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Author(s): Mayara A. Martins, William Douglas De Carvalho , Daniela Dias, Débora De S. França, Marcione B. De Oliveira, and Adriano Lúcio Peracchi

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Bat species richness (Mammalia, Chiroptera) along an elevational gradient in the Atlantic Forest of Southeastern Brazil

MAYARA A. MARTINS[1, 5, 6], WILLIAM DOUGLAS DE CARVALHO[1, 2, 3], DANIELA DIAS[4], DÉBORA DE S. FRANÇA[5], MARCIONE B. DE OLIVEIRA[1, 5], and ADRIANO LÚCIO PERACCHI[5]

[1]*Programa de Pós-graduação em Biologia Animal, Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro (UFRRJ), BR 465, km 7, CP 74507, CEP 23890-000, Seropédica, RJ, Brazil*
[2]*Laboratório de Diversidade de Morcegos, Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, UFRRJ, BR 465, Km 7, CP 74507, CEP 23890-000, Seropédica, RJ, Brazil*
[3]*Centro de Biologia Ambiental, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal*
[4]*Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, IOC, Fundação Oswaldo Cruz, Avenida Brasil, 4365, Manguinhos, CEP 21040-360, Rio de Janeiro, RJ, Brazil*
[5]*Laboratório de Mastozoologia, Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, UFRRJ, BR 465, Km 7, CEP 23890-000, Seropédica, RJ, Brazil*
[6]*Corresponding author: E-mail: mamartinsbio@gmail.com*

The effect of elevational gradients on the richness and composition of communities are reflected by different biotas. The objective of this study was to document changes in the species richness and composition of bats along a tropical elevational gradient between 500 and 2,500 m of elevation in southeastern Brazil. We carried out fieldwork from June 2009 to December 2012 with the use of mist nets. During 32 sampling nights we recorded 270 bats from 22 species. Species richness peaked around low-elevation (500–1,000 m a.s.l.) and there was richness decrease at higher elevations. The analysis of bat assemblage between the elevational range showed a significant difference in species composition along an elevational gradient. Bat richness and abundance were negatively related to altitude.

Key words: high altitude, species composition, trophic guilds, vegetation types

INTRODUCTION

The spatial distribution of organisms is the result of the interaction between geological, ecological, and evolutionary processes that determine the structure of a community (Rahbek, 1997; Brown, 2001; Lomolino, 2001). The regional variation in species richness has been discussed for many years by ecologists and biogeographers (Pianka, 1966; Lomolino, 2001; Guo *et al*., 2013). The effect of altitudinal gradients on the composition of communities is reflected in a general trend observed in several groups: species richness decreases with altitude. This pattern, observed in a variety of taxa and geographic areas, is known as Stevens' Rule (e.g., Terborgh, 1977; Stevens, 1992; Rahbek, 1995). Those changes in species richness and abundance related to altitude are influenced by ecological factors as climate, productivity and habitat heterogeneity (Brown, 2001; McCain and Grytnes, 2010).

A remarkable characteristic of elevational gradients is a succession of habitats, which is directly related to climate. Studies have pointed out on complex climate changes happen along an elevational gradient, which can affect the diversity and functional composition of the mammals fauna (Soriano 2000; Brown, 2001; Tews *et al*., 2004; McCain and Grytnes, 2010).

Elevational variations influence the abundance, richness, and distribution of mammal species and each species responds differently to altitude. Two patterns are acknowledged for mammals: (i) the clinal pattern, in which richness is higher in lower areas and decreases with altitude (e.g., Stevens, 1992; Patterson *et al*., 1998; Contreras and Huerta, 2001; Pinares, 2006); and (ii) the modal pattern, with a peak in richness at medium altitudes (e.g., Heaney, 2001; Nor, 2001; Rickart, 2001; Sánchez-Cordero, 2001; McCain, 2007; Rowe and Lidgard, 2009). Rahbek (1995) concluded that the modal pattern (hump-shaped curve) is the most common in tropical biomes for mammals and birds. Studies on bat species richness along altitudinal gradients have shown that both patterns may be found: clinal (Graham, 1983, 1990; Patterson *et al.*, 1996; Pinares, 2006; Flores-Saldaña, 2008) and modal (Sánchez-Cordero, 2001; McCain, 2005; Dias *et al.*, 2008; Piksa *et al*., 2013).

