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The heterogeneity of Caatinga biome: an overview of the bat fauna

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Abstract: In semiarid regions like the Brazilian Caatinga, the long dry season suggests that it is a homogeneous environment. However, differences in climate, soil, relief, and duration of the dry season across this biome has prompted the division of Caatinga in eight ecoregions. Here, we test the validity of these ecoregions for bats, which play a fundamental role in the balance of ecosystems. A literature review was carried out to investigate the distribution of bat species in all Caatinga ecoregions, and the lack of sampling efforts. In total, 90 chiropteran species were recorded in the biome. Bat distribution is not homogeneous, and almost all ecoregions present exclusive species. Gaps in chiropteran sampling efforts occur in all ecoregions. A robust and significant correlation was observed between the number of studies reporting samples and bat richness of each ecoregion, indicating that more research will increase recorded richness in these areas, and in the Caatinga as a whole. The existence of at least four ecoregions in the Caatinga was also supported. This underlines the importance of these areas to conservation initiatives.

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Introduction

Chiroptera is surpassed only by rodents in richness and abundance among mammals (Peracchi et al. 2011). They play a fundamental role in the balance of ecosystems. Several tropical plant species are pollinated by bats (Dobat and Peikert-Holle 1985). Additionally, numerous species feed on fruit and spread seeds through their feces to different areas, promoting the recovery of deforested areas and the maintenance of the more advanced succession stages (Fleming 1988, Sato et al. 2008). Moreover, insectivore bat species act as controlling agents against insect populations, some of which are pests in agriculture (Cleveland et al. 2006, Boyles et al. 2011).

Brazil comes second in chiropteran species richness, with approximately 15% of known species (Alberico et al. 2000). Nine families, divided into 68 genera and more than 170 species occur in the country, and distribute across its biomes (Nogueira et al. 2014). In the Caatinga, bats stand out against other mammals as to species richness. In that biome, chiropterans represent as much as 45% of all mammals (Oliveira et al. 2003). However, the Caatinga is one of the Brazilian biomes that has least been studied in terms of bat fauna, with several knowledge gaps (Pacheco et al. 2008, Garcia et al. 2014).

The Caatinga is the only biome that exists solely within the Brazilian territory (Leal et al. 2003). It is formed by seasonally dry tropical forests whose physiognomy and floristic composition varies considerably, from open, shrub-like covers, to closed-canopy forest patches (Bullock et al. 1995). The Caatinga climate is characterized by long dry seasons (Eiten 1982) and irregular rainfall (Andrade-Lima 1981), which is concentrated between November and June (Ab'Sáber 1977).

Many studies underscore the fact that the Caatinga exhibits a considerable number of physiognomies (Egler 1951, Hueck 1972, Andrade-Lima 1981, Rizzini 1997, Rodal and Sampaio 2002, Prado 2003). In order to conserve and to better understand the biodiversity of the Caatinga, Velloso et al. (2002) divided the biome into eight natural ecoregions: Chapada Diamantina Complex (CDC), Campo Maior Complex (CMC), Ibiapaba-Araripe Complex (IAC), Southern Sertaneja Depression (SSD), Northern Sertaneja Depression (NSD), São Francisco Dunes (SFD), Borborema Highlands (BOH), and Raso da Catarina (RAC) (See Supplemental Text S1 for details). These ecoregions were defined based on soil types, climate, temperature, relief, altitude, rainfall, and fauna and flora taxonomic groups typically observed in the regions covered by the biome.

This division of the Caatinga into ecoregions was totally of partially supported for plants, invertebrates and vertebrates (Queiroz 2006, Hernández 2007, Cardoso et al. 2008, Ferreira et al. 2009, Maciel et al. 2012, Santos et al. 2012, Guedes et al. 2014).

In this study, bat richness in the Caatinga and in the ecoregions was determined. We investigated the relationship of species richness with the area of each ecoregion and with the number of studies carried out. We identified the Caatinga zones where bats have been poorly studied, underscoring the species with wide and restricted distribution as well as the importance of these data in conservation efforts. Finally, we verified whether the ecoregions model proposed by Velloso et al. (2002) is supported by bat species distribution pattern.

