



Inside or out? Cave size and landscape effects on cave-roosting bat assemblages in Brazilian Caatinga caves

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Cave bats have an intimate association with their roosts. Size, structural heterogeneity, and microclimatic conditions are traits of caves known to affect the structure of these assemblages. The effects of the natural and anthropogenic landscape factors around caves on the structure of these assemblages are poorly known, especially in areas with large cave clusters. We assessed the effects of cave size and surrounding landscape attributes on the richness and species composition of cave-roosting bats in 13 caves distributed in two landscapes with large cave clusters in Caatinga dry forests, Brazil. In a 1-km buffer around caves, we obtained 13 internal cave and external landscape variables. Candidate univariate models using generalized linear models were constructed and the Akaike information criterion was used for model selection. The cave size model explained richness and variance in the species composition; larger caves tended to have greater richness and assemblage composition varied depending on the cave size, hence affecting the occurrence of certain species, some of conservation concern (*Natalus macrourus*, *Furipterus horrens*). The cave connectivity model affected only the richness; caves located in denser cave clusters had higher richness likely attributed to movement of bats among caves by a more diverse array of species. Both environmental and anthropic variables affected species composition, but differently depending of the landscape context of cave location (protected versus nonprotected area). The extent these landscape variables affected the species composition was due to species-specific responses, and observed in the mean colony sizes of the species shared between the cave systems. All the landscape variables that we tested affected the structuring process of cave-roosting bats assemblages, and evidences that variables found in disturbed karstic landscapes also affect the structure of the assemblage (e.g., large colonies of vampire bats). However, the ubiquitous effect of cave size on both richness and species composition reinforces the critical importance of the roost in the life of these flying mammals.

Os morcegos que se abrigam em cavernas têm uma associação muito íntima com seus abrigos. Sabe-se que as características de caverna, como o tamanho, heterogeneidade estrutural e condições microclimáticas estáveis, afetam a estrutura das assembleias dos morcegos cavernícolas. No entanto, os efeitos dos fatores externos naturais e antrópicos da paisagem em torno de cavernas na estrutura das assembleias destes morcegos são pouco conhecidos, especialmente em paisagens cársticas com grandes aglomerados de cavernas. Assim, avaliamos os efeitos do tamanho da caverna e dos atributos da paisagem circundante na riqueza e composição de espécies de morcegos em 13 cavernas distribuídas em duas paisagens de Caatinga com grandes aglomerados de cavernas no Rio Grande do Norte. Em um buffer de 1 km ao redor de cada caverna, obtivemos 13 variáveis de paisagem interna (tamanho da caverna) e externa (número de cavernas circundantes, variáveis antropogênicas e ambientais); Modelos candidatos univariados usando GLM foram construídos e o Critério de Informação de Akaike foi usado para a seleção dos modelos. O modelo de tamanho das cavernas explicou a riqueza e a variação na composição

das espécies; cavernas maiores tendem a ter maior riqueza e composição da assembleia variando de acordo com o tamanho da caverna, afetando, portanto, a ocorrência de certas espécies, algumas vulneráveis (*Natalus macrourus*, *Furipterus horrens*). O modelo de conectividade da caverna afetou apenas a riqueza; cavernas localizadas em aglomerados maiores tinham maior riqueza. As variáveis ambientais e antrópicas afetaram diferentemente a composição das espécies dependendo do contexto da paisagem da localização da caverna (área protegida versus não protegida). As variáveis da paisagem afetaram a composição das espécies ocorreu de uma forma específica em algumas espécies e foi observada no tamanho médio das colônias das espécies compartilhadas entre os sistemas de cavernas. Todas as variáveis da paisagem que testamos afetaram o processo de estruturação de assembleias de morcegos cavernícolas, incluindo aquelas que são características de uma paisagem cárstica perturbada. Todas as variáveis de paisagem que testamos afetaram o processo de estruturação de assembleias de morcegos que pousam em cavernas e evidenciam que variáveis encontradas em paisagens cársticas perturbadas também afetam a estrutura da assembleia (por exemplo, grandes colônias de morcegos vampiros). No entanto, o efeito ubíquo do tamanho da caverna sobre a riqueza e a composição das espécies reforça a importância crítica do abrigo na vida desses mamíferos voadores.

Key words: cave connectivity, Chiroptera, dry forest, karst, livestock, richness, species composition, structure, vampire bat

Caves and other underground cavities are commonly used by bats as roosts. They provide humid and thermally stable conditions for bats to reproduce, socialize, and find protection against predators and adverse climate (Kunz 1982). In these underground ecosystems, bats are classified as troglonemes, organisms found regularly in the underground environment, but need to return periodically to the surface to complete their life cycle (Trajano and Bichuette 2006).

As any other trogloneme, bats have a strong association with their cave roost. The diversity and structure of cave bat assemblages are strongly influenced by factors related to cave structure and size (Arita 1996; Brunet and Medellín 2001; Cardiff 2006; Niu et al. 2007; Luo et al. 2013; Phelps et al. 2016; Torquetti et al. 2017), where larger and more geomorphologically complex caves tend to harbor richer bat assemblages. However, other studies have also found that the diversity and structure patterns of cave bat assemblages are affected by other factors such as intra- and interspecific interactions (Arita and Vargas 1995; Rodríguez-Durán and Soto-Centeno 2003), species-specific microclimate preferences (Rodríguez-Durán and Soto-Centeno 2003; Avila-Flores and Medellín 2004), relative humidity (Brunet and Medellín 2001; Rocha and Bichuette 2016), roost disturbances by humans (Luo et al. 2013; Voigt and Kingston 2016), and the external environment or “landscape context” (Furey and Racey 2016; Phelps et al. 2016). Nevertheless, the landscape context where a particular cave is located and how this affects the structure of the assemblages has been poorly explored (Furey and Racey 2016), considering the vital ecological relation of bats with the exterior or surrounding landscape, such as access to water and food.

In general, the structural patterns of a bat assemblage in Neotropical landscapes are determined by species-specific and guild-specific traits in responses to the composition and configuration of both natural and human-modified landscapes, despite the high mobility of bats (Medellín et al. 2000; Pinto and Keitt 2008; Klingbeil and Willig 2009; Avila-Cabadiilla et al. 2012). The abundances of certain aerial insectivorous bats (Estrada-Villegas et al. 2012) and gleaning-animalivorous bats decline in response to habitat loss (e.g., fragmentation; Medellín et al.

2000; Meyer and Kalko 2008; Farneda et al. 2015), whereas nectarivorous and frugivorous bats often increase (Sampaio et al. 2003; Delaval and Charles-Dominique 2006; Meyer and Kalko 2008; Bernard et al. 2011). As for the hematophagous bats, they may be rare in undisturbed areas; however, in human-inhabited landscapes these bats can be very abundant as a result of the stable food resource provided by domestic animals year-round (Trajano 1985; Delpietro et al. 1992; Medellín et al. 2000).

