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Differences in the structure of the bat community between a cloud forest refuge and a surrounding semi-arid Caatinga scrubland in the northeastern Brazil

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ABSTRACT

The present study compared the structure of the bat communities in semi-arid Caatinga scrub and humid cloud forest habitats in the northeastern Brazilian state of Sergipe. A sampling effort of 185,790 h.m2 resulted in the capture of 157 bats representing 12 species in the Caatinga, and 259 individuals belonging to 14 species in the cloud forest. Overall, a total species richness of 18, although highly significant differences were recorded between habitats in the abundance of individuals. *Glossophaga soricina* was the most abundant species in the Caatinga, while *Carollia perspicillata* was the most abundant in the cloud forest. The Glossophaginae was the principal group in the Caatinga, and the Stenodermatinae in the cloud forest. Frugivores were the most abundant in the cloud forest, and many of these species appeared to be concentrated in this habitat during the dry season, dispersing into the Caatinga during the rainy season. Nectarivores were more abundant in the Caatinga during both seasons, indicating that, even during the dry season, this habitat provides an adequate resource base to support this guild. The present study of the Serra da Guia reinforces the importance of these enclaves of humid forest on the diversity and ecology of Caatinga bats.

1. Introduction

The semi-arid Caatinga scrublands of northeastern Brazil cover an area of almost one million square kilometers, but while this biome has suffered intense anthropogenic impacts over the past few centuries, its fauna and flora are still relatively poorly-known (Sá et al., 2004). The most recent data indicate the occurrence of 81 bat species in the Caatinga biome (Paglia et al., 2012; Moratelli and Dias, 2015; Feijó et al., 2015a; 2015b; Rocha et al., 2015a), as compared with 101 species for the neighboring Cerrado savanna, and 113 for the Brazilian Atlantic Forest. In addition to the scarcity of studies of the local chiropteran fauna, most surveys have been conducted in the vicinity of the regions principal urban centers (Leal et al., 2005).

The Caatinga is characterized by an unpredictable and low precipitation regime, with annual rainfall of 400–800 mm, generally concentrated into a short, irregular rainy season. This marked seasonality, together with the intense solar radiation and highly permeable soils typical of the region, tends to impose strict limitations on the characteristics of its fauna and flora (Rodal and Melo, 1999). These characteristics originally led many authors to consider the Caatinga to be a region of relatively reduced faunal diversity and low rates of endemism (Mares et al., 1981; Willig and Mares, 1989). In one of the earliest studies of the chiropteran fauna of the Caatinga, in the Brazilian state of Pernambuco, Willig (1983) recorded 33 species in distinct types of habitat over a three-year period. Over the subsequent three decades, taxonomic revisions, the identification of new species, and inventories (Feijo et al., 2015a; Williams et al., 1995; Marinho-Filho and Sazima, 1998; Oliveira et al., 2003; Sousa et al., 2004; Gregorin and Ditchfield, 2005; Sá-Neto and Marinho-Filho, 2012; Novaes and Laurindo, 2014) more than doubled this total, although up until now, only a few sites have been surveyed systematically, and there are few data from the southern half of the biome, south of the São Francisco River, which includes the Brazilian state of Sergipe.

Small enclaves of humid or cloud forest – known locally as "brejos de altitude" – can be found at a number of localities throughout the semiarid Brazilian Caatinga domain (Andrade-Lima, 1982). These

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enclaves are typically located on high plateaus subject to the formation of orographic precipitation, which results in relatively humid environments suitable for the establishment of dense rainforest, quite distinct from the typical Caatinga scrub (Sales et al., 1998). The vegetation of these enclaves may include elements typical of the Caatinga, Atlantic Forest, and Amazonian Hylea (Tabarelli and Santos, 2004; Rodal et al., 2005; Rodrigues et al., 2008). Historically, these enclaves appear to have expanded considerably during periods of more humid climate, providing the basis for formation of corridors of rainforest vegetation linking the Atlantic Forest to the Amazon basin (Clapperton, 1993; Vivo, 1997), and more recently, refuges for different components of the faunas of these biomes. Here, the chiropteran fauna of a small cloud forest enclave was surveyed in the Brazilian state of Sergipe, and compared with that of the surrounding Caatinga scrub, and the differences in the composition of species and guilds are discussed in the context of the ecological contrasts between sites.

2. Material and methods

2.1. Study site

Serra da Guia (9°58′ S, 37°52’ W) is a small mountain range located within the semiarid Brazilian Caatinga biome, which straddles the frontier between the states of Sergipe (municipality of Poço Redondo) and Bahia, in Pedro Alexandre (Fig. 1). Altitudes vary from 300 m above sea level at the base of the range, to 750 m asl, at the summit.

Two sampling points were selected within the study area (Fig. 2), based on differences in elevation and habitat type. Point 1 (Fig. 2A) was located at the base of the range (300 m asl), in typical Caatinga scrub, characterized by a predominance of shrubs and small trees of the families Fabaceae and Euphorbiaceae, in particular *Caesalpinia pyramidalis* (catingueira) and *Amburana cearensis* (umburana), as well as ouricuri palms, *Syagrus coronata*. This natural vegetation is interspersed with extensive areas of cattle pasture and smaller subsistence plots plant with maize and beans.

