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Does size matter? Bat diversity and the use of rock shelters in Brazil

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Abstract: A positive correlation between cave size and bat diversity has been recorded by some authors for different cave areas in South America. We analyzed published and otherwise available data from three Brazilian karst areas and phytogeography domains, including NE and SE Atlantic Forest and Cerrado (savannah-like vegetation), encompassing a wide range of cave sizes. We found no such correlation, as expected in view of previous observations by researchers and speleologists. We discuss the ecological implications of different ways to measure bat diversity, i.e. the accumulative number of species (sequential use of caves) vs. the number of species at a given occasion (species in actual cohabitation) vs. bat abundance (numbers of individuals), as well as speleological topics related to the concept of caves (based on an anthropomorphic definition, not applicable to other species), the problems of estimating topographic variables such as cave area and volume, and the value of including cave temperatures in the analyses. Multiple interacting variables may influence the composition of cave bat communities and bat species richness and abundance. The most important ones would be the density of caves in a given area (related to lithology – calcareous vs. siliciclastic caves), regional climates, and degree of preservation of epigean habitat. Cave morphology, number and size of entrances, and presence of water bodies, as well as interactions with other species, must also be considered. In conclusion, as a general statement for tropical and subtropical bats, cave size (in the human sense) by itself does not matter, except perhaps for one-off situations. Finally, a brief overview of the diversity of cave bats in Brazil is presented.

Key words: bats; caves; Brazil; use of shelter; cave size.

Introduction

Bats have long been the organisms most frequently associated with caves. Caves are favored shelters for many taxa due to the protection against climatic extremes and scarcity of predators, especially for relatively large-bodied animals. On the other hand, due to the low diversity and species richness and abundance of subterranean organisms, rock shelters in general do not offer enough food for the maintenance of self-sustained populations of these high

energy-demanding homeothermic animals. Hence, bats must leave their shelter daily (or nearly) to feed.

Subterranean organisms (cavernicoles sensu lato) have been defined as evolutionary units responding to subterranean selective regimens. Subterranean habitats provide resources, e.g. food, shelter, substrate, and climate, which directly affect survival/reproductive rates (Trajano and Carvalho 2017).

Animals that use subterranean spaces regularly but must leave periodically (following daily, annual and other cycles) to complete their life cycles are classified as trogloxenes according to the Shiner-Racovitza system (Barr 1968; Camacho 1992; Trajano and Carvalho 2017). Bats are typical trogloxenes, using subterranean habitats as shelter, which favors survival and reproduction, hence affecting population dynamics. They may use caves and smaller rocky spaces as diurnal shelter, permanently or cyclically, or as nocturnal roost, in a temporary way between feeding bouts as a safe place to rest, digest, or even escape night predators. They may be found as isolated individuals or in small groups, to more or less stable colonies, with dozens to hundreds or thousands, or even millions of individuals (Dalquest and Walton 1970; Nowak 1994).

Obligatory trogloxenes depend on both epigean and subterranean resources (Trajano and Carvalho 2017); therefore, their distribution is correlated with the occurrence of rocks favoring the opening of subterranean spaces. Recognition of obligatory trogloxenes depends on good data on biology, population ecology, and distribution of species, indicating that the epigean distribution is strongly correlated to the presence of rocky shelters in the area. There are instances of obligatory trogloxenes among bats in temperate regions, such as *Myotis sodalis* (Miller & Allen, 1928) and *M. lucifugus* (Le Conte, 1831), which have a relatively wide distribution in North America, but are dependent on a small number of caves for hibernation (Kunz and Reichard 2010; Menzel et al. 2001). Bats from tropical and subtropical regions do not hibernate, and there is no selective physiological pressure for large aggregations. When such aggregations occur, with hundreds to thousands of individuals, it is mostly a result of large regional population sizes combined with low shelter availability (Trajano 1985).

Several variables are potentially involved in the use of rocky shelters by bats. Lithology and regional climate, as major determinants not only of cave morphology (size, shape, number, and position of entrances), and, consequently, of speleoclimate (cave temperature, humidity, air circulation), but also the density of caves in a given area, are probably the most important factors. The presence of permanent water bodies, species in cohabitation, phytogeography, and preservation degree of contiguous epigean habitats are other variables (Trajano 1996; Vargas-Mena et al. 2020).