Regarding the relationship between caves and landscapes, Phelps et al. (2016) found that in a karstic landscape in the Philippines, the diversity of cave bat assemblages responded positively to increasing cave complexity and negatively to increasing anthropic variables related to decreased forest cover, increased urbanization, and road development. Studies with such an approach are needed, especially in karstic landscapes that harbor high cave densities. These areas are known to be key for the maintenance of local bat populations by offering abundant cave roost resources throughout the landscape (Trajano 1985; Struebig et al. 2009; Furey et al. 2010; Torquetti et al. 2017; Vargas-Mena et al. 2018b). In turn, cave bats provide invaluable ecosystem services to vast areas surrounding caves, including seed dispersal, plant pollination, and control of pest insects (Medellín et al. 2017). Karstic landscapes with high densities of caves offer a greater number of favorable roosts for a high diversity of cave-roosting bats and assure the perpetuation of the ecosystem services provided by these mammals.

In Brazil, karstic landscapes with a large number and density of caves are commonly found (Jansen and Pereira 2014), and this might be another landscape factor structuring these bat assemblages. For instance, in a karstic area with large cave clusters in southeast Brazil, cave bat assemblages were greater and more diverse the more isolated the cave was, regardless of the cave dimensions, while in areas with large cave clusters, factors related to the cave size were more important in the structuring process of the assemblages (Trajano 1985). In areas with the occurrence of cave clusters with a large number and proximity of potential cave roosts for bats, different species may be moving among caves and potentially affecting the structure

of the assemblage. Although this translocation of cave bats is poorly known, evidence of movements among cave roosts has been recorded in areas with the occurrence of clusters of caves (Campanha and Fowler 1993; Trajano 1996; Bredt et al. 1999). Potentially, this connectivity promoted by the movement of bats among caves is another variable to take into account for a better understanding of the structure of cave-roosting bat assemblages inhabiting these particular karstic landscapes.

We tested the effects of the surrounding landscape structure and number of caves, and the internal cave dimensions on the richness and species composition of cave-roosting bats in two karstic landscapes in the western portion of the state of Rio Grande do Norte in northeastern Brazil. Rio Grande do Norte has the peculiarity to harbor more than 1,000 caves with several areas of cave hotspots (>100 caves; Bento et al. 2017) and with a diverse bat fauna where one-third of the recorded species are cave dwellers (Vargas-Mena et al. 2018a).

Based on the premise that cave size, cave isolation (connectivity), and landscape factors affect the richness and species composition of cave bat assemblages, we predicted that species richness 1) will be affected positively by cave size, where larger caves will harbor greater bat richness; and 2) will be affected by the connectivity of caves found in the landscape because of the higher probability of a larger array of different species moving among caves and hence increasing the species richness in each cave. Regarding species composition, we predicted that 3) the assemblages will be correlated with

specific landscape variables depending on the landscape context in which the cave is located. Caves in areas with high levels of disturbance such as low forest cover and high levels of anthropic activities (e.g., domestic animals, human settlements) will have assemblages poor in species richness, and be dominated by species favored by human-modified landscapes (e.g., hematophagous and generalist frugivorous bats); and 4) conversely, caves in areas with low levels of anthropic activities, high forest cover, and close to water resources will have relatively more diverse assemblages with the presence of more forest-dependent bats (e.g., carnivorous, gleaning-insectivorous bats).

MATERIALS AND METHODS

Study area.—This study was conducted in two karstic areas in different landscape contexts, both within in the Caatinga domain of Rio Grande do Norte state (RN) in northeastern Brazil (Fig. 1). The Caatinga is a seasonal tropical dry forest composed of mosaics of xeric spiny shrub lands, columnar cacti, succulents, and deciduous woody forest stands (da Silva et al. 2017). Natural forested areas of Caatinga have been deeply altered in the last decades by human activities (e.g., lumber extraction, agriculture, livestock) that are causing rapid environmental damage and desertification (Leal et al. 2005). The Caatinga covers 95% of the state's territory, which harbors several cave hotspots (>1,000 caves in the state), most of them

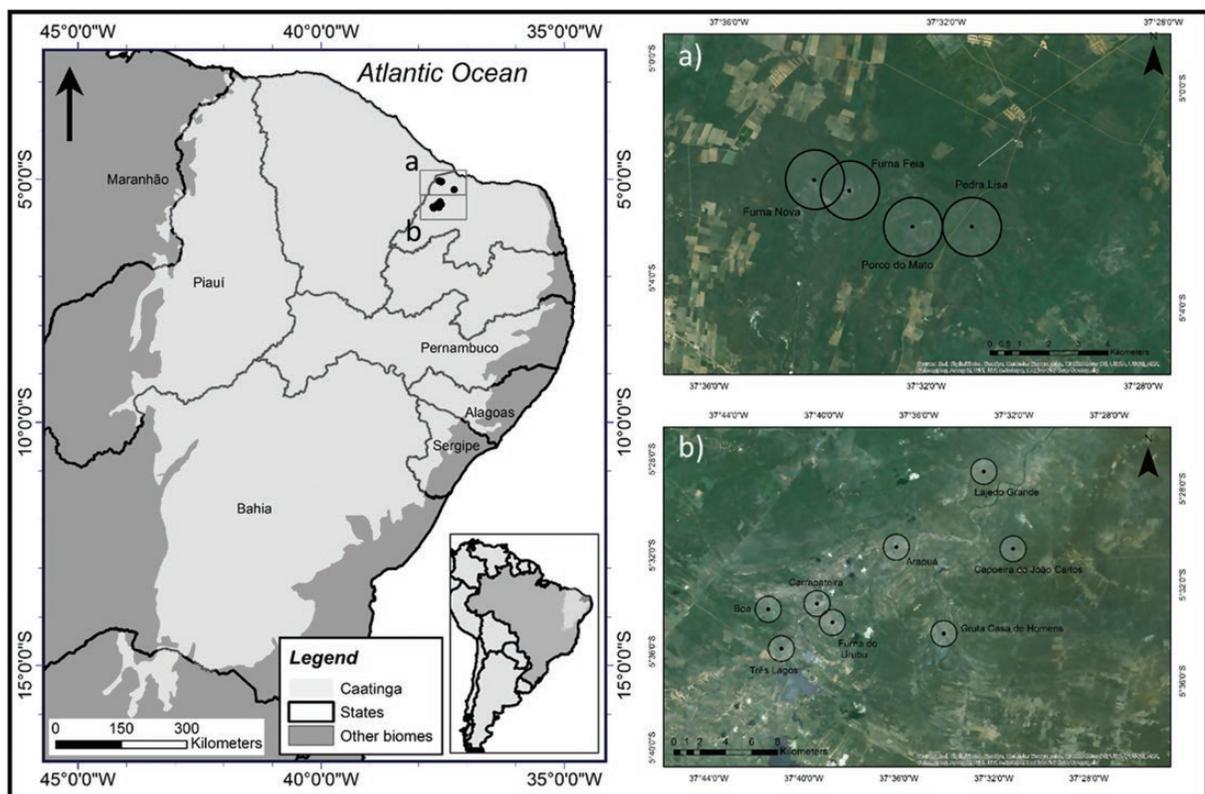


Fig. 1.—Map of the study area with 13 selected caves. Each cave shows a 1-km buffer around it. (a) Furna Feia National Park, (b) Felipe Guerra Cave System in the municipalities of Felipe Guerra, Governador Dix-sept Rosado and Caraúbas. The Gruta dos Trinta cave in Mossoró is not shown.

found in large calcareous outcrops in the western region (Bento et al. 2017).