Point 2 (Fig. 2B) was located at 750 m asl, and covers an area of approximately 20 ha. This humid forest has emergent trees of between 10 m and 20 m in height, with a predominance of the Fabaceae and Poaceae families, and 13 species of orchid (Machado et al., 2012). This study found a similarity of only 26.7% in the composition of the two habitats, and considerable differences in their phytosociological structure. Mean annual precipitation in the study area is approximately 500 mm, with a wet season typically between April and August, and a dry season during the rest of the year, from September to March.

2.2. Data collection

This study was authorized by the Chico Mendes Institute for Biodiversity Conservation - ICMBio (licence number 8516-1), and adhered to the current legislation of the Brazilian Committee for Animal Experimentation. Bats were sampled in the of shrubby Caatinga and cloud forest at Serra da Guia between October, 2008, and September, 2009, following a standardized monthly schedule in which mist-nets (2.5 m high and 100 m long) were set along a trail system within an area of typical habitat between 18:00 h and 05:00 h on three consecutive nights during the new moon. During the first six h of each session, the nets were visited every 20 min for the removal of captured bats, but after midnight, the nets were only checked every 90 min, given that the capture rate declined considerably during this part of the night. All captured specimens were placed in cotton bags until the following morning for processing.

Each specimen was examined and identified to the species level, and its sex, age, reproductive condition, weight, and forearm length were recorded. The specimens were marked with numbered plastic rings, which were attached to the distal portion of the forearm and then released. Voucher specimens (no more than four individuals per species) were collected for taxonomic verification. These specimens were euthanized by asphyxia with ethyl ether, fixed in 10% formaldehyde and preserved in 70% ethanol. The individuals were deposited as voucher specimens in the Adriano Lúcio Peracchi collection (ALP) at the Federal Rural University of Rio de Janeiro in Seropédica, Brazil. Identification was based on the keys of Anderson (1997), Simmons and Voss (1998), Lim and Engstrom (2001), and Gardner (2007).

2.3. Data analyses

Sampling effort was calculated by multiplying the total area of the mist-nets by the number of hours they were set (Straube and Bianconi,

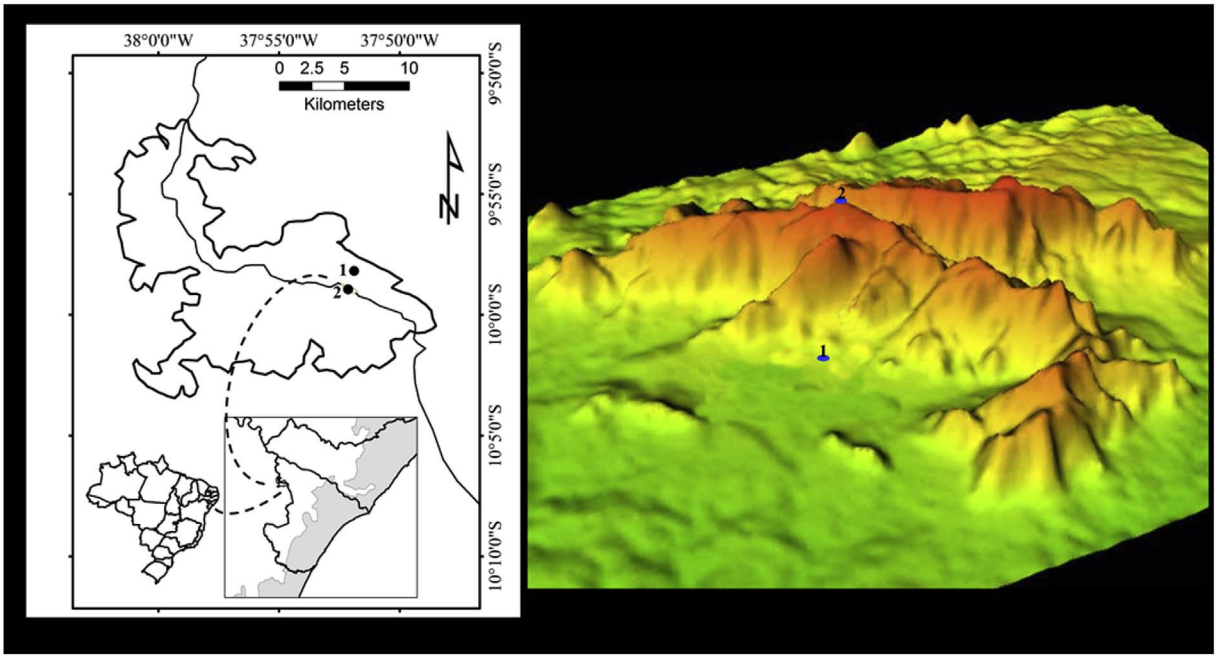

Fig. 1. Location of the two study sites at Serra da Guia, Poço Redondo, Sergipe, northeastern Brazil. (1) Caatinga and (2) cloud forest.

Fig. 2. Caatinga (A) and cloud forest (B) habitats at Serra da Guia, Poço Redondo, Sergipe, Brazil.

2002). Species were considered dominant if their relative abundance was higher than 1/S, where S = species richness (Uramoto et al., 2005).