Some authors have found some positive correlation between cave length and bat richness in South American cave areas such as Lagoa Santa karst area/MG, eastern Brazil (Torquetti et al. 2017), Rio Grande do Norte State, northeastern Brazil (Vargas-Mena et al. 2020), Tocantis State, Central Brazil (Barros et al. 2020), and eastern Bolivia, Brazilian-Paranaense biogeographic region (Lizarro et al. 2020). However, the studied caves were quite small, most less than 200 m long.

Aiming to test the generality of the hypothesis of correlation between cave size and bat diversity in a much wider range of cave sizes, we analyzed data from the literature concerning three well-studied Brazilian karst areas with a focus on cave size vs. bat richness and abundance: the Alto Ribeira, São Paulo State, southeastern Brazil (Arnone 2008; Trajano 1985) the Rio Pardo karst area, southern Bahia State, northeastern Brazil (Santos 2001) (both in the Brazilian Atlantic Forest), and the Distrito Federal, central Brazil (Bredt et al. 1999), in the Cerrado (savannah-like biome). For comparison, we re-analyzed data from Vargas-Mena et

al. (2020) with a focus on the caves' lengths.

We also discuss the pitfalls of quantifying variables that could influence the use of rock shelters by bats, including the problem of using speleometry, which is based on a human perspective of size (distinct from the perspective of other subterranean animals, usually smaller and with different locomotor and sensorial abilities), and also the different ways of measuring bat diversity, which have distinct ecological meanings.

Many studies on cave bats reveal an incomplete understanding of the habitat actually used by these and other subterranean animals, based on an anthropocentric approach to the subject. In order to provide an ecological and taxonomic context for the analyses, we also present a review of the diversity and composition of bat communities in Brazilian caves, with comments on shelter preferences based on the literature and our own observations on Brazilian caves.

Bats and caves: the problem of using speleomorphometric data in biology

Few researchers working on cave bats realize that the term "cave" corresponds to an operational concept. According to the widely accepted definition, caves are natural spaces in the subsurface accessible to humans (Ford and Williams 2007). This is clearly an anthropocentric concept devoid of general biological meaning, as it is dependent on the body size of a particular species. As a matter of fact, caves are the human-accessible components of much wider networks of interconnected spaces in the subsurface, with heterogeneous sizes and filled with water and/or air.

Most caves, including the largest ones, are karst caves. Karst areas consist of surface-relief and surface-underground hydrographic networks resulting from water circulation and its aggressive chemical and physical action in conduits, joints, fractures, bedding plains, and cracks along the layers of soluble rocks, especially carbonate rocks (such as limestones and dolomites), and, to a lesser extent, siliciclastic rocks (quartzites, sandstones). Karstification results in structurally complex features, both in surface and smaller spaces and, consequently, in heterogeneous substrates (Bonacci 2009; Ford and Wiliams 2007). Sheltered crevices, concavities in the ceiling and walls, and other discontinuities with favorable microclimate for bats, are common in limestone caves (E. Trajano pers. obs.).

Bats are much smaller than humans, therefore it is reasonable to suppose that the extension of habitat potentially used by bats for shelter, life activities such as grooming, social activities and reproduction, and movements (exploratory flights, emergence, and return to the shelter) may considerably exceed that of humans. Also, bats may use openings to the surface too small for humans. Hence, the minimum distances traveled by bats inside caves do not necessarily correspond to the distance between their roosts and the entrances used by humans. As a matter of fact, speleologists frequently use bat movements as a clue to reveal openings to the surface, including new accessibility. Therefore, it would be more appropriate and biologically meaningful to refer to bats using caves (in the human sense) and smaller rock spaces as lithophiles (bats that use some abiotic substance such as rock, soil, etc. – Verschuren's classification apud Dalquest and Walton 1970).

It is noteworthy that most caves with high concentrations of bats are isolated caves or those located in small karst areas, with relatively low availability of rock shelters. This situation is more common in non-calcareous areas, less prone to the opening of subterranean spaces. That is the case of caves in siliciclastic rocks, such as quartzites and sandstones. On the other hand, in large karst areas, such as the Alto Ribeira, bats frequently form itinerant colonies, moving between caves both on seasonal and non-seasonal bases (Trajano 1985).