Materials and methods

Bat species richness in the eight Caatinga ecoregions was assessed reviewing data in articles, abstracts published in science events, books, book chapters, technical reports, monographs, dissertations and theses. The literature reviewed included studies in which bat populations were sampled and species of the order Chiroptera were recorded in the Caatinga. The information from these sources was analyzed with special care to detect synonymy, validations of genera and species, and restrictions and expansions of geographical distribution.

Based on the Caatinga ecoregions defined by Velloso et al. (2002) map that considered the geo-environmental units (Silva et al. 1993) was constructed using the softwares Google Earth® (Google Inc. 2013), Terra View (INPE 2010), Adobe® Photoshop® CS6 (Dayley and Dayley 2012), and ZANE (Silva et al. 2000). This map shows the municipalities where bats were sampled, and was used to identify areas where the bat fauna has been poorly investigated.

The methodology used assessed the correlations between (i) the area of each ecoregion and bat fauna richness, and (ii) the number of studies including bats and bat richness in each ecoregion. The Kolmogorov-Smirnov test was used to evaluate normality of data. Subsequently, Spearman' correlation coefficient (p value=95%) was calculated. Both analyses were conducted in the software Graphpad 5.01 (PRISM 2007). The classification of correlations was carried out according to Callegari-Jacques (2003).

The division of the Caatinga into ecoregions was validated considering the presence of exclusive bat species and performing two cluster analyses. Cluster analyses were based on the Euclidean distance and evaluated (1) bat species composition in each of the eight ecoregions, and (2) bat species composition in the ecoregions that have been more effectively surveyed. In this analysis, studies that investigated chiropterans more broadly in each ecoregion carried out by highly experienced researchers were selected, namely Guerra (2007) and Sá-Neto and Marinho-Filho (2013) for SSD; Fabián (2008) and Piccinini (1974) for NSD; Novaes and Laurindo (2014) and Novaes et al. (2015) for IAC; and Silva (2007), who investigated chiropteran diversity in two areas in BOH. Cluster analyses were computed using the Past software.

Results

Of the more than 1280 municipalities located in the Caatinga biome (CNRBC 2004), studies on bat fauna were carried out only in 119 (Figure 1). Among these, a little over 11% of townships were included in three or more studies. This survey identified 90 bat species in the biome, distributed in eight families: Phyllostomidae (51 species), Molossidae (14), Vespertilionidae (12), Emballonuridae (6), Mormoopidae (3), Noctilionidae (2), Furipteridae (1) and Natalidae (1) (Supplemental Table S1).

Ecoregions SFD and RAC were the least studied, and presented the lowest recorded chiropteran richness in the Caatinga (Supplemental Tables S1; S2). In SFD, only four species were recorded, with sampling gaps in much of this ecoregion (Figure 1). In RAC, 15 species were recorded. Bat occurrences remain to be established in a considerable area to the south of RAC.

Most studies on the bat fauna in CMC were carried out in its western portion, near the Amazon biome. Twenty-one chiropteran species were recorded, among which *Chiroderma vizottoi* (Taddei and Lim, 2010), which is endemic to the Caatinga, but has been recorded only in this ecoregion. *Eumops hansae* (Sanborn, 1932), *Nyctinomops aurispinosus* (Peale, 1848), *Saccopteryx canescens*