The Shannon-Wiener diversity index, Jackknife 1 species richness estimator and species accumulation curves (observed and estimated) based on 1000 replications (see Colwell and Coddington, 1994) were run in the EstimateS 8.0 program (Colwell, 2005). Shannon-Wiener's equitability (*E*) was obtained using the equation $E = H'/\ln S$, where *H'* = Shannon-Wiener diversity index and LnS = natural logarithm of species richness. The differences in the species composition between sites were evaluated using a Non-Metric Multidimensional Scaling (NMDS), based on the abundance data, using the Bray-Curtis distance as a measure of similarity. The significance of the dissimilarity between sites was tested using an Analysis of Similarities (ANOSIM). These analyses were run in PAST (Hammer et al., 2001).

The bat species recorded were classified according to their feeding niche, based on Nowak (1994), as insectivore, frugivore, nectarivore or sanguivore. The analysis of the relative contribution of the different guilds to the two bat communities was based on both the abundance and total biomass (sum of the body weights of the specimens captured for each species). The plant-feeding bats (frugivores + nectarivores) were grouped by body size as (a) large (forearm length > 55 mm), (b) medium (forearm length 40–55 mm), and (c) small, with forearm length < 40 mm (adapted from Fleming et al., 1972).

Between-season differences in species diversity (*H'*) were evaluated using a modified *t*-test (Zar, 1996). Differences in abundance and/or biomass were tested using Chi-square. This tests were run in BioStat 5.0 (Ayres et al., 2007), considering $\alpha = 0.05$ (Zar, 1996).

3. Results

The study was based on a total sampling effort of 185,790 h m^2, resulting in the capture of 416 individuals belonging to three families, 14 genera, and 18 species. Overall, Shannon-Wiener's diversity was 2.01, with equitability of 0.69 reflecting the presence of few abundant species and many rare species. The Phyllostomidae was the most diverse family, with 412 specimens belonging to 16 species, representing 88.8% of the species richness and 99.0% of the abundance. The two other families (Emballonuridae and Vespertilionidae) were each represented by only a single species (Table 1). The Jackknife 1 procedure estimated a total of 21.7 species (Fig. 3), a significantly higher number than that actually recorded, i.e., 18 ($t = -6.27$, $df = 22$, $p < 0.05$).

Overall, 12 species were recorded in the Caatinga and 14 in the cloud forest. There was no significant difference in species richness ($\chi^2 = 0.15$; $df = 1$; $p > 0.05$), as confirmed by the expected species abundance curves (Fig. 3).

While no significant difference was found in species diversity ($t = -1{,}11$; $p > 0.05$), considerable variation was observed between habitats in species composition and community structure. Eight of the 18 bat species recorded at Serra da Guia were encountered in both habitats, four were exclusive to the Caatinga, and six to the cloud forest (Table 1). While phyllostomids predominated in both habitats, a significantly ($\chi^2 = 25.56$; $df = 1$; $p < 0.05$) larger number of bats were captured in the cloud forest (n = 257) in comparison with the Caatinga (n = 155).

This predominance of the cloud forest bat species persisted throughout most of the study period (Fig. 4), with the number of specimens being captured in the Caatinga surpassing that of the cloud forest in only three months, December, February, and July. Two main patterns can were observed here. One was a gradual decline in abundance during the dry season, followed by a peak in the subsequent months, when precipitation increased. This peak in abundance was most pronounced in the Caatinga, with a threefold increase in numbers in July, in comparison with all other months. The second pattern was a more prolonged peak in abundance in the cloud forest. In fact, the period between August and November accounts for the majority of the difference in abundance between habitats. Between December and June, while bats were still more abundant in the cloud forest in most months, they were far less numerous in general, and the difference between sites was much less pronounced in most months.

The larger numbers of bats found in the cloud forest were due entirely to the relative contribution of the frugivorous stenodermatines and carollines, whereas the Caatinga community was dominated by nectarivores, in particular the glossophagines and *Lonchophylla mordax*, the only lonchophylline recorded in the study, which was exclusive to the Caatinga. Insectivorous bats were also predominant in the Caatinga, and *Desmodus* was also much more common (Fig. 5).

The structure of the two communities was also quite distinct in terms of the relative contribution of the different species and guilds. In the cloud forest, the frugivore guild predominated, with 90% (n = 233) of the individuals captured, of which, 151 (60%) belonged the subfamily Stenodermatinae. In the Caatinga, the nectarivore guild was the most abundant, with 74 individuals, or 47% of the total (Fig. 6). Only three (*Carollia perspicillata*, *Glossophaga soricina* and *Desmodus rotundus*) of the eight species common to both habitats were captured in both dry and rainy seasons. While they were dominant in the cloud forest, the frugivores *Artibeus lituratus* and *Platyrrhinus lineatus* were only captured in the Caatinga during the rainy season, and even then, were rare, with two and six individuals being caught, respectively (Fig. 5).