In Brazil, only a few authors studied the relationship between mammal species richness and altitude; among them, the studies by Bonvicino *et al.* (1997), Geise *et al.* (2004), and Pardini and Umetsu (2006) stand out. Few studies assessed the variation in bat species richness with altitude in Brazil (e.g., Dias *et al*., 2008; Bordignon and França, 2009). In the Atlantic Forest of the states of Rio de Janeiro and Minas Gerais, where some mountain ranges surpass 2,000 m, most bat inventories have been conducted at altitudes below 500 m (Esbérard and Bergallo, 2005). The scarcity of bat sampling in high areas is explained by their high declivity, low availability of plain clearings, and low temperatures, which together with fieldwork logistics result in a lower sampling success (Dias *et al*., 2008; Mello *et al.,* 2008). As a result, little is known about bat species composition at higher altitudes (Carvalho *et al.*, 2013; Moras *et al.*, 2013) and how bat abundance and richness varies with altitude.

The present study aimed to investigate patterns of bat species richness along an elevational gradient in the Atlantic Forest of Southeastern Brazil. We predicted that the altitudinal pattern of assemblages of bats would vary with altitude and species richness and abundance would decline with increasing elevation.

Material and Methods

Study Area

The study was conducted in Itatiaia National Park, southeastern Brazil. The park has an area of 30,000 ha (Fig. 1), and is located in the Itatiaia Massif, Mantiqueira Mountain Range. The Itatiaia Park is within the Mantiqueira Mountain Range Environmental Protection Area, Atlantic Forest biome, which is part of a global protection system classified as highly irreplaceable in terms of biodiversity (Saout *et al.*, 2013).

The Itatiaia Park is characterized by montane relief and rocky slopes, with altitudes ranging from 650 to 2,789 m. Its orography is one of the main factors that determine the climate of Itatiaia Park, as it contains the highest surfaces of the Mantiqueira Mountain Range. There are two climate types, according to Köppen system: Cwb (mesothermal with mild summer and rainy season concentrated in summer) in the highlands above 1,600 m, and Cpb (mesothermal with mild summer and no dry season) in the lowlands. Severe frosts are common in the winter, hail is observed frequently, and light snowfall occurs rarely. The annual rainfall recorded in Itatiaia Park is ca. 2,400 mm, and is concentrated mainly in the summer (IBDF, 1982).