Vargas-Mena et al. (2020) included cave width and volume among variables potentially

influencing bat diversity in caves; by definition, the width axis is the shorter of the horizontally oriented axes (Chabert and Watson 1981). However, these data are not fully comparable among caves from distinct regions and mapped by different speleologists.

For bats using rocky shelters, the morphometric variables most likely to influence bat diversity and the position of colonies are the distance to the openings used for the emergence and return and the area of the ceiling plus walls above 2 m of height, where bats are usually seen (E. Trajano pers. obs.).

Currently, cave scanning is the only method producing realistic and comparable morphometric data, but its use is still very limited in Brazil. Therefore, data on cave lengths available in national cadasters are usually based on the horizontal projections on maps (map length). Map length is projected onto a horizontal plane without consideration of vertical components, whereas linear development is on a line that follows the actual orientation of cave passages in three-dimensional space (Chabert and Watson 1981). Therefore, using map lengths results in length sub-estimations at variable levels depending on the conduit inclination.

Conduit widths, used to calculate areas, pose additional difficulties because there are different ways of measuring them: some authors measure the width at the level of the compass, which may be on the floor, at the waist, or at the eyes level, while others estimate an average width best representing the conduit (Rubbioli and Moura 2005; E. Rubbioli pers. comm. 2022). This is a problem because cave walls are rarely vertical – in cross-section, cave conduits may be elliptical or bell-shaped (young passages), or quite irregular (older conduits). This absence of standardization introduces an element of subjectivity, which is amplified when height is added to calculate volume, because cave ceilings are usually quite irregular.

In order to determine volumes, a large number of width and height measurements is required, and linear development must be measured in a way that excludes counting any space more than once, i.e., using discontinuous linear developments (Chabert and Watson 1981). Consequently, areas and volumes inferred directly from maps are prone to random errors, which can be up to 300 percent (Calux 2018). In other words, strictly speaking, volume is a parameter that can only be used in case all of the sampled caves have been scanned.

These data only make sense in the speleomorphometry context, which is an anthropocentric activity. For terrestrial animals, the relevant variable is the actual ground area. For bats, which roost on the ceiling and high in the walls, this is the area to be considered. Moreover, in view of the delicate energetic balance between the costs of homeothermy, flight, and other activities and the amount of food ingested, it is reasonable to hypothesize that bats tend to optimize foraging movements, minimizing distances traveled inside the shelter. Thus, it is expected that bats select roosting places which are both ecologically favorable and as close as possible to emergence points practicable to bats.

How to measure cave bat richness? Simultaneous vs. sequential use of rock shelters

Taxonomic diversity (species richness) may be expressed in two ways: the number of species simultaneously inhabiting a site, i.e., species recorded at a given collecting occasion, and the cumulative number of species recorded at a given time in this site (Trajano 1985). These ways of expressing diversity have distinct ecological meanings: the former refers to species actually sharing resources and potentially interacting, whereas the latter includes both species in actual cohabitation and those intermittently using such habitat.

Due to methodological limitations, a single collecting occasion is hardly sufficient for a sample representative of the target taxon or community living in the studied habitat. The increasing number of species in accumulation curves may be due to: i) the addition of species that were there from the beginning but that are difficult to sample, such as rare species or

those with aggregate or mosaic distributions; ii) intermittent presence in the locality, due to recruitment and to cyclical and non-cyclical movements. The occurrence of intermittent species should not be underestimated, because such organisms are ecologically relevant – their presence may affect other species and, on the other side, the use of a given habitat, even sporadic, may have consequences for the whole species.

Trogloxenes, such as bats, are a good example: the sheltered conditions in subterranean habitats may increase the survival chances and favor reproduction, thus affecting the population dynamics of the species, including individuals which do not use such habitats. On the other hand, trogloxenes interact with other subterranean organisms, as predators, competitors, and food (guano and dead bodies), affecting the whole community.

Unfortunately, few authors, such as Trajano (1985), Arnone (2008) and Santos (2001), make the necessary distinction between the maximum number of species recorded on one occasion and the accumulative number of species in a given habitat. In general, only cumulative numbers of species are presented.