The abundance of six of the eight universal species varied significantly between habitats, with *Carollia perspicillata* ($\chi^2 = 27.69$; $df = 1$; $p < 0.05$), *Artibeus lituratus* ($\chi^2 = 40.33$; $df = 1$; $p < 0.05$), *Platyrrhinus lineatus* ($\chi^2 = 54.87$; $df = 1$; $p < 0.05$), and *Artibeus cinereus* ($\chi^2 = 9.94$; $df = 1$; $p < 0.05$) being more abundant in the cloud forest, and *Desmodus rotundus* ($\chi^2 = 4.56$; $df = 1$; $p < 0.05$) and *Glossophaga soricina* ($\chi^2 = 38.4$; $df = 1$; $p < 0.05$) being more common in the Caatinga (Fig. 5). Only *Carollia perspicillata* was among the three most abundant species in both habitats. While *Lonchophylla*

Table 1
Bat species recorded during the present study at Serra da Guia, Poço Redondo (Brazil), showing their feeding guilds and the number of records collected.

Species	Number of individuals captured:			Relative abundance (%)	Guild
	Cloud forest	Caatinga	Total		
Family Emballonuridae					
Peropteryx macrotis (Wagner, 1843)		1	1	0.2	Insectivore
Family Phyllostomidae					
Subfamily Desmodontinae					
Desmodus rotundus (E. Geoffroy, 1810)	12	25	37	8.9	Hematophagous
Subfamily Phyllostominae					
Lophostoma brasiliense (Peters, 1866)	1		1	0.2	Insectivore
Subfamily Micronycterinae					
Micronycteris microtis Miller, 1898	1		1	0.2	Insectivore
Micronycteris aff. *sanborni* (Simmons, 1996)		8	8	1.9	Insectivore
Subfamily Glossophaginae					
Anoura geoffroyi (Gray, 1838)	2	1	3	0.7	Nectarivore
Glossophaga soricina (Pallas, 1766)	6	54	60	0.144	Nectarivore
Dryadonycteris capixaba Nogueira et al., 2012	2		2	0.005	Nectarivore
Subfamily Lonchophyllinae					
Lonchophylla mordax (Thomas, 1903)		19	19	0.046	Nectarivore
Subfamily Carollinae					
Carollia perspicillata (Linnaeus, 1758)	95	35	130	0.313	Frugivore
Subfamily Stenodermatinae					
Dermanura cinerea (Gervais, 1855)	15	2	17	0.041	Frugivore
Artibeus planirostris (Spix, 1823)	3		3	0.007	Frugivore
Artibeus lituratus (Olfers, 1818)	46	2	48	0.115	Frugivore
Artibeus obscurus (Schinz, 1821)	1		1	0.002	Frugivore
Platyrrhinus lineatus (E. Geoffroy, 1810)	71	6	77	0.185	Frugivore
Sturnira lilium (E. Geoffroy, 1810)	2		2	0.005	Frugivore
Uroderma magnirostrum Davis, 1968		3	3	0.007	Frugivore
Family Vespertilionidae					
Myotis lavali (Moratelli, Peracchi, Dias & de Oliveira, 2011)	2	1	3	0.007	Insectivore
Total abundance	**259**	**157**	**416**		
Species	**14**	**12**	**18**		
Estimated species richness (Jackknife 1)	**16.7**	**14.7**	**21.6**		
Diversity (Shannon-Wiener)	**1.69**	**1.8**	**2.01**		

mordax was the fourth most abundant species in the Caatinga (n = 19), it was not captured in the cloud forest. *Myotis lavali* was the only insectivore captured in both habitats (Fig. 5).

Nectarivores were present in the Caatinga throughout the year, with no seasonal variation in abundance (see Rocha et al., 2015bb). This guild was much rarer in the cloud forest, however, where it increased slightly during the rainy season (Fig. 5). While frugivores were abundant in the cloud forest throughout the year, they tended to be restricted to this habitat during the dry season. During this season, only *Carollia perspicillata* (n = 8) and *Dermanura cinerea* (n = 2) were captured in the Caatinga (Fig. 5). Other frugivores, such as *Artibeus lituratus and Platyrrhinus lineatus*, were only captured in the Caatinga after the seventh month of the study, at the beginning of the rainy season. It is interesting to note that two of the six *Platyrrhinus lineatus* captured in the Caatinga were recaptures coming from the cloud forest.

Sanguivorous bats were more abundant during the dry season in both habitats, although they were more common in the Caatinga. The insectivore guild was the least abundant, with *Micronycteris* aff. *sanborni* (n = 8) being the most common, captured in the Caatinga in both seasons.