Cave selection.—The surveyed caves are separated in two karstic areas, or cave systems (Fig. 1). One system, the Felipe Guerra Cave System (FGCS) located in three municipalities (Felipe Guerra, Governador Dix-sept Rosado, and Caraúbas), is about 80,560 ha, and contains the largest concentration of caves in RN (341 cavities); however, the area is unprotected, with high pressures from mining and deforestation (Bento et al. 2015). The second cave system is the protected karstic areas of Furna Feia National Park (FFNP) in Mossoró and Baraúna municipalities, with 8,494 ha of primary and secondary Caatinga. The FFNP is the national park that protects the largest number of caves in Brazil, with around 250 underground cavities (Bento et al. 2013). Close to the FFNP, we surveyed one cave, the Gruta dos Trinta, located about 24 km from the FFNP in Mossoró municipality.

Because of the large number of caves in the state, we consulted the available database of the Brazilian Center of Research and Conservation of Caves (CECAV) (<http://www.icmbio.gov.br/cecav/canie.html>) in search of cavities that had available topographic data, confirmed presence of bats, and at least 2 km of distance among each other. Logistics and access permits were also considered during cave selection. Thirteen caves fit our criteria (Table 1). A 1-km buffer (314 ha) was established around each cave for further landscape variable extraction and analysis (Fig. 1). Although home range size for most of the species recorded in this study is unknown, we expected that the foraging area of some species may be larger than the buffer area; nonetheless, the landscape over a 1-km buffer area likely represents the land use around each cave on a larger spatial scale. Additionally, because of the short distance between some caves, the 1-km buffer was the

maximum size possible to avoid overlap between buffers to achieve statistical independence between samples. Finally, based on the premise that bat species remain close to their roosts if nonperturbed foraging habitat (e.g., forest, water) is found nearby, disturbances at this 1 km scale could make a cave an unsuitable roost for a bat as a result of the increase in energetic cost of commuting larger distances to reach suitable foraging habitats (Kingston 2013).

Bat data collection.—From June 8 to October 23 of 2015, we sampled each cave during three consecutive days to assess the richness and species composition of their bat assemblages. Due to logistic problems, the Gruta dos Trinta was sampled only during two consecutive days. In each of the days, active searches and bat captures were conducted. The active search consisted of an exhaustive search inside the cave by illuminating colonies and individuals during daylight, which ensures that all the bats that were found at that moment were using the cave as a day roost (Kunz et al. 2009).

Bat richness was determined by the record of a species either by direct observation during the day or by the capture of any individual entering or leaving the cave. For each species, we estimated their colony size for each cave. When encountering small clusters of bats (< 30), we were usually able to count all individuals. Counting was done exclusively by the same two observers (JCVM and ECS). When medium-sized colonies were found (< 100–200; e.g., *Desmodus rotundus*, *Glossophaga soricina*), we took photos for a later counting on the camera screen or computer. However, the direct counting method may be acceptable for small and compact colonies, but for large colonies, estimation of colony size through direct observation may not be reliable (Kunz et al. 2009). We encountered large-sized colonies (> 200; *Phyllostomus discolor*, *G. soricina*, and *Pteronotus gymnotus*) on only three

Table 1.—Caves selected for analysis in this study with bat species occurrence and values of internal variables per cave in Rio Grande do Norte, Brazil. Acronyms of the 16 bat species recorded are: *Peropteryx macrotis* (Pm), *Desmodus rotundus* (Dr), *Diphylla ecaudata* (De), *Glossophaga soricina* (Gs), *Lonchophylla mordax* (Lm), *Chrotopterus auritus* (Ca), *Lonchorhina aurita* (La), *Micronycteris* sp. (Msp.), *Phyllostomus discolor* (Pd), *Tonatia bidens* (Tb), *Trachops cirrhosus* (Tc), *Artibeus lituratus* (Al), *Artibeus planirostris* (Ap), *Pteronotus gymnotus* (Pg), *Natalus macrourus* (Nm), and *Furipterus horrens* (Fh). Internal cave variables are: cave linear development extension (LD), cave horizontal projection (HP), cave area (A), cave volume (V), and cave internal unevenness (Unev).

Site	Cave name	Species recorded	Richness	HD (m)	HP (m)	A (m ²)	V (m ³)	Unev. (m)	Coordinates	
									Lat.	Long.
FFNP	Furna Nova	Pm, Dr, De, Gs, Pd, Tb, Nm	7	239.3	211.3	2,786.6	6517	29.8	−5.034226	−37.571167
	Furna Feia	Pm, Dr, De, Gs, Pd, Tb, Al, Ap, Fh, Nm	10	739.1	707.5	2,1251.0	49,699.6	30.0	−5.036878	−37.560177
	Caverna Porco do Mato I	Pm, De, Gs, Tb, Ap, Fh	6	140.4	137.5	1,636.4	2,062.1	3.9	−5.046638	−37.540114
FGCS	Caverna da Pedra Lisa	Pm, Gs, Tb, Fh	4	149.7	142.3	2,558.9	1,557.7	6.0	−5.045527	−37.521902
	Gruta dos Três Lagos	Pm, Dr, De, La, Msp, Tc, Fh	7	65.0	62.0	148.2	410.2	12.0	−5.593288	−37.687155
	Caverna Boa	Dr, De, Pd, Tb, Ap, Nm, Fh	6	264.5	255.7	13,966.1	10,165.2	17.8	−5.566527	−37.697897
	Gruta da Carrapateira	Pm, Dr, De, Gs, Ca, Ap, Fh	7	242.2	229.5	4,631.6	5,064.1	10.5	−5.560618	−37.663979
	Furna do Urubu	Pm, Dr, De, Tb, Ap, Pg	6	283.5	274.6	7,760.9	9,264.8	19.2	−5.573047	−37.65242
	Caverna do Arapuá	De, Fh	2	110.0	97.0	564.0	1,466.0	12.0	−5.518367	−37.610706
	Gruta Capoeira João Carlos	Pm, De, Gs, Tb, Ap, Fh	6	55.0	49.0	324.6	650.1	12.2	−5.514716	−37.52877
	Caverna do Lajedo Grande	Pm, Dr, De, Ap	4	155.4	136.1	1,600.8	5,465.9	15.9	−5.462278	−37.552471
	Gruta Casa de Homens	Pm, Dr, De, Tb, Fh	5	31.0	30.0	278.1	248.9	3.6	−5.576272	−37.573807
Mossoró	Gruta dos Trinta	Pm, Dr, Gs, Lm, Nm	5	271.6	270.8	645.0	558.1	1.3	−5.212322	−37.264153

occasions, and estimation of those colonies sizes was assessed by the most experienced author (RAM).