Bat abundance is another measure of richness sensu lato. Total numbers of individuals are the outcome of resource availability, especially shelter, and food, and are not necessarily correlated with taxonomic richness. They provide a rough measure of abundance, somewhat biased towards phyllostomids, because aerial insectivores such as vespertilionids, emballonurids, and mollossids escape capturing more easily by detecting mist-nets (and other collecting devices) and flying around them. Therefore, such numbers must be used with caution.

Materials and Methods

Study sites

The studied sites are limestone karst areas, with distinct climatic and phytogeographic characteristics. The Alto Ribeira and Rio Pardo karst areas are located respectively in the southeastern and the northeastern Brazilian Atlantic Forest, whereas the Distrito Federal (referred to as DF from now on) is in the Cerrado biome, Central Brazil.

The study area (24°26'-24°45'S 48°35'- 49°00'W) in the Alto Ribeira karst area is situated in SE São Paulo/NE Paraná States, Upper Ribeira river basin, mostly in Iporanga Co. It is defined geologically by the presence of Pre-Cambrian metasediments of the Açungui Group, consisting mostly of carbonates such as limestones and dolomites-oriented NE-SW, intercalated with insoluble rocks, mainly phyllites (Rubbioli et al. 2019). The area is in the transition between the Tropical Atlantic and the Araucaria Forest domains; the climate is subtropical humid, without a typical dry season, and the mean annual temperature is around 18-19°C. It represents one of the last continuous, relatively well-preserved remnants of the Brazilian Atlantic Forest, mostly protected by two contiguous conservation units, the Parque Estadual Intervales (PEI), and the Parque Estadual Turístico do Alto Ribeira (PETAR) (Trajano et al. 2016). Nevertheless, the intense visitation, mostly as speleotourism, and the presence of residents with livestock and family agriculture inside and around these parks impact the natural ecosystems (Arnone 2008; E. Trajano pers. obs.).

The Alto Ribeira presents a high concentration of subterranean spaces. Due to the hilly landscape, the caves greatly vary in morphology – from nearly horizontal to vertical caves (the majority among the deepest in the country); from large, spacious to labyrinthine narrow conduits; from one to multiple entrances with variable dimensions – and size – from a couple of meters to the largest in the area, Santana Cave, with more than 8 km in horizontal projection, including permanently and seasonally dry caves and those crossed by permanent streams (updated from Trajano 1985). Thirty-seven caves and two abandoned mines caves in the Alto

Ribeira, lengths from 25 to ca. 8,700 m, were surveyed by Trajano (1985) (four caves and the mines have been excluded from the present analysis due to the absence of reliable data on length); 10 caves (60-8,700 m) were chosen for the subsequent population study (Table S1b). Ca. 25 years later, Arnone (2008) replicated the population study by Trajano (1985), in the 10 caves previously selected (Table S1c). Santos (2001) studied eight caves, 45 – 250 m long, in the Rio Pardo karst area, southern Bahia State, northeastern Brazil (Table S2). Bredt et al. (1999) surveyed 20 caves, their length varying from 20 to 432 m, in the DF region, Central Brazil (Table S3). We also re-analyzed data from Vargas-Mena et al. (2020) in order to compare them with our own (Table S4).

The Rio Pardo karst area (15°20'-16°00'S 39°10'-39°45'W) is a small and isolated region at South Bahia State, Low Pardo and Jequinhonha river basins. It is situated at the SE edge of São Francisco Craton, Rio Pardo geological Group, characterized by the presence of metacarbonates, with few notable karst features. The Rio Pardo area encompasses two climatic types in the Koppen classification: type Af, humid tropical climate without a defined dry season, annual precipitation above 1,400 mm and mean temperatures above 24° C; and type Am, with a short dry season in August-September (Santos 2001). The Atlantic Forest is suitable for shade cacao plantations ("cabruca"), which helps to preserve many forest species, including bats (Faria et al. 2007; Sambuichi and Haridasan 2007). However, due to the decline of cacao prices in international markets, "cabrucas" have been replaced by much more disturbing economic activities such as livestock farming and traditional agriculture. There are few notable features, and the caves are relatively small (up to 300 m). Compared to the Alto Ribeira, the caves of Rio Pardo are more homogeneous, generally small (less than 300 m of linear development), horizontal and dry, except for Pedra Suspensa Cave (see Table S2), which is described as constantly humid.