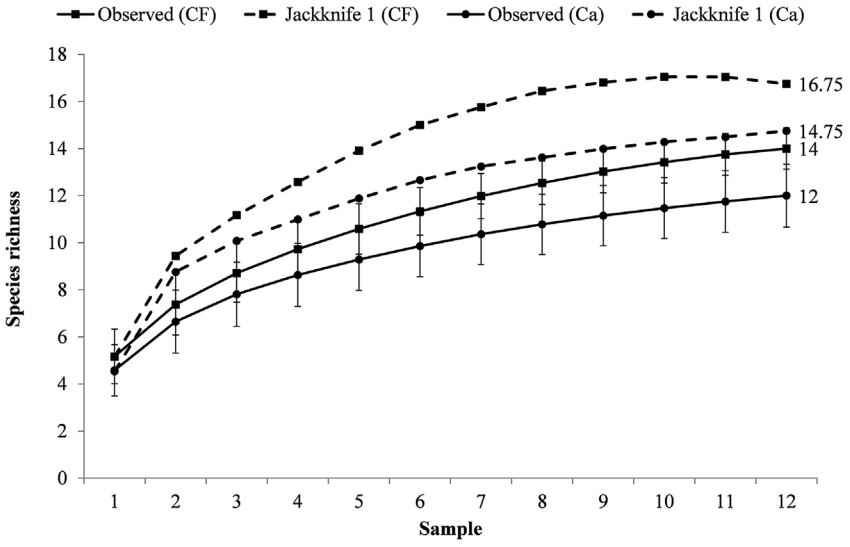

Fig. 3. Observed and expected (Jackknife 1) bat species richness at Serra da Guia, Poço Redondo, Sergipe (Brazil). CF = Cloud Forest, Ca = Caatinga.

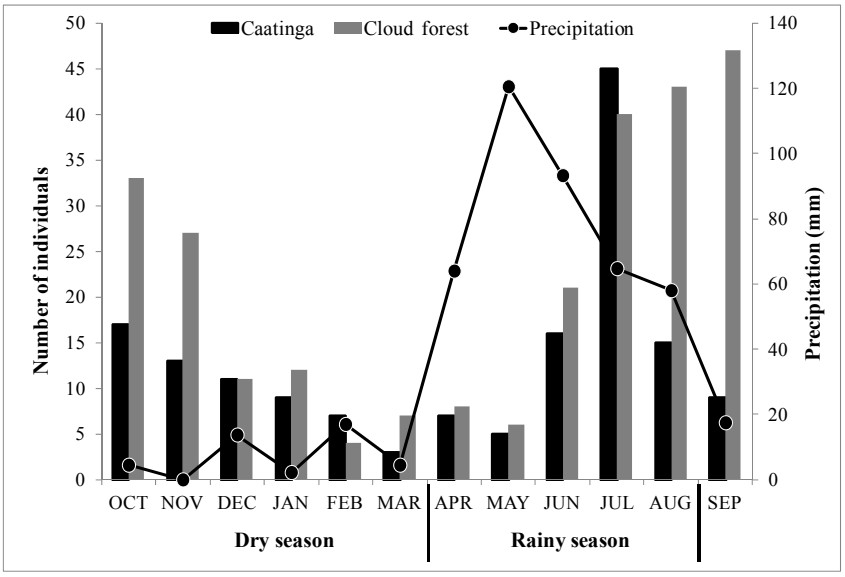

Fig. 4. Number of individuals captured per month in the habitats of Caatinga and cloud forest habitats at Serra da Guia, Sergipe, and monthly precipitation recorded during the study period, between October 2008, and September 2009.

