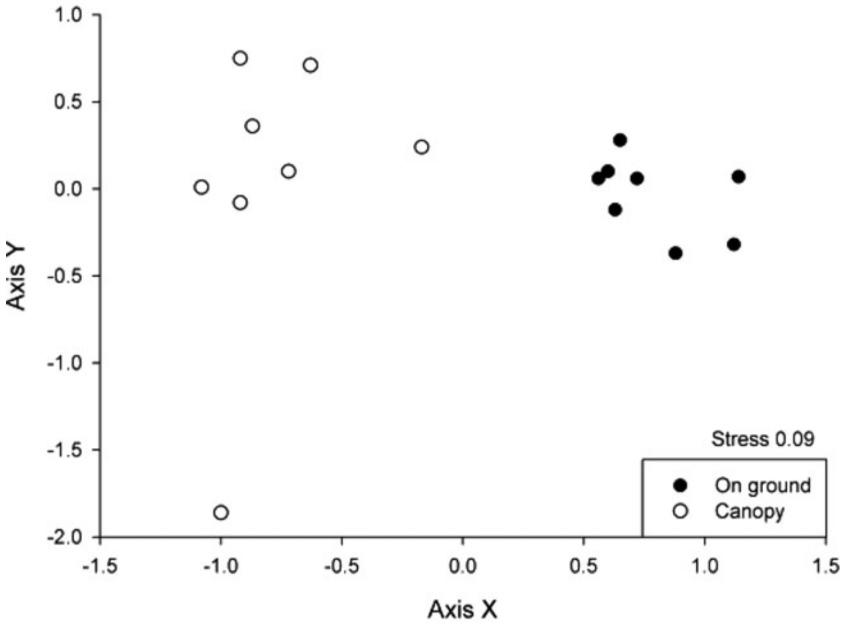

Figure 2. Ordination of understorey (solid circle) and canopy (open circle) bat faunas in eight sampling sites in the Atlantic Forest of Rio Doce State Park, eastern state of Minas Gerais, Brazil. A non-metric multidimensional scaling ordination was performed based on 31 bat species recorded.

the vertical space of PERD employing the Bray–Curtis index which quantifies the compositional dissimilarity between two different sites using previously standardized data (number of captures/sampling effort). We also tested the similarities of strata by using a one-way analysis of similarity (ANOSIM–Clarke 1993) of the results produced by our NMDS analyses. ANOSIM is a non-parametric statistical test used to test whether the similarity between groups is greater or equal to the similarity within the groups. The NMDS and ANOSIM were performed using the Primer and Permanova software (Anderson *et al.* 2008). We identified species that had dissimilar distribution among the strata by the Indicator Value test (INDVAL test – Dufrene & Legendre 1997). The INDVAL quantifies the fidelity and specificity of species in relation to groups of sites in a user-specified classification of sites, and tests for the statistical significance of the associations by permutation tests. Only species with ≥ 10 captures were considered for the ordinations. INDVAL associated with the Monte Carlo test were performed in PC-ORD.

We classified all species into trophic guilds as proposed by Kalko *et al.* (1996). In such classification, trophic guilds are defined by a combination of predominant diet (based on most consumed food items), foraging strategies, and main habitat used (cluttered and uncluttered space). We also used *t*-test to verify the significance among trophic guilds by strata (canopy versus understorey) based on bat captures with the help of the software Bioestat 5.0 (Ayres *et al.* 2007).

RESULTS

We captured a total of 429 bats in the understorey and 189 bats in the canopy. We recorded 31 bat species distributed in the families Emballonuridae, Phyllostomidae, Vespertilionidae and Molossidae. *Carollia perspicillata*, *Artibeus lituratus* and *Desmodus rotundus* accounted for > 70% of the captures (265, 154 and 37 bats, respectively). We captured representatives of a total of eight out of the 10 guilds expected to occur in tropical bat communities (Table 1).

The NMDS ordination indicated that the bat assemblages of PERD were different between canopy/sub-canopy and understorey sets ($P < 0.001$; R global $= 0.768$) (Figure 2), and site A1 appears as an outlier (Figure 2). A total of 16 species were predominantly or exclusively captured in the canopy, and eight in the understorey (Table 1). Nine out of 31 recorded species were separated by stratum, but only *A. lituratus* considered as having affinities with the canopy, and *C. perspicillata* and *D. rotundus* as typically understorey species had statistical support for the INDVAL test (Table 2).