From the quantitative data of direct bat counting, we assigned each species to a colony size for each cave, in six categories (ranking colony size). This method may lead to an over- or underestimation of the colony sizes by the observers, but we aimed to obtain only a preliminary insight into the bat colonies in order of magnitude and did not attempt to estimate the absolute population size or census of the bat colonies. The categories for colony size were based on and modified from [Arita \(1996\)](#): 1 (night visitor); 2 (< 10 individuals); 3 (11–100); 4 (101–1,000); 5 (1,001–10,000); 6 (> 10,000). The night visitor category corresponded to captured bats entering a cave at night with no colony of that species spotted during the diurnal active search, suggesting those individuals were probably using the cave as a feeding perch.

Mist-nets were set at the cave entrances from 1730–2400 h to capture emerging bats to confirm species identification and to detect other roosting species overlooked during the day active search. The number and size (3–12 m long) of the mist-nets depended on the size and number of cave entrances. Detected bat species were assigned to trophic guilds based on [Hill and Smith \(1984\)](#) using the available primary diet information of bats in Brazil ([dos Reis et al. 2007](#)). However, we merged the foliage-gleaning insectivorous and carnivorous guilds of [Hill and Smith \(1984\)](#) into a gleaning animalivorous guild. Bats belonging to these guilds can have both an insectivorous and carnivorous diet (e.g., Phyllostomine bats; [Gardner 2007](#)). Guilds used in this study were aerial insectivores, gleaning animalivores, piscivores, frugivores, nectarivores, omnivores, and sanguinivores.

Collecting permits were issued by the Brazilian environmental agency (SISBIO license number 48325-2 MMA, IBAMA and ICMBIO) and handling protocols followed the guidelines of the American Society of Mammalogists ([Sikes et al. 2016](#)).

Extraction of cave and landscape variables.—The following 13 variables were obtained from various available databases ([Supplementary Data SD1](#)) and extracted from the 1-km buffer of each cave: 1) percentage of Caatinga forest coverage, obtained from the “MapBiomas Project” using the coverage of year 2017 - collection 3.1. The percentage was estimated using the “ZONAL STATISTICS” tool from the spatial analysis module of ArcGis 10.1. software; 2) distance to lakes or water reservoirs, and 3) distance to rivers were obtained using the “NEAR” tool also from the ArcGis 10.1 software. External anthropic variables referred to human activities in the landscape. We obtained data for 4) sheep density, 5) goat density, and 6) cattle density from the 2006 Brazilian agricultural census; and 7) human demographic density from the national census of 2010, both by the IBGE (Instituto Brasileiro de Geografia e Estatística) of each census sector (district) where each cave is located. From the numbers of individuals (livestock and people), we calculated the density (number of individuals/hectare) to subsequently calculate the density in the 1-km radius buffer of each cave. All analyses were performed in ArcGIS

10.1. The projection was WGS84 on the UTM zone 25 projection system. We used the CECAV data base (see [Supplementary Data SD1](#)) to obtain the number of underground cavities in a buffer of 3 km around each of the surveyed caves to estimate 8) cave connectivity. Finally, from the same CECAV data base, we obtained topographical data for each cave for the internal cave size variables: 9) linear development (LD), 10) horizontal projection (HP), 11) volume (Vol), 12) area (A), and 13) vertical unevenness (VU). All data for each cave that were used for the analysis can be found in [Supplementary Data SD2](#).

Statistical analysis.—To analyze the species composition of the sampled assemblages, we used the Bray-Curtis index of dissimilarity to generate a distance matrix between caves and perform a nonmetrical multidimensional analysis (NMDS; [Kruskal 1964](#)) in two-dimensional solution for the ordinal data of colony sizes (0–6). The stress was used as an adjustment measure between the obtained values of the analysis and the original matrix of community distance. We calculated Spearman correlations with the scores of axes I and II of the NMDS, with the environmental, anthropogenic, cave connectivity, and cave-size dimension data and the bat species colony size to interpret which variables and species affected the scores in the ordination space.

A similarity percentage analysis (SIMPER) was performed to estimate the weight of each species in the assemblage dissimilarity between the FGCS and FFNP. Data from the Gruta dos Trinta cave were excluded from this analysis. Finally, we performed a multivariate analysis of variance (MANOVA) to compare differences between these two cave systems (FGCS and FFNP) using the scores of the two axes of NMDS analysis.

To assess the effects of landscape and cave size on the bat assemblages, the 13 variables were grouped into four sets of variables, one set of internal variables (cave structure) and three sets of external landscape variables (connectivity, environmental, and anthropogenic). Then, using a principal component analysis (PCA), we reduced the predictor data for three multivariate variable sets and scores were used as explanatory variables for simple linear regressions ([Supplementary Data SD3](#)). The first axes of PCA of the sets of internal variables (cave structure) and environmental variables presented 85.65% and 80.79%, respectively, of the variance, while the second axes both presented low percents of the variance and were not used for subsequent analysis. The anthropogenic variable set presented a solution in both axes. Axis 1 represented 54.51% of the variation in the sheep (axis 1 loading = 0.981), cattle (axis 1 loading = 0.807), and goat (axis 1 loading = 0.753) densities, while the second axis explained 34.70% of the variance in human demographic density. In this case, we used these two axes for the subsequent analysis.