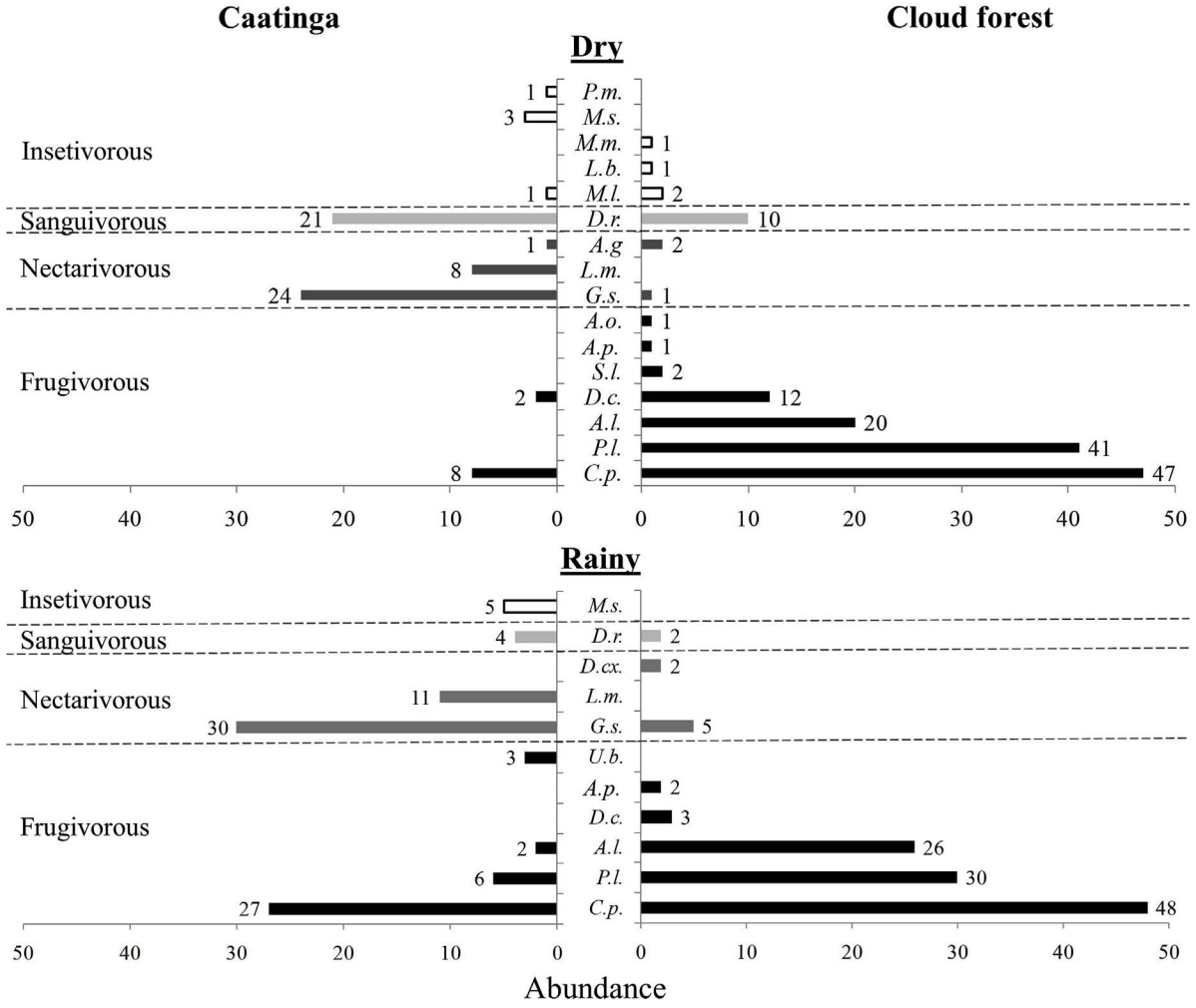

Fig. 5. Abundance of bats in the Caatinga and cloud forest at Serra da Guia, Poço Redondo, Sergipe (Brazil), during the dry and rainy seasons. C.p.: *Carollia perspicillata*; P.l.: *Platyrrhinus lineatus*; A.l.: *Artibeus lituratus*; D.c.: *Dermanura. cinerea*; A.p.: *Artibeus planirostris*; A.o.: *Artibeus obscurus*; U.m.: *Uroderma magnirostrum* S.l.: *Sturnira lilium*; G.s.: *Glossophaga soricina*; L.m.: *Lonchophylla mordax*; D.cx: *Dryadonycteris capixaba*; A.g.: *Anoura geoffroyi*; D.r.: *Desmodus rotundus*; M.l. *Myotis lavali*; L.b.: *Lophostoma brasiliense*; M.m.: *Micronycteris microtis*; M.s.: *Micronycteris* aff. *sanborni;* P.m.: *Peropteryx macrotis*.

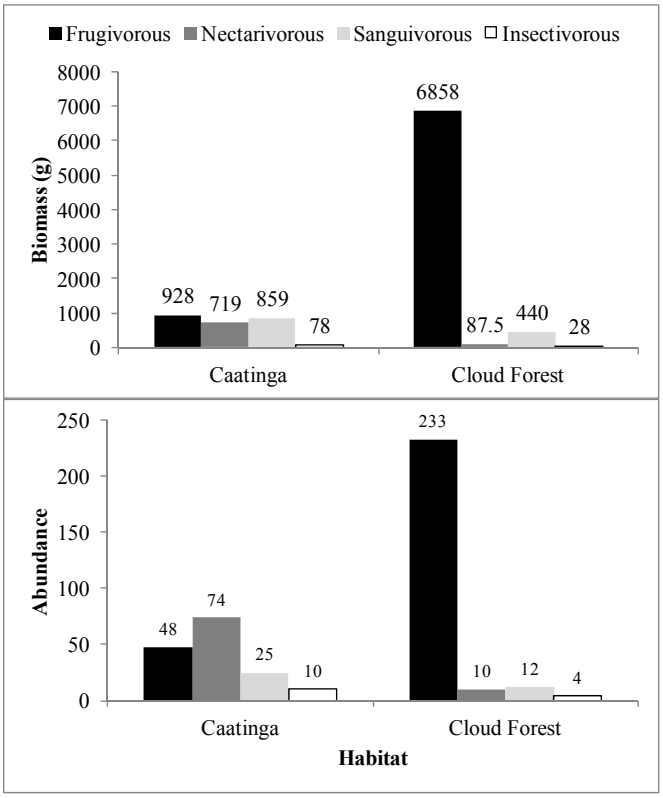

Fig. 6. Biomass (g) and abundance of bat guilds in the Caatinga and cloud forest habitat of Serra da Guia, Poço Redondo, Sergipe (Brazil).

If total biomass is considered rather than abundance, the contrasts between the communities increase even further (Fig. 6). While frugivores are 4.8 times more abundant in the cloud forest, the biomass of this guild is 7.2 greater, reflecting the relatively larger body size of the species.

Small plant feeders (forearm < 40 mm) were the most abundant in the Caatinga throughout the year, with no significant variation between seasons (χ^2 = 0.65; df = 1; p > 0.05), whereas the abundance of medium-sized feeders (forearm 40–55 mm), while rare overall, was significantly greater during the rain season (χ^2 = 18.75; df = 1; p < 0.05), when they were as common as the smaller-bodied individuals. Large plant feeders (forearm > 55 mm) were represented only by two *A. lituratus,* captured during the rain season (Fig. 7).