The study area of Bredt et al. (1999) (15°30'-16°03'S 47°25'48o12'W) is situated in the Distrito Federal (DF) and surroundings, the territory of the Brazilian capital, Brasilia, inserted in East Goiás State, Central Brazil. It is characterized by the presence of limestones and silicyclastic rocks (sandstones, siltstones, mudstones) of the Bambui Group, Paraopeba Formation, at the Cerrado (savannah-like vegetation) core area. The climate is tropical with two distinct seasons, a warm and rainy season from October to April, and a cool, dry season from May to September. Twenty caves have been surveyed, which were predominantly horizontal and dry, except for Gruta dos Morcegos, Água Rasa, and Dança dos Vampiros, crossed by permanent creeks, and Volks Club, crossed by a temporary watercourse; some caves have been excluded from the present analyses due to absence of reliable data on length. Caves of the DF area are small; among caves known in the late 1990s, 60% were less than 100 m long, and 25% were 100 - 300 m long; the largest cave studied by Bredt et al. (1999) was Fenda II, 430 m long (Table S2).

Methods

This study is based on a re-analyses of literature data (published papers and unpublished theses). Cave length was updated based on the Cadastro Nacional de Cavernas do Brasil (CNC), Sociedade Brasileira de Espeleologia (SBE). In the few cases when linear development was unavailable, we used the horizontal projection when it was higher than the length recorded in the original publication.

We analyzed bat richness in terms of the cumulative number of species and bat abundance recorded in the three presently studied Brazilian karst areas; in the case of Trajano (1985), the only publication also showing the maximum number of species at a single collecting occasion, these data are included in the analyses. Comparison with literature data is based on

the cumulative numbers of species. We used the total number of individuals captured in each cave to measure bat abundance (infants carried by mothers were not counted). This is an approximation because the number of bats flying above the mist-nets used for capture was higher in high entrances (where most collections have been done) and conduits.

For a possible relationship between abundance, richness, and maximum richness with development, Spearman's correlation was calculated and analyzed using the "ggpubr" package and the R software (version 4.1.). For the relationship of richness with development, temporal data for the Alto Ribeira karst, the Rio Pardo karst, and the Distrito Federal karst were analyzed separately and grouped (Group 1). For the relationship of abundance with development, we analyzed the two temporal data for the Alto Ribeira karst, the Rio Pardo karst, the Distrito Federal karst, and the group of all three karsts (Group 2). Data from the Caatinga karst studied by Vargas-Mena et al. (2020) were also analyzed but not included in the groups because the sampling methodology differed from the others. For the relationship of maximum richness with development, we used one sampling occasion for Alto Ribeira karst. First, the analysis was performed using all caves of the same series, and later the cave with the biggest development was removed in order to see the influence of possible outliers.

Results

Diversity of lithophilous bats in Brazil

Patterns of cave occupancy and preference have emerged from studies in limestone and sandstone karst areas, including sets of caves and isolated ones, carried out in the 1980-90s and situated in different phytogeographic domains: Atlantic forest – Alto Ribeira/SP (Arnone 2008; Trajano 1985), Corumbataí/SP (Campanhã and Fowler 1993), Rio Pardo/BA (Santos 2001); Cerrado – Distrito Federal (Bredt et al. 1999) and Mambaí/GO (Ésberard et al. 2001); Amazon Forest – Altamira-Itaituba/PA (Trajano and Moreira 1989); and isolated caves in different biomes (Gregorin and Mendes 1999; Silva et al. 2001; Trajano and Gimenez 1998; Uieda et al. 1980;). These patterns were corroborated by studies in the last decades in various biomes, mostly Caatinga (semiarid dry forest) and Cerrado (e.g., Bichuette et al. 2018; Cajaiba 2014; Cajaiba et al. 2021; Esbérard et al. 2005; Felix et al. 2016; Guimarães and Ferreira 2014; Otálora-Ardila et al. 2019; Portella 2010; Schmaedecke et al. 2019; Silva et al. 2009; Zortéa et al. 2015;). We present a summary of these data.