Once the scores of the PCA of each variable set were extracted, we used these values as explanatory variables to construct candidate models using generalized linear models (GLM) with Gaussian error for species composition and with Poisson error for species richness ([Crawley 2002](#)). Because of the small sample size ($n = 13$ caves), the GLMs were constructed only with univariate models, as recommended by

Burnham and Anderson (2002). Before starting the model selection analysis, we tested the correlation between geographic distance and dissimilarity (Bray Curtis index) of cave bat assemblages, but no correlation was found (Mantel test, $r = 0.018$; $P = 0.874$), thus we did not use spatial variables in the candidate models. Therefore, we had six candidate models, including the null model, as explanatory variables of the observed patterns of richness and composition of the sampled cave bat assemblages (Supplementary Data SD6). We followed the approach of Burnham and Anderson (2002) for model selection based on the second-order Akaike information criterion corrected for small sample size (AICc). The AIC compares the different models through a combination of maximum likelihood that determines which model better explains the observed data (Williams et al. 2002). The lower the value of AIC scores ($\Delta\text{AIC} < 2$), the more plausible the model adjustment is to the data. All analyses were done using SYSTAT software version 12 and packages *MuMIn* and *jtools* of R software version 1.1.447 (R Development Core Team 2019)

RESULTS

Bat assemblage composition.—We recorded 16 bat species from five families in the 13 sampled caves. Bat species richness ranged from two species (Caverna do Arapuá in FGCS) to 10 species (Furna Feia cave in FFNP). The FGCS had the highest richness (14 species), followed by the FFNP (10) and the Gruta dos Trinta (5; Fig. 1). Phyllostomidae was the most common family with 12 species, followed by Emballonuridae, Mormoopidae, Furipteridae, and Natalidae, all with one species each. Of the 16 species recorded, nine (*G. soricina*, *D. rotundus*, *Diphylla ecaudata*, *Artibeus planirostris*, *P. discolor*, *Tonatia bidens*, *Furipterus horrens*, *Natalus macrourus*, and *Peropteryx macrotis*) occurred in both cave systems. Five species (*P. gymnonotus*, *Lonchorhina aurita*, *Trachops cirrhosus*, *Chrotopterus auritus*, and *Micronycteris* sp.) were found only in the FGCA, while *Artibeus lituratus* only occurred in FFNP. The MANOVA showed a significant difference

in the bat species composition between FGCS and FFNP (MANOVA-Pilai Trace = 0.511; $d.f. = 2,9$; $P = 0.04$). The univariate tests showed a marginal difference only in the second axis ($F_{1,10} = 3.9$, $P = 0.077$). The SIMPER analysis (Table 2) showed that the highest mean difference of the colony sizes of bat species that occurred in both FGCS and FFNP belonged to *G. soricina* with a percentage of contribution to the assemblage dissimilarity of 12.53%, followed by *D. rotundus* (12.40%), *A. planirostris* (9.92%), and *P. discolor* (9.56%). These species explained 44.4% of the total dissimilarity between the cave systems. Both *G. soricina* and *P. discolor* had larger colonies (higher mean colony size) in the FFNP, whereas *D. rotundus* and *A. planirostris* had bigger colonies in the FGCS.

The NMDS ordination showed a separation between FGCS and FFNP in the rank colony sizes (stress = 0.169; Fig. 2). We found that axis 1 of the ordination was positively correlated with the ranking colony size of only *N. macrourus* (Spearman's $\rho = 0.771$), *D. rotundus* (Spearman's $\rho = 0.629$), and *P. discolor* (Spearman's $\rho = 0.615$), and negatively correlated with *F. horrens* (Spearman's $\rho = -0.645$). Axis 2 was positively correlated only to *G. soricina* (Spearman's $\rho = 0.886$), and negatively correlated with *D. ecaudata* (Spearman's $\rho = -0.811$) and *D. rotundus* (Spearman's $\rho = -0.567$; Supplementary Data SD4).

Model selection.—Among all candidate models, the only ones selected to explain bat richness were the set of internal cave size variables ($R^2 = 0.406$; $\omega\text{AICc} = 38.46$) and cave connectivity (3 km; $R^2 = 0.337$; $\omega\text{AICc} = 29.11$), representing 67.57% of the variance explained by all models (Table 3). Regressions were not significant for either model but were selected because they presented a $\Delta\text{AICc} < 2$. However, the set of cave size variables presented a regression with marginal significance (Fig. 3a). Information added by the other variables related to the external anthropogenic and environmental variable sets were not important for explaining bat richness.

Regarding species composition, we found that axis 1 of the NMDS ordination of the single cave size model ($R^2 = 0.510$; $\omega\text{AICc} = 85.41$) was the best to explain the

Table 2.—Results of the similarity percentage analysis (SIMPER) for comparisons of the Bray Curtis dissimilarity index between mean colony size of cave bats in Felipe Guerra Cave System (FGCS) and Furna Feia National Park (FFNP) in Rio Grande do Norte State, Brazil. The overall average dissimilarity was 43.47. The table indicates average dissimilarity, percentage of contribution to dissimilarity, cumulative percentage, and mean abundance of each species in FGCS and FFNP.

Species	Average dissimilarity	% Contribution	Cumulative %	FGCA mean abundance	FFNP mean abundance
<i>Glossophaga soricina</i>	6.734	12.53	12.53	0.5	2.25
<i>Desmodus rotundus</i>	6.663	12.40	24.93	2.25	1.5
<i>Artibeus planirostris</i>	5.329	9.92	34.85	1.5	0.75
<i>Phyllostomus discolor</i>	5.137	9.56	44.4	0.25	1.75
<i>Tonatia bidens</i>	4.858	9.04	53.44	0.5	1.75
<i>Furipterus horrens</i>	4.826	8.98	62.42	1.5	1.75
<i>Natalus macrourus</i>	4.754	8.85	71.27	0.25	1.5
<i>Diphylla ecaudata</i>	4.581	8.52	79.79	2.25	1.25
<i>Peropteryx macrotis</i>	3.562	6.63	86.42	1.75	2.25
<i>Pteronotus gymnonotus</i>	2.553	4.75	91.17	0.75	0
<i>Lonchorhina aurita</i>	1.233	2.29	93.46	0.375	0
<i>Trachops cirrhosus</i>	1.233	2.29	95.76	0.375	0
<i>Micronycteris</i> sp.	0.8218	1.53	97.29	0.25	0
<i>Chrotopterus auritus</i>	0.8218	1.53	98.82	0.25	0
<i>Artibeus lituratus</i>	0.6357	1.18	100	0	0.25

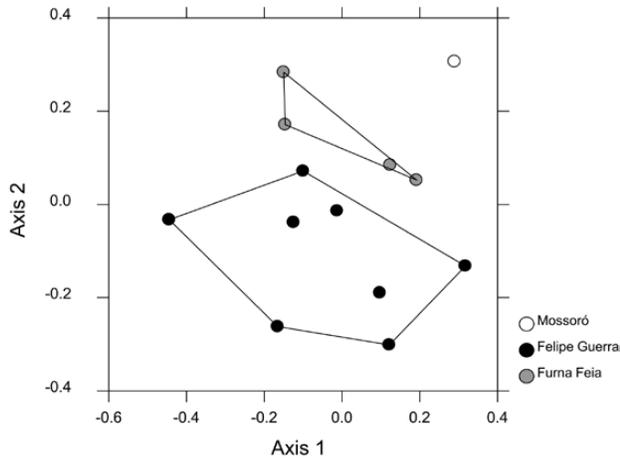


Fig. 2.—NMDS ordination for ranking size colonies of bat species of all sampled caves in RN State, Brazil. Of the original Bray-Curtis dissimilarity index, axis 1 retained 46.1% and axis 2 retained 23.7% with a stress = 0.169. Each point in the ordination represents a cave. Black points represent caves from the Felipe Guerra Cave System. Gray points represent caves from the Furna Feia National Park. Unfilled point represents the Gruta dos Trinta cave in Mossoró.