In the cloud forest, medium-sized plant feeders, principally *C. perspicillata* and *P. lineatus*, predominated, followed by the larger class,

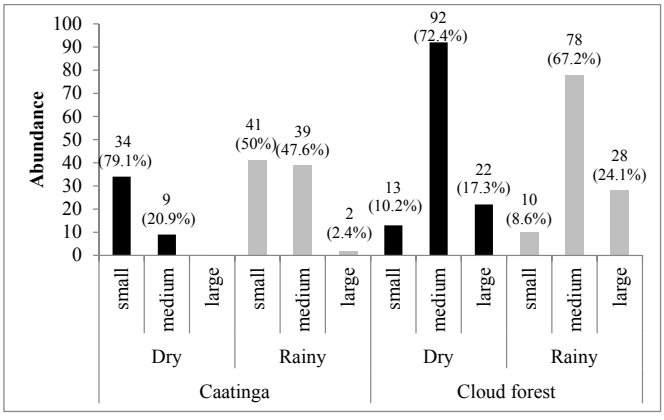

Fig. 7. Seasonal variation in the abundance of plant-feeding bats of different sizes in the Caatinga and cloud forest habitats at Serra da Guia, Poço Redondo (Brazil).

primarily *A. lituratus* (Fig. 7). In this habitat, no significant seasonal variation was found in the distribution of the size classes. (small: χ^2 = 0.39, df = 1, p > 0.05; medium: χ^2 = 1.15, df = 1, p > 0.05; large: χ^2 = 0.72, df = 1, p > 0.05).

The NMDS plot (Fig. 8) shows the differences in the structure of the two communities. The ANOSIM confirmed that the difference in the structure of the two communities was highly significant (R = 0.69; p = 0.001).

4. Discussion

The compilation of species inventories from an ecologically diverse area may provide misleading insights into the structure and dynamics of local communities. In the present study, the comparison of the structure of the Caatinga and cloud forest communities revealed clear differences on a microgeographic scale within the study region. While no significant differences were found between habitats in the species diversity, considerable variation was found between habitats in the abundance of different species, guilds, and body size classes.

Most of the 18 bat species recorded during the present study are amply distributed in South America (Marinho-Filho and Sazima, 1998; Paglia et al., 2012), and most can be considered to be common in the Caatinga, in particular *G. soricina*, *A. lituratus*, *P. lineatus*, *C. perspicillata*, and *D. rotundus* (Oliveira et al., 2003). However, the exclusive presence of *D. capixaba* in the cloud forest enclave reinforces the association of these species with forest habitats (Marinho-Filho and Sazima, 1998; Nogueira et al., 2012). In fact, Rocha et al. (2014) concluded that populations of this species may be restricted to cloud forest enclaves within the Caatinga, and are thus isolated and vulnerable.

Of the six most abundant species found at Serra Guia, only *C. perspicillata* was dominant in both habitats, while two (*P. lineatus* and *A. lituratus*) were considered dominant only in the cloud forest, and the remaining three (*G. soricina*, *L. mordax*, and *D. rotundus*) in the Caatinga. Interestingly, the dominant species in the cloud forest are medium-large sized frugivores, while those in the Caatinga are nectarivores and hematophages.

Habitat diversity is an intrinsic characteristic of the Caatinga scrublands (Silva et al., 2003; Araújo et al., 2005). This heterogeneity contributes to the formation of a mosaic of habitats that provide distinct conditions and resources, supporting micro-scale variation in community structure. In a pioneering comparative analysis of Caatinga habitats in Pernambuco, Willig (1983) found marked variation in the composition of communities, and identified preferences of some species for certain habitats. In an area of Caatinga scrub and deciduous forest in Ceará, Silva et al. (2004) only captured frugivores (such as *A. lituratus* and *P. lineatus*) in the more humid habitats during the dry season. Gregorin et al. (2008) captured much larger numbers of frugivores in the more humid habitats of the Serra das Confusões National Park in the Brazilian state of Piauí.

The habitat heterogeneity hypothesis predicts that the number of species found in a landscape will increase as the number of habitats increases (MacArthur and MacArthur, 1961). In this context, Cramer and Willig (2005) predicted that, in the absence of barriers to dispersal, the habitat preferences of some species may reduce their competitiveness in other environments, leading to distinct patterns of species abundance and composition among the habitats found within the landscape. In this case, the diversity of the landscape will be reinforced by the presence of specialists that prefer distinct habitats. As the two habitats at Serra da Guia are separated by only 1.5 km, which is unlikely to impede the dispersal of bats, it seems reasonable to conclude that the differences in community structure were linked directly to the seasonal variation in the availability of resources. Despite their proximity, Machado et al. (2012) found marked differences in the composition (Jaccard index = 0.267) and structure of the two habitats.