According to Ururahy *et al.* (1983), the vegetation of the area is classified as dense rainforest and is composed of different habitats that follow the altitudinal gradient: lower montane forest (ca. 50 to 500 m a.s.l.), montane forest (ca. 501 to 1,500 m a.s.l.), upper montane forest (ca. 1,501 to 2,000 m a.s.l.) and high altitude fields (campos de altitude) (above 2,000 m a.s.l.). Studies carried out by Segadas-Viana (1965) and Segadas-Viana and Dau (1965) along the elevational range of Itatiaia Park showed that the habitats are well delimited and easily recognizable by climate and vegetation structure. The lower montane forest was not sampled due to it was occupied by an urban area. We carried out sampling in four habitats, wherein Montane Forest was sampled into two habitats: 1 — Montane Forest (500 to 1,500 m a.s.l.): it has the largest altitudinal range and is divided into two areas: (i) a lower area (500 to 1,000 m a.s.l.) almost entirely covered by secondary forest; its climax is an open forest, with a moderately dense understory and trees with 30 to 40 m in height; (ii) an upper area (1,001 to 1,500 m a.s.l.) covered by an open climax forest, with trees that vary from 20 to 30 m in height and a dense understory. In both areas, the warmest months have an average temperature of 20°C and in the coldest months the average temperature is 15°C. The average annual rainfall is 1,699 mm; 2 — Upper montane forest (1,501 to 2,000 m a.s.l.): a low, moderately dense climax forest, with few trees of 15 m in height. The climate is *Cfb*, temperate and humid due to the plant cover and the altitude. The dry and cold season is more severe than in lower physiognomies. The warmest months have an average temperature of 18°C and in the coldest months the average temperature is 13°C. The average annual rainfall is 2,000 mm; 3 — High-altitude fields (above 2,000 m a.s.l.): it has an irregular and very diverse topography; its climax is grassland vegetation with a steppe structure. In the warmest months the average temperature is 13°C and in the coldest months the average temperature is 9°C. The average annual rainfall is 2,407 mm. The rocky peaks found in this region, such as the Agulhas Negras Peak (Itatiaiuçu, 2,789 m), reach the highest altitudes in the state of Rio de Janeiro. Safford (1999) compared the high-altitude fields (campos de altitude) with the highlands of the Andes (páramos) and found similarities in floristics, climate, and soil. Due to these different vegetation types along the altitudinal gradient, the Itatiaia Park has attracted special attention because of its fauna (Ávila-Pires and Gouvêa, 1977; Holt, 1928; Pinto, 1951), which was studied for the first time by Ule (1896).

Fieldwork

Capture and handling protocols followed the guidelines of the American Society of Mammalogists (Sikes *et al*., 2011). We carried out fieldwork in Itatiaia Park from June 2009 to December 2012 in areas within the states of Minas Gerais and Rio de Janeiro (Fig 1). We carried out sampling over 32 nights in the park, comprising eight nights in each elevational range: four nights in the rainy season and four in the dry season. In each altitudinal range, we made captures aiming at sampling the largest number of points (Simmons and Voss, 1998; Bergallo *et al.,* 2003; Marques *et al.*, 2013). All new captures in the field were realized under license provided by the corresponding local agencies and governments.

At each sampling night, we set up mist nets (12 m × 2.5 m; mesh, 40 mm) at ground level on trails or gaps close to plants in blossom or bearing fruits, and at sites where bat occurrence is expected, such as buildings, tunnels, rock crevices, rocks, and hollow trees. We set up mist nets also over rivers and water bodies, or near them. Considering that in higher elevations landscape usually changes drastically, in high-altitude fields we set nets at ground level combining units of different lengths and were linked in lines. We also placed mist-nets in shrubs, rocky areas and human building that are possible roosts, and near water. We set up nets before sunset, kept them open for six hrs, and checked them every 20 min. The calculation of sampling effort followed Straube and Bianconi (2002). After removed from the mist nets, bats were placed in individual numbered cloth bags. We identified the captured bats in the field using the keys in Gardner (2008) and the species accounts provided by Simmons and Voss (1998) and Dias and Peracchi (2008)

We collected representatives of all species, and they were prepared as vouchers, preserved in spirit, and deposited at the Adriano Lúcio Peracchi Collection (ALP) of the Institute of Biology, Federal Rural University of Rio de Janeiro (UFRRJ) (Table 1). The other individuals were released after identification and recording of field data.