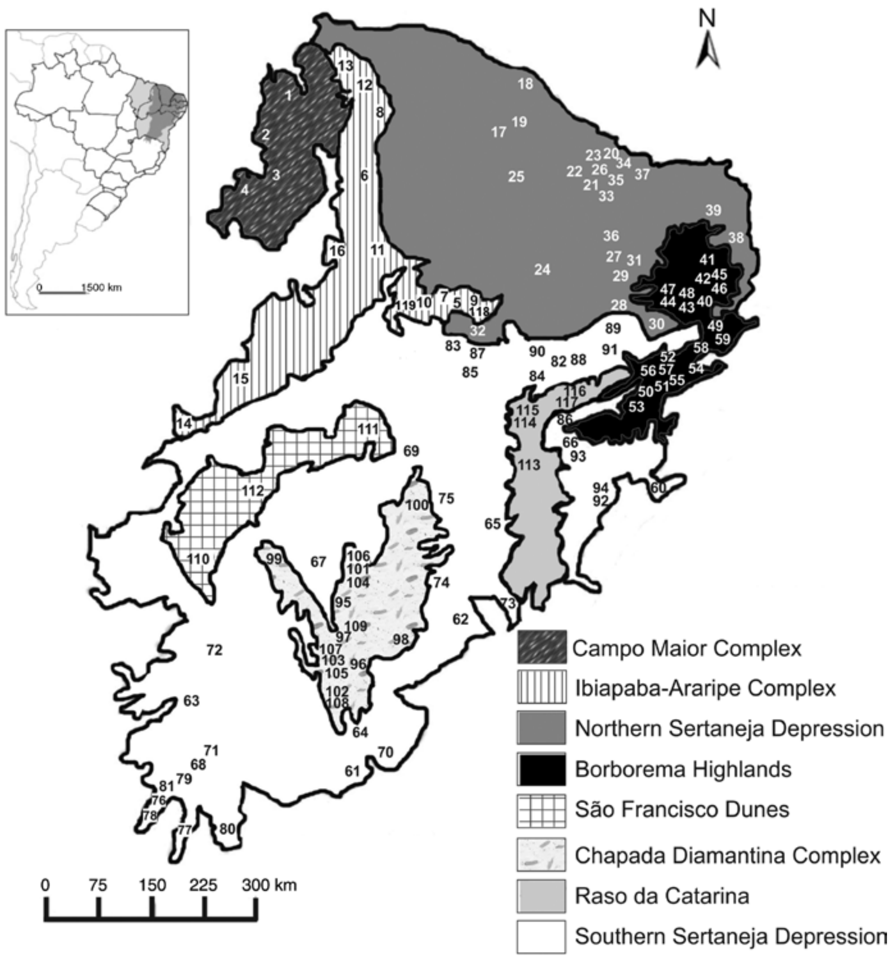

Figure 1: Map of Caatinga ecoregions and municipalities surveyed for chiropteran fauna.
Inset shows the South American continent and Brazil, more specifically northeastern Brazil (light gray) and the area covered by the Caatinga biome (dark gray). The numbers indicate the names of municipalities, as follows. Superscript numbers in brackets indicate the studies that cite the municipality, as listed in Supplementary Table S1. **1** – Batalha – PI [(39)]; **2** – José de Freitas – PI [(36)]; **3** – Teresina – PI [(28; 35; 54)]; **4** – Monsenhor Gil – PI [(25)]; **5** – Arajara – CE [(23,64)]; **6** – Crateús – CE [(4; 21; 52)]; **7** – Crato – CE [(23; 28; 55; 60; 61)]; **8** – Ipu – CE [(57)]; **9** – Juazeiro do Norte – CE [(2)]; **10** – Nova Olinda – CE [(53; 28)]; **11** – Parambú – CE [(24)]; **12** – Ubajara – CE [(20; 50)]; **13** – Cocal – PI [(25)]; **14** – Guaribas – PI [(19)]; **15** – São Raimundo Nonato – PI [(28)]; **16** – Valença do Piauí – PI [(28; 61)]; **17** – Canindé – CE [(7; 8)]; **18** – Fortaleza – CE [(7; 27; 63)]; **19** – Guaramiranga – CE [(7; 63)]; **20** – Jaguaruana – CE [(7; 8)]; **21** – Limoeiro do Norte – CE [(7; 8; 32)]; **22** – Morada Nova – CE [(7)]; **23** – Palhano – CE [(7)]; **24** – Pereiro – CE [(7; 8)]; **25** – Quixadá – CE [(2; 7; 8; 32; 63)]; **26** – Russas – CE [(7; 8; 32)]; **27** – Brejo dos Santos – PB [(10)]; **28** – Maturéia – PB [(32)]; **29** – Santa Terezinha – PB [(10; 32)]; **30** – São José dos Cordeiros – PB [(10; 13; 32)]; **31** – Pombal – PB [(32)]; **32** – Exu – PE [(2; 18; 23; 28; 53; 60; 61)]; **33** – Apodi – RN [(12)]; **34** – Baraúna – RN[(12)]; **35** – Felipe Guerra – RN [(12)]; **36** – Martins – RN [(12)]; **37** – Mossoró – RN [(5)]; **38** – Nova Cruz – RN [(11; 32)]; **39** – Pedra Grande – RN [(12)]; **40** – Alagoinha – PB [(32)]; **41** – Araruna – PB [(4; 9; 10; 32)]; **42** – Areia – PB [(32)]; **43** – Boqueirão – PB [(32)]; **44** – Cabaceiras – PB [(10; 32)]; **45** – Cacimba de Dentro – PB [(32)]; **46** – Guarabira – PB [(32)]; **47** – Juazeirinho – PB[(2)]; **48** – Soledade – PB [(18)]; **49** – Umbuzeiro – PB [(10)]; **50** – Arcoverde – PE [(2; 22)]; **51** – Belo Jardim – PE [(2; 23)]; **52** – Brejo da Madre de Deus – PE [(2; 23; 32; 47; 49)]; **53** – Buíque – PE [(2; 23)]; **54** – Caruaru – PE [(2; 