observed variation (Table 3). Additionally, in the second axis of the NMDS, the environmental variables (PCA1; $R^2 = 0.350$; $\omega\text{AICc} = 31.93$), human demographic density (PCA2; $R^2 = 0.330$; $\omega\text{AICc} = 26.83$), and livestock density ($R^2 = 0.330$; $\omega\text{AICc} = 26.53$) explained together 85.29% of the variance explained by all models. Models selected revealed that the species composition among the cave systems was affected strongly by the size of the cave, however, the natural environment and anthropogenic activity variables found around the caves also affected the structure of the sampled assemblages.

DISCUSSION

Effects on bat richness.—As predicted, the species richness in our study responded significantly to cave dimensions and cave connectivity. Although the regression of the cave size variable had a marginal significance on the richness, the model explained more than a third (38.46%) of the variance of all models. Larger caves tended to harbor relatively richer bat assemblages (Fig. 3a). This result supports a positive relationship between species richness of cave bats and cave dimensions, as reported in other caves (Arita 1996; Brunet and Medellín 2001; Cardiff 2006; Niu et al. 2007; Luo et al. 2013; Phelps et al. 2016; Torquetti et al. 2017). This relationship has been attributed to the higher probability of a larger and more structurally heterogeneous cave to offer more roosting sites for a greater array of species than a relatively smaller and less heterogeneous cave.

Such a correlation can be explained by the species–area relationship (Preston 1962). A factor that can affect the species–area relationship is habitat heterogeneity, where larger areas have a higher probability to contain more types of habitats and hence sustain more species than a smaller area (Connor and McCoy 1979). Brunet and Medellín (2001) addressed this relationship and found that the number of bat species in the studied

Table 3.—Model selection by Akaike information criteria (AIC) of all candidate models for explaining bat richness and species composition in a Caatinga of Rio Grande do Norte, Brazil. The R^2 in bold indicates significant regressions. Models in bold with $\Delta\text{AICc} \leq 2$ were selected. The Akaike weight (ωAICc) is provided by maximum likelihood estimates for all of the models. Cum ωAICc is the cumulative Akaike weight.

Models	R^2	ΔAICc	ωAICc	Cum ωAICc
Bat richness				
Cave (PCA1)	0.406	0.00	38.46	38.46
Cave connectivity (3 km)	0.337	0.56	29.11	67.57
Environmental (PCA1)	0.064	2.76	9.69	77.27
Livestock density (PCA 1)	0.0008	3.21	7.74	85.00
Human demogr. density (PCA 2)	0.0006	3.27	7.51	92.51
Null model	0.0000	3.27	7.49	100.00
Bat composition (axis 1 of NMDS)				
Cave (PCA1)	0.510	-1.54	85.41	85.41
Null model	0.000	3.34	7.43	92.84
Environmental (PCA1)	0.035	5.73	2.26	95.11
Cave connectivity (3 km)	0.002	5.73	2.25	97.36
Human demogr. density (PCA 2)	0.023	6.73	1.37	98.73
Livestock density (PCA 1)	0.011	6.88	1.27	100.00
Bat composition (axis 2 of NMDS)				
Environmental (PCA1)	0.350	0	31.93	31.93
Human demogr. density (PCA 2)	0.330	0.35	26.83	58.77
Livestock density (PCA 1)	0.330	0.37	26.53	85.29
Null model	0.000	2.17	10.81	96.11
Cave connectivity (3 km)	0.005	5.56	1.98	98.08
Cave (PCA1)	0.000	5.63	1.92	100.00

caves was significantly correlated with the cave surface area as a result of the higher spatial variation in microclimate conditions (humidity) and internal structural substrates (e.g., ceiling erosion domes) in larger caves. In our cave system for instance, the Furna Feia cave was both the largest surveyed cave and the richest in bat species (see Vargas-Mena et al. 2018b) with numerous erosion domes, tunnels, walls, cracks, and large halls.

Cave connectivity presented an effect on bat richness as well, consistent with our second prediction. In caves where the number of other surrounding caves was higher, the species richness tended to increase (Fig. 3b). This suggests that in clusters with more numerous caves, connectivity between caves would be more likely, hence affecting the richness of cave bats. The reasons why bat species are commuting and visiting other caves include search for new or better conditions for roosting (e.g., species microclimate preferences), social interactions, or search for a night roost (Kunz 1982). Night roosts promote digestion of food, provide retreat from predators, and serve as centers of social interactions and information transfer (Kunz 1982). Five species (*D. ecaudata*, *D. rotundus*, *A. planirostris*, *A. lituratus*, and *T. bidens*—see Vargas-Mena et al. 2018a) were detected using caves as a night roost and various individuals were captured entering into four different caves, some carrying food items (e.g., *A. planirostris* and *T. bidens*). Records of consumption of leaves have been recorded under *A. planirostris* night roosts in some of the surveyed caves (Cordero-Schmidt et al. 2016).

Other studies also have detected several species entering caves at night and presenting colonies with signs of exchange of individuals among caves (Campanha and Fowler 1993;