Indeed, the highly cluttered space/gleaning frugivore (HCGF) *A. lituratus* was captured mostly at the canopy as indicated by the INDVAL test ($P = 0.04$; Table 3) while highly cluttered space/gleaning omnivores (HSGO) and uncluttered space/aerial insectivores (USAI) were captured only in the canopy, although a single individual of *M. aztecus* (an aerial insectivorous bat)

Table 2. Outputs from an Indicator Value test using the more representative species (≥ 10 individuals) in a study on the vertical stratification of bat communities of eight Atlantic Forest sampling sites at Rio Doce State Park, eastern state of Minas Gerais, Brazil. *Indicates statistically significant. Note that only three species had significantly distinct abundances between the strata.

Taxon	Stratum	Indicator Value	Mean	P
*Artibeus lituratus**	Canopy	82.4	61.9 ± 7.39	0.001
Artibeus obscurus	Canopy	36.9	34.6 ± 10.8	0.281
Artibeus planirostris	Canopy	39.7	34.7 ± 10.8	0.266
*Carollia perspicillata**	Understorey	89.1	58.2 ± 9.47	0.000
Chiroderma villosum	Canopy	50	25 ± 10.2	0.076
*Desmodus rotundus**	Understorey	69.6	41.4 ± 11	0.024
Glossophaga soricina	Understorey	23.2	28.6 ± 10.7	0.718
Molossus aztecus	Canopy	12.3	18.2 ± 6.35	1.000
Nyctinomops laticaudatus	Canopy	37.5	22.4 ± 9.36	0.205

Table 3. Bat trophic guilds and their most associated vertical strata (C – canopy, U – understorey) based on data from eight Atlantic Forest sampling sites at Rio Doce State Park, eastern state of Minas Gerais, Brazil. Guild acronyms as in Table 1. *Indicates statistically significant. Note that HSGF was only guild distinct in abundance between strata.

Trophic guild	Strata	*t*-value	Degree of freedom	P
HSGN	C, U	0.026	14	0.48
HSGF *	C, U	– 1.77	14	0.04
HSGC	U	1.69	14	0.06
HSGS	C, U	1.48	14	0.08
HSGI	C, U	– 1.33	14	0.11
USAI	C, U	– 1.08	14	0.15
BSAI	C, U	– 0.132	14	0.44
HSGO	C	– 1.00	14	0.17

was netted in the understorey (Table 1). Highly cluttered space/gleaning nectarivores (HSGN) and highly cluttered space/gleaning sanguinivore (HSGS) were mostly captured in the understorey, and highly cluttered space/gleaning carnivore species were captured only in the understorey (Figure 3).

DISCUSSION

Our data from the Atlantic Forest in south-eastern Brazil shows that local bat communities are not homogeneously distributed across vertical strata of the forest, and are structured in canopy and understorey assemblages. Canopy foragers include *A. lituratus* and *C. villosum*, and other species represented by few captures such as small frugivores (*Vampyressa pusilla* and *Platyrrhinus recifinus*), some small gleaning insectivores (*Micronycteris minuta* and *Gardnerycteris crenulatum*) and aerial insectivorous molossids (*Molossus* and *Nyctinomops*). Patterns similar to ours have been observed for other tropical forests in the Amazonia (Bernard 2001, Henry *et al*. 2004, Hodgkison *et al*. 2004, Kalko & Handley 2001, Marques *et al*. 2015, Pereira *et al*. 2010, Sampaio *et al*. 2003, Simmons & Voss 1998). In studies in Belém, Brazilian Pará State, *C. villosum* was also considered a canopy species (Kalko & Handley 2001), while in the Manaus area, in Brazilian Amazonas State, molossids of the genus *Molossus* and *Nyctinomops* have also been recorded usually flying above the trees and roosting in or foraging very close to the canopy (Bernard 2001, Kalko & Handley 2001, Sampaio *et al*. 2003). Moreover, in our sampled sites, *C. perspicillata* and *D. rotundus* have affinities with the understorey stratum (P ≤ 5%; Table 2), a similar pattern to that observed in Amazonian sites (Bernard 2001, Kalko & Handley 2001, Pereira *et al*. 2010, Sampaio *et al*. 2003).

Several other species have been strictly or mostly sampled in understorey, such as the nectarivore *G. soricina*, several gleaning insectivores and carnivores, and the recently described disk-winged bat *Thyroptera wynneae* (Velazco *et al*. 2014). *Thyroptera* roosts mainly in unrolled leaves of *Heliconia* and *Musa*, dead leaves of *Cecropia*, and palm trees found in the understorey, edges and gaps of PERD. Indeed understorey roost selection may increase the chances of captures of several bat species in ground level mist-nets, including species of gleaner insectivore phylostomids, and aerial insectivore emballonurids and thyropterids that use ground hollows, termite hollows and fallen trunks (Dalponte *et al*. 2016, Simmons & Voss 1998, Voss *et al*. 2016). Our second hypothesis, addressing the absence of stratification by trophic guild was just partially confirmed because most of the recorded guilds occurred in both strata though with distinct captures in each stratum (Table 1). For example, molossids – which are exclusive insectivores – were caught only in canopy nets (with one exception – Table 1), while frugivores were mostly in the understorey. On the other hand, gleaning frugivore (HSGF) guild presented differences between strata (Table 3).