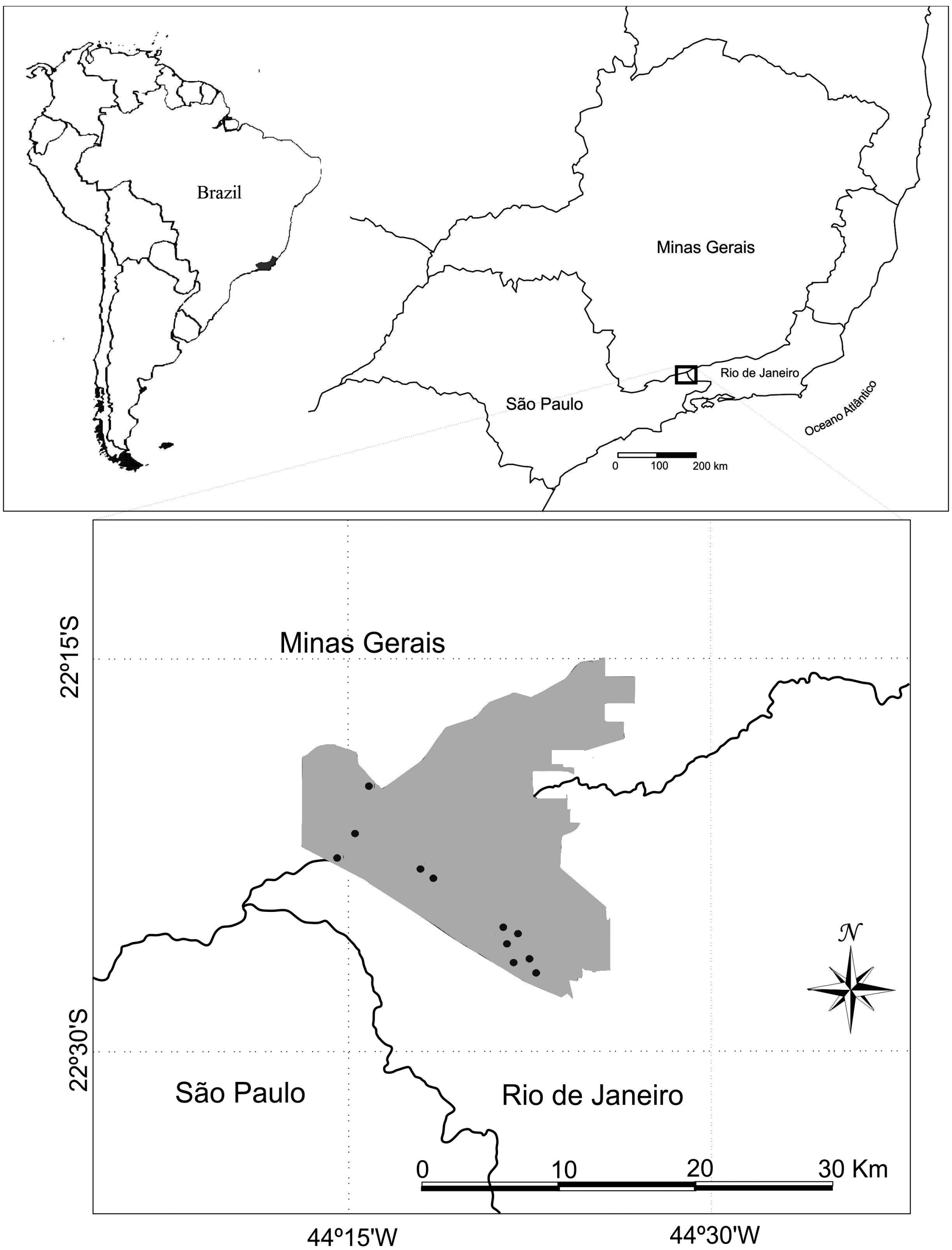

FIG. 1. Map of Itatiaia National Park, showing the sampling sites (•) from 2009 to 2012

Data Analysis

We calculated the relative frequency of each species by dividing the total number of captures in each species by the total number of individuals captured in the study area (Magurran, 1988). To describe the functional composition of the bat fauna in Itatiaia Park, we grouped the species in trophic guilds based on their predominant feeding habit reported in the literature (sensu Kalko *et al.*, 1996; Kalko and Handley, 2001).

We grouped the captures in elevational ranges and the species in trophic guilds in order to test for a distribution pattern along the elevational gradient. To check for differences in species composition related to elevational, we tested the similarity between the communities found in each elevational range with a one-way analysis of similarities ANOSIM (Clarke, 1993). This technique allows, through a permutation procedure, detecting differences between groups of samples. In this analysis, the degree of discrimination between sites is given by the magnitude of R, which usually ranges from 0 to 1. For this analysis we used the program PRIMER 5 (PRIMER-E Ltda, 2001).