In rural areas and nearby, where livestock represent an abundant food source for hematophagous animals, common vampire bats, *Desmodus rotundus* (Geoffroy 1810), may be by far the commonest cave bats, forming colonies with dozens to hundreds of individuals. The hairy-legged vampire, *Dyphilla ecaudata* (Spix 1823), occurs in caves throughout the country, but usually in small numbers.

In accordance with the observed in epigean habitats, the omnivorous/frugivorous *Carollia perspicillata* (Linnaeus 1758) is ubiquitous in caves throughout the country, forming colonies with dozens to hundreds of individuals. Nectarivores (glossophagines and lonchophyllines) are also common in caves, their diversity increasing in tropical areas. *Anoura caudifer* (Geoffroy 1818) is common in the subtropical Alto Ribeira, whereas the common glossophagine *Glossophaga soricina* (Pallas, 1766) and *A. geoffroyi* (Gray, 1838) are rare in these caves, contrary to caves observed northwards. Diversity at genus and species levels increase in tropical caves, especially in open areas, where representatives of the genera *Lonchophylla* (Thomas, 1903), *Lionycteris* (Thomas, 1913), and *Choeroniscus* (Thomas, 1928) have been found, in addition to *Anoura* (Gray, 1838) and *Glossophaga* (Geoffroy, 1818).

The "phyllostomines" (including Lonchorhininae, Micronycterinae, Glyphonycterinae)

are cave bats par excellence. These bats are frequent in karst areas, indicating frequent and intense use of such shelters. Most genera have subterranean representatives throughout Brazil, such as *Chrotopterus auritus* (Peters, 1856), *Lonchorhina aurita* (Tomes, 1863), *Micronycteris* spp., *Mimon bennetti* (Gray, 1838), *Trachops cirrhosus* (Spix, 1823), *Tonatia bidens* (Spix, 1823), *Phyllostomus hastatus* (Pallas, 1767) (frequent in tropical areas), and, to a lesser extent, *Phylloderma stenops* Peters, 1865, *Phyllostomus* spp., *Glyphonycteris* spp., *Macrophyllum* (Schinz, 1821), and *Lophostoma brasiliense* Peters, 1867. *Vampyrum spectrum* (Linnaeus, 1758) is limited to a record of one individual in a sandstone cave in Pará State, Amazonian region (Zortéa et al. 2015), probably in an exploratory flight or hunting other bats.

On the other hand, sternodermatines are less frequent in caves than expected in view of their diversity in epigean habitats. Few exceptions are *Platyrhinus lineatus* (Geoffroy, 1810) which may be frequent in tropical caves, *Artibeus* bats such as *Artibeus lituratus* (Olfers, 1818) and *A. planirostris* (Spix, 1823), and *Sturnira lilium* (Geoffroy, 1810); *A. fimbriatus* (Gray, 1838) is common in the Alto Ribeira karst area. A few other sternodermatines have been recorded in collections at cave entrances, e.g., *Chiroderma doriae* (Thomas, 1891), *Pygoderma bilabiatum* (Wagner, 1843), *Sturnira tildae* (de la Torre, 1959), *Artibeus cinereus* (Gervais, 1856)), probably as individuals in exploratory flight. In fact, stenodermines are known to use vegetation as shelter, and their diversity in caves is lower than expected in view of the diversity in epigean habitats (Arnone 2008; Ésberard et al. 2005).

In accordance with the epigean distribution, mormoopids (*Pteronotus* spp.) may form huge colonies in tropical caves, especially in relatively well-preserved areas with few caves. Among the small aerial insectivorous bats, *Natalus macrourus* (Gervais, 1856), *Furipterus horrens* (Cuvier, 1828), and emballonurids, in particular *Peropterix* spp., occur in caves throughout the country.