Other approaches may help to refine the information on the use of the space by bats in tropical forests. Findings based on the study of stable isotopes (N and C) point to a more complex scenario for bats. For example, Rex *et al*. (2011) revealed that some frugivores (including

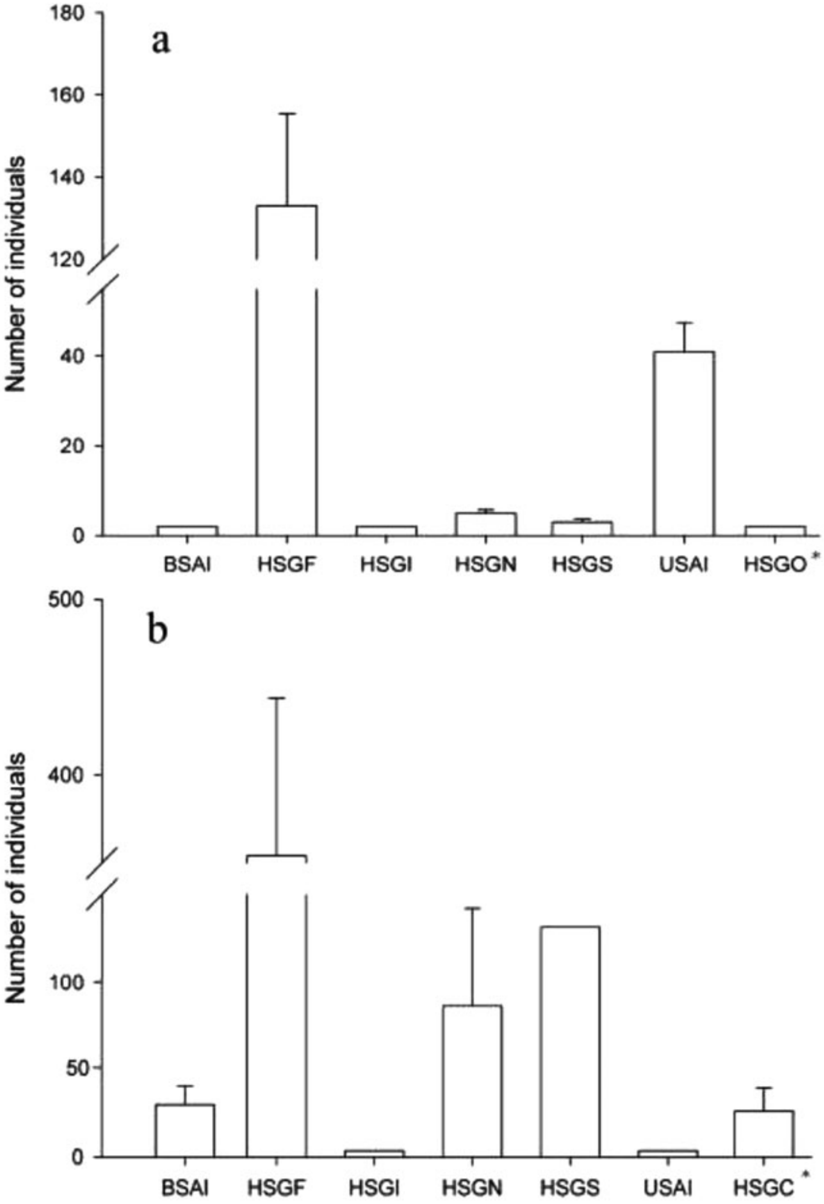

Figure 3. Mean and standard deviation of captures of bats in the canopy (a) and understorey (b) in eight sampling sites in the Atlantic Forest of Rio Doce State Park, eastern state of Minas Gerais, Brazil. Bat species were grouped in trophic guilds (acronyms as in Table 1). *Indicates trophic guilds restricted to only one stratum.

A. lituratus) were mostly netted in the understorey but, in fact, they had fed on plant species of canopy, as indicated by isotopic analyses. In our study, *A. lituratus* was netted in both strata, but mostly in the canopy.