To test whether species richness and abundance vary with different elevations, we used simple linear regressions (Vieira, 2003). For this analysis we exclude the highest elevational range due to the small sample size. The individuals captured in roost were not considered in the analysis. The results of all analyses were considered significant when $P < 0.05$.

Results

We captured 270 individuals of 22 species, 14 genera, and three families: Phyllostomidae (14 species), Vespertilionidae (seven species), and Molossidae (one species) (Table 1). The species with highest capture frequency in Itatiaia Park was *Sturnira lilium* (46.7% of all captures), followed by *Anoura caudifer* (11.8%) and *Carollia perspicillata* (8.1%).

Elevational range I (500−1,000 m a.s.l.) we recorded the highest species richness (15) and its fauna was represented by Phyllostomidae and Vespertilionidae. *Sturnira lilium* (n = 58) was the most frequent, followed by *A. caudifer* (n = 20) and *Artibeus lituratus* (n = 19). Elevational range II (1,001−1,500 m a.s.l.) we recorded a richness of 10 species, represented by Phyllostomidae and Vespertilionidae. *Sturnira lilium* (n = 32) was again the most frequent, followed by *A. caudifer* (n = 11) and *Platyrrhinus recifinus* (n = 9). In elevational range III (1,501–2,000 m a.s.l.) we recorded six species

Table 1. Voucher number, family, trophic guild and number of individuals captured for each species in Itatiaia National Park, Brazil from 2009 to 2012

Species	Sex/Voucher number (ALP)	Family	Trophic guild	Number of individuals	Relative abundance (%)
Sturnira lilium	♀9415, ♂9418, ♂9425, ♀9426, ♀9434, ♀9442, ♀9452	Phyllostomidae	F	126	46.7
Anoura caudifer	♂9448	Phyllostomidae	N	32	11.8
Carollia perspicillata	♂9417, ♂9419, ♀9423	Phyllostomidae	F	22	8.1
Artibeus lituratus	♀9414, ♂9416	Phyllostomidae	F	20	7.4
Platyrrhinus recifinus	♂9424, ♀9453, ♂9457	Phyllostomidae	F	15	5.6
Myotis riparius	♀9443, ♂9444, ♀9445, ♀9446, ♂9449, ♀9451	Vespertilionidae	AI	11	4.1
Glossophaga soricina	♂9421, ♂9422	Phyllostomidae	N	8	2.9
Tadarida brasiliensis	♀9460, ♂9463	Molossidae	AI	8	2.9
Artibeus fimbriatus	♂9412, ♀9440	Phyllostomidae	F	5	1.8
Myotis izecksohni	♀9432, ♀9447, ♀9450, ♀9454	Vespertilionidae	AI	4	1.5
Myotis levis	♂9461, ♂9464	Vespertilionidae	AI	4	1.5
Tonatia bidens	♂9411, ♀9439	Phyllostomidae	O	2	0.7
Chrotopterus auritus	♂9438, ♂9455	Phyllostomidae	C	2	0.7
Micronycteris microtis	♀9429, ♀9458	Phyllostomidae	G	2	0.7
Lasiurus blossevillii	♂9462, ♂9465	Vespertilionidae	AI	2	0.7
Anoura geoffroyi	♂9448	Phyllostomidae	N	1	0.4
Desmodus rotundus	♂9431	Phyllostomidae	H	1	0.4
Mimon bennettii	♀9427	Phyllostomidae	O	1	0.4
Myotis ruber	♂9410	Vespertilionidae	AI	1	0.4
Lasiurus cinereus	♀9459	Vespertilionidae	AI	1	0.4
Artibeus obscurus	♀9456	Phyllostomidae	F	1	0.4
Myotis nigricans	♀9437	Vespertilionidae	AI	1	0.4
Total				270	100.0

F — frugivore, N — nectarivore, AI — aerial insectivore, G — gleaner, O — omnivore, C — carnivore, and S — sanguivore represented by Phyllostomidae, Vespertilionidae, and Molossidae. *Sturnira lilium* (n = 36) was again the most frequent species. In the elevational range IV (2,001−2,500 m a.s.l.) we recorded four species, represented by Molossidae and Vespertilionidae (Table 2).