23)]; **55** – Panelas – PE [(23)]; **56** – Pedra – PE [(2)]; **57** – Sanharó – PE [(23)]; **58** – Toritama – PE [(2; 23)]; **59** – Vertentes – PE [(32)];**60** – Penedo – AL[(25; 58)];**61** – Anagé – BA [(32)]; **62** – Aporá – BA [(15)]; **63** – Bom Jesus da Lapa – BA [(43)]; **64** – Contendas do Sincorá – BA [(41; 42)]; **65** – Euclides da Cunha – BA [(18)]; **66** – Glória – BA [(2)]; **67** – Irecê – BA [(17)]; **68** – Iuiú – BA [(43)]; **69** – Juazeiro – BA [(28, 32)]; **70** – Malhada – BA [(43)]; **71** – Palmas de Monte Alto – BA [(43)]; **72** – Paratinga – BA [(43)]; **73** – São Gonçalo dos Campos – BA [(32)]; **74** – São José – BA [(32)]; **75** – Senhor do Bonfim – BA [(14; 28)]; **76**- Itacarambi – MG [(32; 40; 56)]; **77** – Jaíba – MG [(33; 34; 37; 56)]; **78** – Januária – MG [(56)]; **79** – Manga – MG [(56)]; **80** – Mocambinho – MG [(32)]; **81** – São João das Missões – MG [(40)]; **82** – Betânia – PE [(4)]; **83** – Bodocó – PE [(2; 23)]; **84** – Floresta – PE [(2; 4)]; **85** – Orocó – PE [(2; 23; 51)]; **86** – Petrolândia – PE [(2; 23)]; **87** – Salgueiro – PE [(2; 23)]; **88** – São Caetano do Navio – PE [(32)]; **89** – São José do Egito – PE [(48)]; **90** – Serra Talhada – PE[(3; 2; 23; 28)]; **91** – Sertânia – PE [(2; 23)]; **92** – Areia Branca – SE [(31)]; **93** – Canindé do São Francisco – SE [(1; 2; 23)]; **94** – Itabaiana – SE [(29; 30; 31)]; **95** – Canarana – BA [(44)]; **96** – Itaeté – BA [(16; 55)]; **97** – Iraquara – BA [(44)]; **98**- Itaberaba – BA [(38)]; **99** – Gentio do Ouro – BA [(32)]; **100** – Jacobina – BA [(32)]; **101** – João Dourado – BA [(44)]; **102** – Jussiape – BA[(38)]; **103** – Lençóis – BA [(38; 46)]; **104** – Morro do Chapéu – BA [(32; 38; 44)]; **105** – Mucugê – BA [(38)]; **106** – Ourolândia – BA [(44)]; **107** – Palmeiras – BA [(44)]; **108** – Rio de Contas – BA [(38)]; **109** – Utinga – BA [(44; 45)]; **110** – Barra – BA [(26)]; **111** – Sobradinho – BA [(2)]; **112** – Pilão Arcado – BA [(32)]; **113** – Canudos – BA [(18)]; **114** – Rodelas – BA [(2)]; **115** – Floresta do Navio – PE [(23)]; **116** – Ibimirim – PE [(2; 23)]; **117** – Inajá – PE [(23; 32)]; **118** – Jardim – CE [(64)]; **119**- São João do Piauí – PI [(65)]. PI, Piauí; CE, Ceará; PB, Paraíba; RN, Rio Grande do Norte; PE, Pernambuco; AL, Alagoas; BA, Bahia; MG, Minas Gerais; SE, Sergipe.