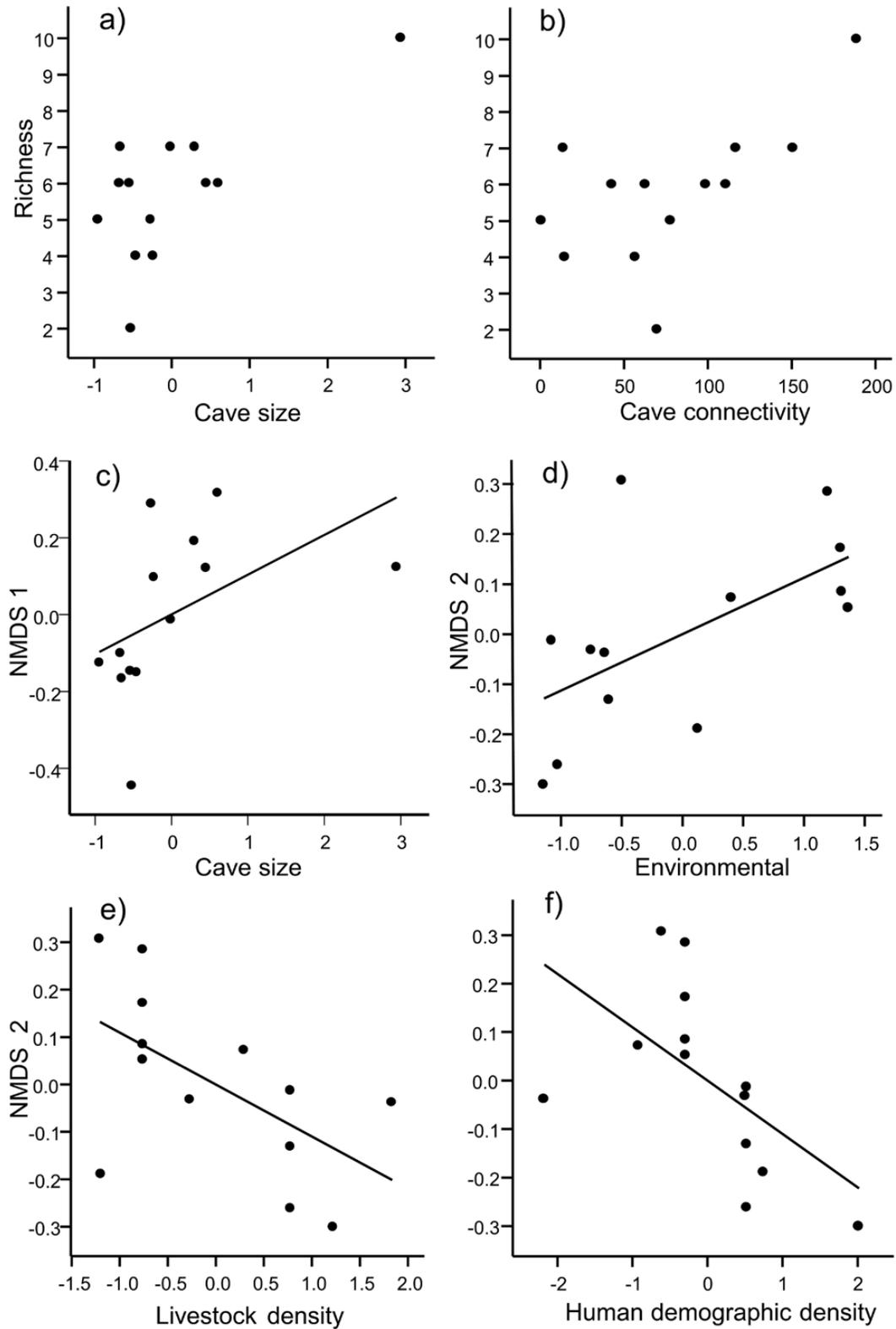


Fig. 3.—Relationships between species richness and (a) cave size and (b) cave connectivity (3 km); between species composition and (c) cave size in axis 1, and (d) environmental, (e) livestock density, and (f) human demographic density variables in axis 2 of the NMDS ordination of cave-roosting bat assemblages in two karstic landscapes in the Caatinga of Rio Grande do Norte, Brazil. Each point represents a cave. The black line presents the tendencies of the regressions.

Trajano 1996; Bredt et al. 1999; Siles et al. 2007). Trajano (1996) found that *D. rotundus* presented low roost fidelity, with individuals using multiple roosts probably attributed to the large number of favorable roosts in the studied area in southeastern Brazil. This might be indirect evidence of how cave proximity may promote movement of bats among caves and therefore increase the species richness of the surveyed caves. More detailed studies of movement and foraging patterns of bats are needed to understand better the landscape use and cave connectivity by bats in these karstic areas.

Effects on species composition.—All landscape variables affected bat species composition as expected, but cave size (internal variables) was found also to affect strongly species composition (Table 3). The cave size model explained 85.41% of the observed variance in axis 1 of the ordination (Table 3); in larger caves, the species composition tended to change (Fig. 3c). Larger caves could offer more roosting area and greater spatial variation of abiotic factors (light, temperature, and humidity) along the cave that may favor the formation of larger colonies by particular bat species.

Consistent with the findings of Arita (1996), Kofoky et al. (2007), and Niu et al. (2007), we observed that relatively larger caves in our study sites were occupied by more abundant assemblages and more intensively used by bats. For instance, the largest colony sizes (>category 4: *P. discolor*, *P. gymnonotus*, *G. soricina*) were found only in caves with relatively high values of HP, LD, Vol, and Area (e.g., Furna Feia, Gruta dos Trinta, Furna do Urubu; Table 1). Particularly, the colony of *P. discolor* found in the Furna Feia, with around 5,000 individuals, was unusually large considering that this species is known to form colonies of fewer than 400 individuals (Kwiecinski 2006). Similarly, common vampire bats (*D. rotundus*) presented colonies of >200 individuals in relatively large caves (Caverna Boa, Furna Feia, Furna Nova—Vargas-Mena et al. 2018b). *Desmodus rotundus* generally form colonies of 20–100 individuals (Greenhall et al. 1983); however, aggregations of 150–500 individuals have been recorded in other areas in Brazil (Uieda et al. 1996; Bredt et al. 1999; dos Reis et al. 2007). Such results suggest that large caves tend to favor the formation of uncommonly large colonies for some phyllostomid bats, at least in our studied Caatinga cave systems.

Additionally, we found that the size of the cave also can favor the occurrence of certain species that select caves of certain size, therefore affecting the species composition of the studied assemblages. The aerial-hawking, insect-eating *N. macrourus* (Spearman $\rho = 0.771$) was positively correlated in Axis 1 of the ordination with most of the internal cave size variables (Supplementary Data SD4, SD5). *Natalus macrourus* occurred only in caves with a large horizontal development and horizontal projection (>200 m; e.g., Gruta dos Trinta, Caverna Boa, Furna Feia, Furna Nova; Table 1). Natalid bats are strictly cave-roosting bats with specific roost microclimate preferences, where they occupy the most humid and hottest parts of caves (Arita and Vargas 1995; Torres-Flores and López-Wilchis 2010). These microclimate conditions are likely to be more stable in long and deep caves.

Conversely, the thumbless bat (*F. horrens*) was negatively correlated (Spearman $\rho = -0.645$) in axis 1 of the ordination with the cave size variables, suggesting that the species tended to occupy and form colonies in caves independently of cave size. However, the species tended to occur in caves that were neither large nor deep (e.g., Gruta Casa de Homens, Caverna do Arapuá, Gruta Capoeira João Carlos, among others) despite the fact that it was recorded also in large caves (e.g., Furna Feia and Gruta da Carrapateira (Table 1). *Furipterus horrens* preferred to roost in the aphotic zones of small chambers or narrow passages rarely surpassing 1.5 m in height and 3 m wide, forming colonies of 10–150 individuals, consistent with colonies studied in other Caatinga caves (Uieda et al. 1980). In the two karst areas studied, due to the large number of caves in these areas, it is likely that roosting sites with these characteristics are abundant and would explain why *F. horrens* had a high occurrence (8 of 13) among the studied caves (see also Vargas-Mena et al. 2018a).