Insectivorous bats, the guild with the largest number of species in Itatiaia Park, were recorded along the entire elevational gradient (Fig. 2). This was also the only trophic guild found in high-altitude fields. Hematophagous and carnivorous bats were restricted to a single elevation range. They were recorded, in the elevational ranges I (500−1,000 m a.s.l.) and II (1,001−1,500 m a.s.l.) respectively. The relative abundance of *S. lilium* was higher in elevational range I, where it represented 54.8% of all captures, followed by 24% in elevational range II, 17.7% in altitudinal range III, and 3.33% in altitudinal range IV.

The results of the ANOSIM showed that the four altitudinal ranges analyzed in the present study differ from each other in terms of fauna (R = 0.367, P < 0.001). The smallest R-value was found between the elevational ranges II and III, which showed no significant difference in species composition, with higher similarity. The R-values of the comparisons that evidenced the highest differences in species composition, such as between the groups I, IV and II, IV, were all very large (≈ 1) (Table 3). Bat species richness (F = 30.84, *d.f.* = 1, R^2 = 0.56, P < 0.001) and abundance (F = 14.33, *d.f.* = 1, R^2 = 0.36, P < 0.001) were negatively related to altitude, i.e., the higher the altitude, the lower the species richness and abundance (Fig. 3).

Discussion

Sturnira lilium was the most abundant species in three elevational ranges. This species is common at high elevation (Moratelli and Peracchi, 2007; Nobre *et al.*, 2009; Luz *et al.*, 2013), which probably points to a more plasticity of this species for highlands. In species of the genus *Sturnira*, importance of plant *Solanum* in the diet increases in elevation (Giannini,

Table 2. Individuals per species and site along the elevational gradient in Itatiaia National Park, Brazil from 2009 to 2012

Species	Range I (500–1,000 m)	Range II (1,001–1,500 m)	Range III (1,501–2,000 m)	Range IV (2,001–2,500 m)
Molossidae				
Tadarida brasiliensis	0	0	4	4*
Phyllostomidae				
Desmodus rotundus	1	0	0	0
Anoura caudifer	20	11	1	0
A. geoffroyi	1	0	0	0
Glossophaga soricina	8	0	0	0
Chrotopterus auritus	0	2	0	0
Micronycteris microtis	1	1	0	0
Mimon bennettii	1	0	0	0
Tonatia bidens	1	1	0	0
Carollia perspicillata	17	5	0	0
Artibeus fimbriatus	5	0	0	0
A. lituratus	19	0	1	0
A. obscurus	0	1	0	0
Platyrrhinus recifinus	6	9	0	0
Sturnira lilium	58	32	36	0
Vespertilionidae				
Lasiurus blossevillii	0	0	0	2
L. cinereus	0	0	0	1
Myotis levis	0	0	2	2
M. nigricans	0	1	0	0
M. riparius	7	0	4	0
M. ruber	1	0	0	0
M. izecksohni	2	2	0	0
Total of individuals	148	65	48	9
Total of species	15	10	6	4
Sampling effort (m^2.h)	12,135	11,025	11,160	11,130