(Thomas, 1901) and *Platyrrhinus incarum* (Thomas, 1912) also occurred in the Caatinga, but only in CMC.

Approximately 50% of the municipalities where chiropterans were sampled in CDC are in its central portion. Of the 26 species inventoried, *Macrophyllum macrophyllum* (Schinz, 1821) was recorded in the Caatinga only in this ecoregion.

In BOH, 43 bat species were recorded. Only two small areas, in the south and in the north of the ecoregion, were never surveyed in studies on chiropteran fauna. Three species were recorded in the Caatinga only in this territory: *Choeroniscus minor* (Peters, 1868), *Platyrrhinus recifinus* (Thomas, 1901) and *Pygoderma bilabiatum* (Wagner, 1843).

The eastern and western areas of NSD have not been surveyed for bat species. However, bat richness was relatively high, 48 species. In the Caatinga, *Histiotus velatus* (I. Geoffroy, 1824) and *Lophostoma brasiliense* (Peters, 1866) are exclusive to the ecoregion.

IAC was second in bats richness. The studies on the chiropteran fauna in this ecoregion were carried out in border zones, and few sampling efforts were conducted in its central area. In total, 56 species have been recorded, six of which are exclusive to the Caatinga, in this ecoregion: *Artibeus concolor* (Peters, 1865), *Carollia brevicauda* (Schinz, 1821), *Cynomops abrasus* (Temminck, 1827), *Mimon bennettii* (Gray, 1838), *Saccopteryx bilineata* (Temminck, 1838), and *Vampyrum spectrum* (Linnaeus, 1758).

The ecoregion presenting the highest number of bat records was SSD, with 64 species, seven of which are exclusive: *Chiroderma doriae* (Thomas, 1891), *Eptesicus brasiliensis* (Desmarest, 1819), *Molossus pretiosus* (Miller, 1902), *Micronycteris schmidtorum* (Sanborn, 1935), *Myotis albescens* (E. Geoffroy, 1806), *Peropteryx kappleri* (Peters, 1867), and *Rhinophylla pumilio* (Peters, 1865). The data obtained place this ecoregion as the best surveyed in terms of chiropteran fauna. As SSD is considerably large, there is a lack of knowledge on bat species in this territory such as in a portion that surrounds SFD and a considerable area near the west of CDC.

Of the bat species observed in the Caatinga biome, only *Molossus molossus* (Pallas, 1766) has been documented in all ecoregions. *Peropteryx macrotis* (Wagner, 1843) has been recorded in all ecoregions, except RAC. *Desmodus rotundus* (E. Geoffroy, 1810), *Carollia perspicillata* (Linnaeus, 1758), and *Artibeus planirostris* (Spix, 1823) are absent only in SFD, while *Glossophaga soricina* (Pallas, 1766) was recorded in all ecoregions, except CMC.

The comparative analysis of bat richness considering the area of each Caatinga ecoregion and the number of studies presenting records of chiropterans are shown in Figure 2. A very robust and significant correlation was observed between area of each ecoregion and the number of bat species recorded (ρ=0.9286; p=0.0009) and between the number of studies documenting chiropteran samples and the number of known species for each ecoregion (ρ=0.9940; p<0.0001).

The cluster analysis for bat species composition in ecoregions revealed two groups. The first group was formed by CDC, SFD, RAC, and CMC. In this group, CDC joined the subgroup formed by SFD and RAC, and these three ecoregions connected with CMC. The second group was composed by a subgroup including BOH and SSD, and a subgroup with IAC and NSD (Figure 3A).

The cluster analysis was also conducted for ecoregions where chiropterans had been more comprehensively surveyed (SSD, NSD, IAC, and BOH). In this analysis, the studies addressing the same ecoregion were grouped, revealing the validation of the four ecoregions surveyed for bat fauna (Figure 3B).