Besides the strong effect of cave size, species composition was also significantly affected by both anthropic and environmental variables in Axis 2 of the NMDS (Figs. 3d–f). This is consistent with our third and fourth predictions since the environmental variables (31.93%), human demographic density (26.83%), and livestock density (26.53%) explained 85.29% of the observed variance of the species composition (Table 3). The extent to which these landscape variables affected the species composition was in a species-specific response and observed in the mean sizes of the colonies of the species shared between the two cave systems.

For instance, in FGCS, where livestock density values were higher than in FFNP, the hematophagous bats *D. ecaudata* and *D. rotundus* had larger colonies in the FGCS than in the protected area of the FFNP (Table 3), probably related to a stable and abundant food resource (blood) around caves in the FGCS. *Desmodus rotundus* is likely to prefer to feed from livestock rather than from native mammals in disturbed landscapes (Voigt and Kelm 2006), and a year-round resource might favor the formation and maintenance of large colonies of vampire bats. Caves in the FGCS such as Furna do Urubu and Caverna Boa contained the largest colonies of *D. rotundus* (>150 individuals), as well the highest densities of cattle, sheep, and goats. Similarly, in the karstic area studied by Trajano (1996) in southeast Brazil, colonies of *D. rotundus* were larger and remain stable year-round in caves that were close to areas where livestock was abundant nearby.

The hairy-legged vampire bat (*D. ecaudata*) also had a positive relationship with livestock and human density variables. *Diphylla ecaudata* is considered a rare bat within its total distribution (Gardner 2007), but in the studied caves this species had a high occurrence, especially in the FGCS (Vargas-Mena et al. 2018b). The high abundance of *D. ecaudata* in FGCS might be related to free-range poultry farming, an activity commonly observed in many houses in FGCS. *Diphylla ecaudata* feeds only on bird blood (Greenhall et al. 1984), but recently Ito et al. (2016) found that in a disturbed area of Caatinga where wild birds are scarce, *D. ecaudata* fed on blood from domestic birds

and humans as well, suggesting its dietary flexibility in a landscape with high human activity.

The environmental natural landscape variables also have their role in the structure of the species composition, and explained 31.93% of the variance (Table 3). Caves located in areas with higher natural environmental components (shorter distance to lakes and rivers, greater percent of Caatinga coverage) tended to present different species composition (Fig. 3d). This was observed, for example, with the species composition of the assemblages of the FFNP. Mean colony sizes of the animalivorous *T. bidens* were larger in the national park than in FGCS (Table 2) and most of the caves in national park had a very high percentage of Caatinga coverage (>94%). This suggests that in karstic Caatinga landscapes with low anthropic activities and high forest cover, animalivorous bats can be more abundant than in disturbed landscapes, consistent with Medellín et al. (2000), Meyer and Kalko (2008), and Farneda et al. (2015).

The distance to a water body (lake or river) also had a role in the species composition in FGCS. The Apodi River, the second largest river in RN, passes through the FGCS. The river is likely creating a heterogeneous landscape with more foraging habitats near the river (e.g., riparian Caatingas, water bodies) and more prey availability for a wider array of animalivorous species (e.g., *C. auritus*, *T. cirrhosus*) than in the FFNP, which lacked the presence of a water body within the park.

Although the FGCS harbored a high richness of forest-dependent species, assemblages showed a predominance of species that adapt easily to human-modified landscapes (e.g., vampire bats). If the disturbance persists in the FGCS, vampire bat colonies are expected to become more numerous, especially in larger caves, as we found in this study. Therefore, larger populations of hematophagous bats would increase not only the risk of epizootic outbreaks (e.g., rabies) affecting local animals and humans (Streicker and Allgeier 2016), but would also lead to species-poor assemblages dominated by vampires and generalist bats.

Inside or outside?—Our approach has led to insights on how both internal and external variables structure the assemblages of cave-roosting bats. The internal factors related to cave size had the strongest effects on richness and species composition, but proximity of cave roosts also was a factor affecting species richness. These results reinforce that the roosts overall are a critical component in the life of the bats. However, in areas with high cave densities, such as the studied karstic system, both anthropic and natural landscape components can also affect the structure of the cave bat assemblages depending on the landscape context in which a cluster of caves is located, at least at the spatial scale evaluated herein.

Finally, although the FGCS presented a very high diversity of cave bats, including colonies of three vulnerable species in Brazil (*F. horrens*, *N. macrourus*, and *L. aurita*), the karstic system harbors a landscape modified by human activities that directly or indirectly affect bat populations in many parts of the world (e.g., illegal mining, ranching, deforestation; Voigt and Kingston 2016). Such a scenario reinforces the need for the protection of the speleological and biological heritage of this area, as proposed by Bento et al. (2015).

Bat conservation efforts in karst landscapes should consider the protection of multiple caves such as those in the Furna Feia National Park (Bento et al. 2013), hence the protection of the assemblages of cave-roosting bats, their associated cave fauna, and the ecosystem services these flying mammals provide. More studies on the cave bats of RN and their ecological dynamics in these cave systems are needed for the generation of accurate data to be used in future conservation of these unique karstic landscapes.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Description of variables used to perform models to explore the effects on the richness and composition (rank colony size) of cave-roosting bat assemblages in the Caatinga of Rio Grande do Norte, Brazil.

Supplementary Data SD2.—Caves selected for analysis in this study, with their corresponding values of internal and external extracted variables in the Rio Grande do Norte, Brazil. Acronyms are: latitude (Lat), longitude (Long), cave linear development extension (LD), cave horizontal projection (HP), cave area (A), cave volume (V), cave internal unevenness (Unev), all in meters (m); human population density (HumD), sheep density (SheepD), goat density (GoatD), cattle density (CattleD), all in individuals per hectare (Ind/ha); distance to rivers (RivD), distance to lakes (LakeD) in meters (m); and Caatinga forest coverage (Caa) in percentage (%).

Supplementary Data SD3.—Loadings of PCAs performed for cave, environmental, and population density variables of sampled caves in RN State, Brazil.

Supplementary Data SD4.—Spearman correlation of NMDS ordination axes with the ranking colony size of each bat species sampled in 13 caves in RN State, Brazil.

Supplementary Data SD5.—Spearman correlation of NMDS ordination axes with the explanatory variables (cave-size, environmental, and population density variables) for the species composition of cave bats in 13 caves in RN State, Brazil.

Supplementary Data SD6.—Candidate models used to test the effect of the explanatory variables on the richness and species composition of cave-dwelling bats in Rio Grande do Norte, Brazil.

Supplementary Data SD7.—Candidate models used to test the effect of the explanatory variables of cave connectivity on the richness and species composition of cave-dwelling bats in Rio Grande do Norte, Brazil.

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