While no data are available on the phonological patterns of the two habitats, the proportion of zoochoric species in the cloud forest (88.8%)

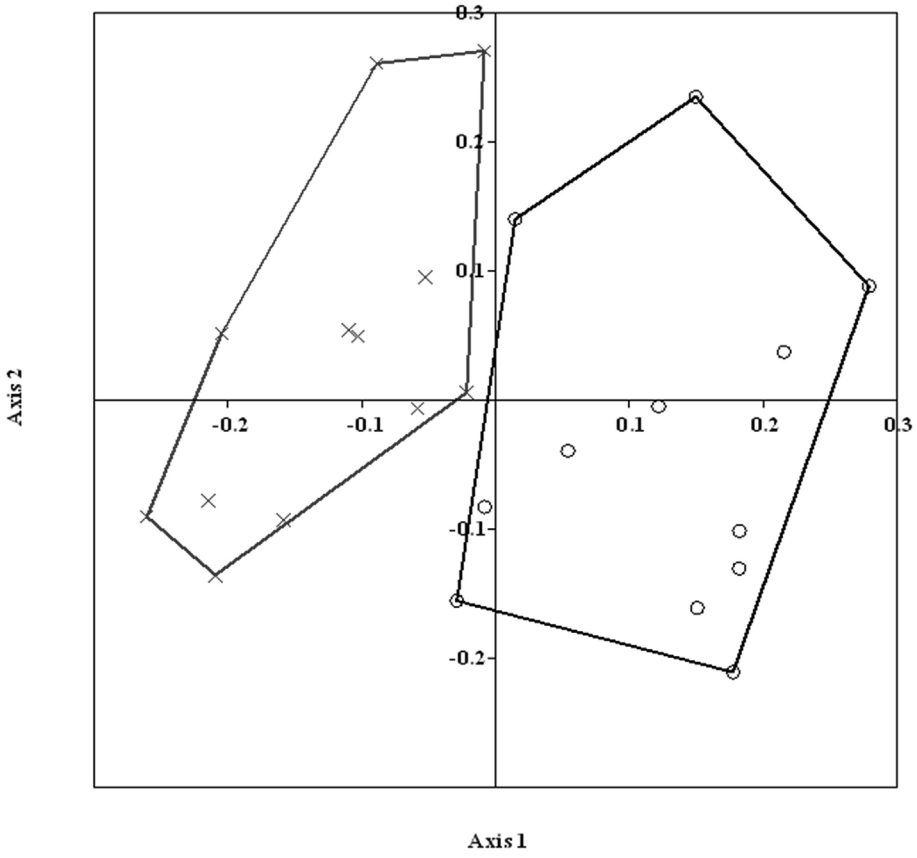

Fig. 8. The NMDS plot illustrating the differences in the structure of the bat communities in the Caatinga (circles) and cloud forest (X) habitats at Serra da Guia, at Serra da Guia, Poço Redondo (Brazil).

is significantly higher than that of the Caatinga (44.1%), where most species are dispersed by mechanical mechanisms (adapted from Machado et al., 2012). This obviously implies a richer resource base for frugivores in the more humid cloud forest, which is not deciduous during the dry season. By contrast, leaf-fall is a characteristic of the Caatinga during the dry season, when most woody species lose their leaves completely, and practically the whole of the herbaceous stratum dies off.

Vicente et al. (2003) found similar variation in the predominant plant dispersal syndromes between the Atlantic Forest and the Caatinga. Only around 20% of the plants were dispersed by vertebrates in the more arid environments, where anemochory predominated. In the more humid habitats, up to 80% of the plant species were zoochoric.

The distribution of feeding resources plays a fundamental role in structure and complexity of communities (Dumont, 2003), as shown by Willig et al. (2003) in equatorial forests, where the number of frugivores was related positively with the number of zoochoric species. In the present study, the cloud forest appears to have a resource base adequate for the maintenance of populations of medium- and large-bodied frugivorous bats. In the Caatinga, by contrast, the scarcity of resources for the guild, leads to its virtual exclusion during seven months of the year. The only frugivores founds in the Caatinga during the dry season were the small-bodied *A. cinereus* and *C. perspicillata*, which may be insectivorous under some circumstances (Gardner, 2007).

By contrast, nectarivores predominated in the Caatinga throughout the year, indicating the availability of resources for this group, even during the dry season. It seems likely that the large numbers of fertile bromeliads of the species *Encholirium spectabile*, which is known to be pollinated by bats (Silva, 2007), in the study area, together with the small fruits of certain climbers and mistletoes, may contribute to the occurrence of nectarivorous bats.

In general, a reduced resource base will tend to favor smaller-bodied species, such as nectarivores (Helversen and Winter, 2003), and this seemed to be the case of the plant-feeding guilds at Serra da Guia. During the dry season, 79% of the bats captured in the Caatinga were small in size, with only a few medium-sized individuals being observed. At the onset of the rainy season, when resource abundance increased, larger bats (*A. lituratus*, *P. lineatus*) appeared to expand their foraging activities into the Caatinga. This is reinforced by the recapture of two *P. lineatus*, encountered originally in the cloud forest.

Willig (1983) and Mares et al. (1985) proposed that cloud forests provide important refuges for many animal species, especially during the dry season. However, few empirical data are available on the influence of cloud forests on the structure and dynamics of Caatinga communities. Tabarelli and Santos (2004) identified 47 cloud forests in the Caatinga biome, although the bat fauna of only eight of these habitats has been inventoried, with species richness varying from two to 26 species (Sousa et al., 2004), and none of these studies have included the systematic collection of data on the surrounding Caatinga matrix or seasonal patterns. The present study reinforces the need for a more systematic approach to the understanding of the influence of these enclaves of humid forest on the diversity and ecology of Caatinga bats.

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