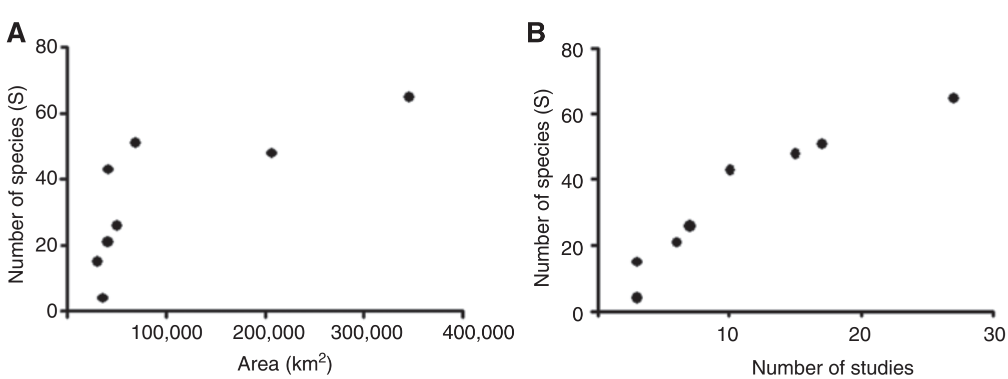

Figure 2: Scatter plot showing the relationship between the number of bat species known to each Caatinga ecoregion and (A) the ecoregion area and (B) the number of studies that included the sampling of chiropterans in each ecoregion.

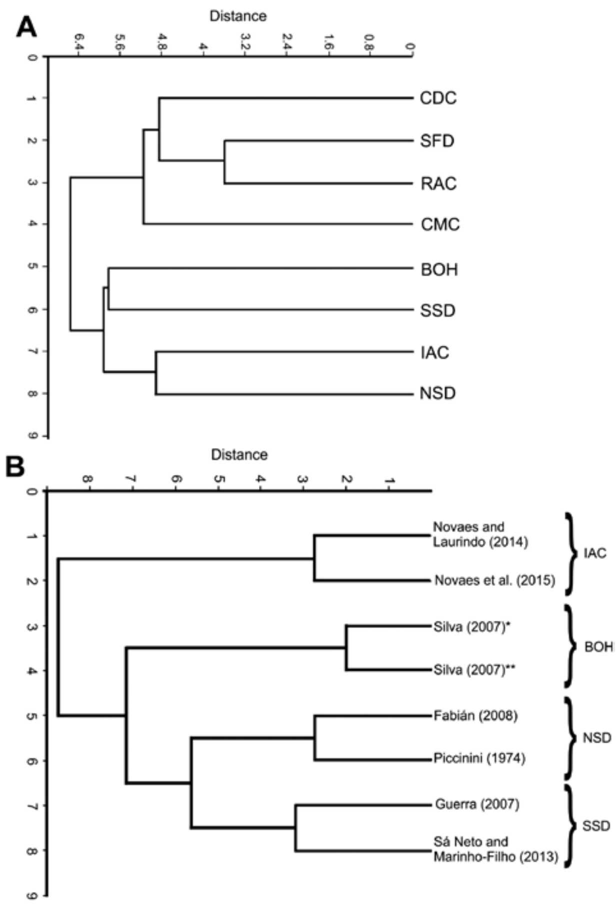

Figure 3: Cluster analyses based on the Euclidean distance for the bat species composition in the eight Caatinga ecoregions (A) and for the main references in the best surveyed ecoregions for the bat fauna. (B) * Fazenda Arara/Caatinga Arbustiva ** Reserva Particular do Patrimônio Natural – Fazenda Bituri/ Floresta Montana. Chapada Diamantina Complex (CDC), São Francisco Dunes (SFD), Raso da Catarina (RAC), Campo Maior Complex (CMC), Borborema Highlands (BOH), Southern Sertaneja Depression (SSD), Ibiapaba-Araripe Complex (IAC), and Northern Sertaneja Depression (NSD).