* — individuals captured in mist nets set up in roost

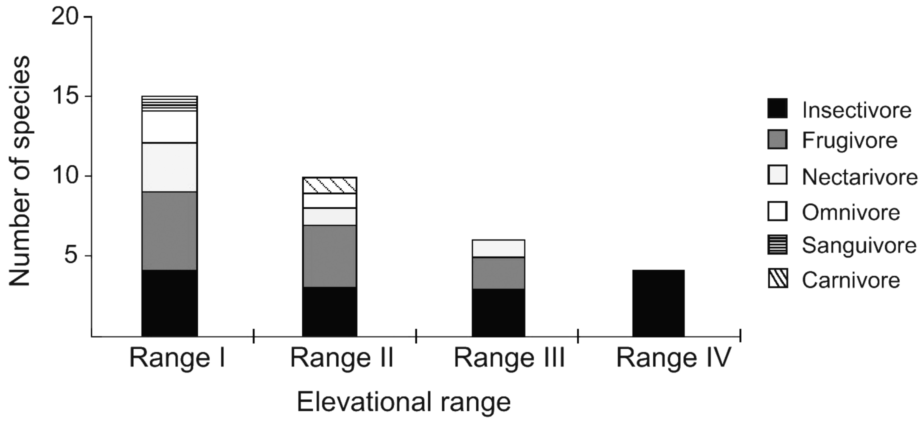

FIG. 2. Number of species per trophic guild recorded in each altitudinal range in Itatiaia National Park from 2009 to 2012

1999), which may favor their occurrence at high altitudes (Sánchez and Giannini, 2014).

The predominance of Phyllostomidae may be a bias of the capture method used. Mist nets set up in the understory favor the capture of phyllostomids (Simmons and Voss, 1998), as most of these bats use the understory to forage and cannot easily detect mist nets, differently from bats of other families. A reduction in the number of phyllostomid species is expected at higher altitudes due to a lower availability of food resources and lower temperature in relation to lowlands (Graham, 1983; Patterson *et al*., 1996; Sánchez-Cordeiro, 2001). Bats of the family Phyllostomidae have higher richness and abundance in warm Neotropical areas (Pereira and Palmerim, 2013) as they do not stand very low temperatures, in spite of being able to regulate their metabolism. This is probably so because of their food, mainly plants, is also limited by altitude and temperature, which leads to food scarcity for frugivorous and nectarivorous species at high altitudes, where plant diversity is lower (Soriano, 2000).

In general Vespertilionidae, whose species are predominantly insectivorous, were broadly distributed in all altitudinal ranges within the studied gradient. This pattern has been found in several studies on bat communities in the high altitudes in the tropics (e.g., Soriano, 2000; McCain, 2007; Bejarano-Bonilla *et al*., 2007). According to Soriano (2000), vespertilionids may be better adapted to higher altitudes with colder climate, because they have broad distribution outside the Neotropics (Arita *et al*., 2014), and many species occupy montane and cold regions in the tropics. The main reason of the insectivorous Molossidae have been recorded in the present study at the highest elevational range, is because they were captured in mist nets set up in front of the exit or near of possible roosts in roof linings of human building. In this places the probability of sampling Molossidae is higher, as the bat species of this family frequently use human residences as roosts (Esbérard, 2003). Molossids are aerial insectivorous and, therefore, have peculiar flight and foraging habitats, which hinders their capture with mist nets. All four individuals of *Tadarida brasiliensis* captured in elevational range IV were caught in mist nets set up in front of the possible roost in roofs.

The mist-netting method linked in line in zigzag formation, detailed by Alberdi *et al*. (2013), showed great success in open environments, particularly for catching low-flying bats in their foraging grounds, in high-mountain areas. Low-flying bats have higher probability of being caught. In the present study, if we have used this method in the highest range in extensive habitats, probably could improve capture success. In this elevational range we captured bats placing nets near the possible roots and water.

The hematophagous species were captured only in lower elevational range. According to Soriano (2000), hematophagous bats are less adapted to high

TABLE 3. Results of the analysis of similarity (ANOSIM) in bat species composition between elevational ranges in Itatiaia National Park from 2009 to 2012

Elevational ranges	*R*-value	*P*-level
I, II	0.193	0.01
I, III	0.376	0.001
I, IV	0.912	0.002
II, III	0.104	0.13
II, IV	0.706	0.002
III, IV	0.381	0.027