Although our effort may not be sufficient to answer questions on vertical stratification for all species, especially those that are rarely captured or able to detect and avoid nets, we would suggest that the main limitation regarding our results is the need for long-term sampling study at PERD to be able to record uncommon species. On the other hand, this is the first attempt to test the vertical stratification of bat assemblages in the Atlantic Forest, and we argue that we have detected significant patterns that may be tested in the long-term studies. Based on the single study of Bergallo *et al.* (2003) approximately 1000 captures may be necessary to estimate the richness of phyllostomid bat communities in Atlantic Forest sites and even an increased number of captures for Amazonian sites (Sampaio *et al.* 2003). In the same way, Meyer *et al.* (2010) proposed that long-term studies (>10 y) and many plots may be necessary to access some patterns and tendencies in tropical bat communities based on abundance. Accessing and sampling the forest canopies have inherent methodological limitations making large sampling efforts frequently impractical (Lowman & Nadkarni 1995, Lowman & Wittman 1996, Nakamura *et al*. 2017). We therefore recognized that the sample sizes, especially in the canopy, are limited, but our data are sufficient to show differences at the level of the assemblages, and for a few common species.

The importance of vertically extended sampling

Bat inventories focused exclusively on understorey sampling in the Atlantic Forest may be particularly limiting to access specific taxa. This is the case of molossids. Because molossids are high-flyers, and usually forage well above the canopy, they are hardly recorded with mist nets set in the forest interior or in the understorey (Kalko *et al*. 1996). Indeed, although PERD now has a diverse record of molossid bats including recently described new species (*Eumops chimaera* – Gregorin *et al*. 2016), most of those records were obtained from roost searching or sporadic captures with nets especially set intercepting flyways or foraging sites. Usually, little or no representation of molossids is observed in datasets from ground-level mist net samples in the Atlantic forests (Dias *et al*. 2002, Martins *et al*. 2015). In our study, with the exception of a single individual of *M. aztecus*, all the molossids recorded came from canopy nets in one of the sites, resulting in a high species richness (five species) and number of captures (41 bats).

Other families and species are also frequently misrepresented in inventories focused on the understorey level. Marques *et al*. (2015), working with bat detectors in the flooded forests of the Amanã Sustainable Development Reserve, in the Brazilian Amazonia, recorded much more activity in Emballonuridae, Molossidae and Vespertilionidae at the canopy level. Emballonurids are also usually recorded in canopy nets (e.g. *Diclidurus* spp., *Saccopteryx* spp. – Kalko & Handley 2001). They were absent from our canopy nets, but have been previously recorded in PERD mostly due to roost searching, and often associated to water bodies (Tavares & Anciães 1998, Tavares *et al*. 2007). Indeed the history of bat species inventories at PERD (Gregorin *et al*. 2015, 2016; Tavares 2013, Tavares & Anciães 1998, Tavares *et al*. 2007; Velazco *et al*. 2014) emphasize the need to adopt mixed methodologies (Marques *et al*. 2015, Meyer *et al*. 2011) to uncover the diversity of the bat fauna at the reserve, including the use of bat detectors, roost searching and canopy sampling.

Conservation implications of changing the vertical structure of the forest

Neotropical forests are heterogeneous environments for bats in terms of vertical strata (Yang *et al*. 2013) and the canopy shelters high richness and dynamic activity (Bernard 2001, Kalko & Handley 2001, Marques *et al.* 2015, Rex *et al*. 2011). Reduction or loss of tree canopy is the first and one of the most harmful effects of deforestation in tropical forests, affecting several bat species (Fenton *et al*. 1998, Russo *et al*. 2007). The Atlantic Forest suffered a severe process of habitat loss, and has been reduced to ~8% of its original size (Ribeiro *et al*. 2009).

As demonstrated in our study and others elsewhere, the loss or lowering of mature forests and, consequently, of the forest canopy may affect whole bat assemblages associated to these upper strata. Besides direct effects on bats per se, this will also affect other bat-mediated ecological processes such as pollination and seed dispersal of many plant species (Tabarelli *et al*. 2010). Such changes in the canopy structure can potentially disrupt seed-delivery services provided by some frugivores, as well as favour the dominance of bat species that feed mostly on small-seeded understorey plant species, or, more dramatically, promote a biotic plant community homogenization in response to a regional-scale proliferation of some pioneer species (Melo *et al.* 2006, Santo-Silva *et al*. 2013).

On the other hand, the increase in relative abundance of bat-associated species in the understorey may produce positive bias, accelerating the colonization and regeneration of disrupted habitats (Tabarelli *et al*. 2010). In all cases, in a scenario where human-modified landscapes prevail – such as in south-eastern Brazil – conserving the integrity of the canopy of mature forests may directly contribute not just to the persistence of bats, but of a large portion of the local biodiversity of inland Atlantic Forest sites.

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