Discussion

The xeric landscapes of the Caatinga are often associated with the notion that the biome is rather poor in species diversity (Vanzolini et al. 1980, Andrade-Lima 1982, Prance 1987). Despite the large gaps in the sampling of chiropteran fauna, the present study indicates that the Caatinga is home to at least 90 bat species. This number is relatively close to the 101 species documented in the Cerrado, in Brazil (Paglia et al. 2012), which is another important biome with seasonally dry tropical forests in the Neotropical region (Pennington et al. 2009). Chiropteran diversity in the Caatinga is, nevertheless, comparatively lower, considering the 113 species recorded in the exuberant Brazilian Atlantic Forest and 146 species that live in the Brazilian Amazon (Bernard et al. 2011). Compared with the compilation carried out by Paglia et al. (2012), the data obtained in the present review add 20 bat species to the Caatinga biome (Supplemental Table S1). Of these, five are recorded only in two ecoregions, while 12 were exclusive to one ecoregion.

The lowest bat richness levels were observed in SFD, RAC, and CMC. These Caatinga ecoregions concentrate the areas with the lowest rainfall means, the highest temperature means, and low soil fertility. Under such conditions, food availability for bats may be negatively affected, which in turn explains the low species diversity recorded in these ecoregions. The low number of chiropterans observed in SFD and RAC may also be a result of the longest distance between these regions and urban centers, which may explain why so few studies have been conducted in the areas.

Another ecoregion with low chiropteran diversity was CDC. A likely reason for this may lie in the fact that several studies conducted in the region investigated only expanses where caves occur (Gregorin and Mendes 1999, Oliveira and Pessôa 2005, Sbragia and Cardoso 2008). In this sense, investigations in other areas may show that bat diversity in CDC is actually higher, since this Caatinga ecoregion features fertile soils and perennial rivers, which may be attractive factors for chiropteran species.

The number of recorded bat species in the different Caatinga ecoregions varies considerably. So, what are the likely factors behind this difference in species richness, besides the abiotic factors cited? Both the number of studies and the area of each ecoregion were strongly and significantly correlated with chiropteran richness. It is likely that the correlation between ecoregion area and respective bat richness will sustain itself when the knowledge gaps about chiropteran fauna are bridged, especially for ecoregions where chiropterans were least sampled. Evidence in support of this notion is given by the fact that two regions of similar area like SFD and RAC presented considerably different richness values. This difference points to the need for further studies on the chiropteran fauna living in places that remain poorly investigated, as some of the regions evaluated in the present study.

Only six bat species were observed in all or virtually all Caatinga ecoregions, and were considered widely distributed species. All ecoregions, except for SFD and RAC, presented exclusive species. Apart from being an indicator of the validity of the subdivision of the biome in ecoregions, this information also points to the importance of conserving these areas, since they are site to a unique biological stock. The ecoregions with the highest number of protected areas are SSD, NSD, and IAC. In the other ecoregions, few protected areas have been implemented, or none at all, which is the case of SFD (Velloso et al. 2002).

The cluster analysis for the best surveyed areas provided support to at least four ecoregions (IAC, BOH, SSD, and NSD), supporting patterns already observed by other authors for distinct groups of plants (Queiroz 2006, Cardoso et al. 2008, Ferreira et al. 2009, Maciel et al. 2012, Santos et al. 2012) and animals (Hernández 2005, 2007, Guedes et al. 2014).

Five bat species documented in the Caatinga are present in the official list of animal species threatened with extinction published in 2014 by the Environment Ministry of Brazil (MMA 2014). Of these, *Lonchophylla dekeyseri* (Taddei et al. 1983) is listed as threatened. *Furipterus horrens* (Cuvier, 1828), *Lonchorhina aurita* (Tomes, 1863), *Natalus macrourus* (Gervais, 1856), and *Xeronycteris vieirai* (Gregorin and Ditchfield, 2005) stand as vulnerable. These five species are found mainly in the four ecoregions supported by the cluster analysis (IAC, BOH, SSD, and NSD, Supplemental Table S1). Therefore, the division into ecoregions may play an important role in promoting more effective strategies to protect bat species.

Bats are the most abundant and diverse mammal group in the Caatinga, and play an essential role in the regeneration and maintenance of this biome. We reviewed bat species richness in the Caatinga, and warn about the areas in each ecoregion where these organisms have not been comprehensively investigated. The recognition of subdivisions or ecoregions in the Caatinga has opened new research and conservation perspectives, and should play a major role both in planning and implementing conservation initiatives in a biome that, in spite of its high species diversity, is significantly threatened by the destruction of natural areas.

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