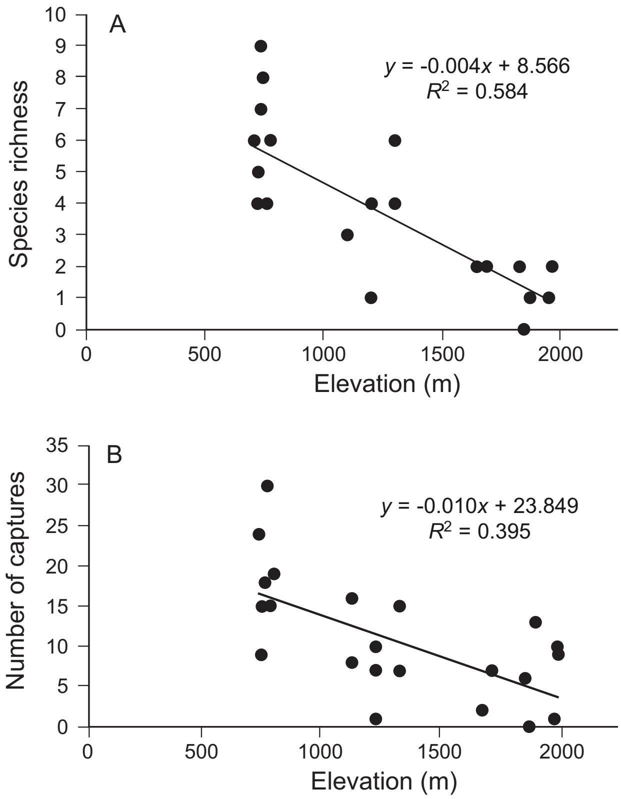

FIG. 3. Simple linear regression between bat richness and altitude (A), and number of individuals and altitude (B) showing the negative relationship in Itatiaia National Park from 2009 to 2012

altitudes because they have slow metabolism and would need abundant food (blood) to compensate for heat loss at low temperatures at high altitudes, where food abundance is extremely low. Carnivorous bats usually occur at low to medium altitudes, where the abundance of prey (amphibians, lizards, birds, rodents, and other bats) is usually higher than in montane environments (Soriano, 2000).

In spite of the difference in species composition, our results point to higher similarity between the elevational ranges II and III. Therefore, it is possible to say that there is higher turnover of bat species between these elevational ranges. According to Lomolino (2001), biotic turnover is not uniform along the elevational gradient. The amount of turnover between biotas depends directly on the richness of the overlapping communities. With an increase in elevation, the potential turnover between higher communities should decrease.

It is important to highlight that most studies in tropical areas recorded higher bat richness at low altitudes in Central America and northern South America (e.g., Graham, 1990; Patterson *et al*., 1996; Contreras and Huerta, 2001; Pinares, 2006). In Brazil, the few studies available point also to a negative relationship between bat richness and elevation (Dias *et al*., 2008; Bordignon & França, 2009). Several studies discuss the possible causes for the decrease in richness and abundance with elevation. Those studies did not point to a single factor, but to a set of factors that interact with each other, such as reduction in habitat heterogeneity, climate, decrease in area, lower productivity, evolutionary processes, niche partitioning and roost microclimate (Rahbek, 1995; Contreras and Huerta, 2001; Heaney, 2001; Lomolino, 2001; McCain and Grytnes, 2010; Dunn and Waters, 2012; Piksa *et al*., 2013; Cisneros *et al*., 2014; Sánchez and Giannini, 2014).

Our research shows that there is a variation in bat species richness and composition along the altitudinal gradient in Itatiaia Park. According to the description of the sampled area in the present study, we noted a change in habitat heterogeneity along the altitudinal gradient. It is probably one of the strong ecological factors that affects the bats species richness and functional composition in Itatiaia Park. In spite of logistic difficulties of carrying out fieldwork at highlands, the results presented here draw attention to the importance of sampling bats in these localities to better understand elevational gradients and to advance the knowledge of several aspects of bat biology. Our results also reinforce the importance of studying the relationship between species richness and elevation, which is poorly explored in bat studies in Brazil.

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