On the other hand, in contrast with temperate regions, the only vespertilonid frequent in Brazilian caves is *Myotis nigricans* (Schinz, 1821), a relatively common bat throughout the country. However, other vespertilionids found throughout the country have not been recorded so far in caves. There are rare records of *M. riparius* (Handley, 1960) and *Lasiurus ega* (Gervais, 1856) (Alto Ribeira karst area) and *Epitesicus brasiliensis* (Desmareste, 1819) (Distrito Federal), probably as individuals in exploratory flights. Likewise, records of Brazilian molossids in rock shelters are rare and localized, with the highest numbers, *Nyctinomops laticaudatus* (Geoffroy, 1805) and *Molossus molossus* (Pallas, 1766), being observed in the Amazonian forest. Except for *M. nigricans*, representatives of these two families are less frequent in Brazilian caves than expected in view of the observed epigean diversity, indicating a preference for other types of shelters.

The three presently studied karst areas are examples of the dominance of vampires, *D. rotundus*, due to the presence of domestic animals nearby. They are not only the most frequent species in the caves, but also the most abundant: in the Alto Ribeira, for instance, 44% of the total number of captured individuals belonged to a single species (among 19 recorded species), the common vampire, *D. rotundus*, with occurrence in 65.6% of the 34 studied caves; they were followed by *C. perspicillata* (11% of individuals in 56% of caves) and *A. caudifer* (8.5% of individuals in 37.5% of caves). In the Distrito Federal area, common vampires correspond to 55% of the total number of individuals captured, occurring in 90% of the studied caves, followed by *G. soricina* (6% of individuals in 75% of caves) and *C. perspicillata* (9% of individuals distributed in 40% of the studied caves).

Anoura geoffroyi is the second most abundant species in DF (10% of the individuals), but occurs in only 20% of the caves. Likewise, in the Alto Ribeira, *A. geoffroyi* corresponded

to 9% of individuals, all from a single cave. In contrast with abundant species such as *C. perspicillata* and nectarivores such as *G. soricina* and *Lonchophylla dekeyseri* (Taddei, Vizotto & Sazima, 1983) (in DF), and *A. caudifer* (in the Alto Ribeira), which spread through the available shelters, *A. geoffroyi* tend to concentrate in few caves, forming colonies that are quite large, with hundreds of individuals.

Cave size versus species richness and abundance

No significant correlation between cave length and bat diversity, including species richness and abundance, was obtained for any of the three studied Brazilian karst areas (Table 1; Figs. S1-14). These areas differ in geomorphology, hydrogeography, and climate, hence in karst features, including caves. The studies were carried out by distinct researchers; thus they may be considered as independent replicas.

Re-analysis of data provided by Vargas-Mena et al. (2020) focusing on cave development vs. bat richness revealed a positive correlation only when Furna Feia cave, a size outlier (ca. 740 m), was included. There was no significant correlation for the remaining 12 caves, their sizes varying between ca. 30 and 285 m.

Discussion

Multiple interacting variables influence the use of rocky shelters by bats. As mentioned above, lithology (including mineral composition, rock structure, stratification, etc.) and regional climate, as major determinants not only of cave morphology (size, shape, number, and position of entrances), consequently of speleoclimate (cave temperature, humidity, air circulation), but also the density of caves in a given area, are probably the most important factors. The presence of permanent water bodies supplying moisture may favor the occupancy by bats, but noisy running water may be a problem for echolocation. The presence of other species may interfere with the occurrence of a species in a given shelter, either in the sense of attraction or avoidance (Trajano 1985). The type and preservation degree of epigean systems (pristine vs. disturbed), which provides food resources, is another important variable to be considered.

Table 1. Spearman (Cor.) and the significance values between the different study areas. Significance values in bold.

Local	Richness x Development		Abundance x Development		Max Richness x Development	
	Cor.	p value	Cor.	p value	Cor.	p value
Alto Ribeira karst A	0,03	0,86	0,21	0,22	-	-
Alto Ribeira karst B	-0,47	0,17	-	-	-0,46	0,18
Alto Ribeira karst C	-0,39	0,26	0,47	0,17	-	-
Rio Pardo karst	0,33	0,42	-0,38	0,36	-	-
Distrito Federal karst	0,14	0,6	0,03	0,9	-	-
Group 1	-0,06	0,57	-	-	-	-
Group 2	-	-	-0,04	0,73	-	-
Caatinga karst	0,67	**0,00**	-	-	-	-
Caatinga karst WO	0,24	0,45	-	-	-	-

WO, without the highest value.

Comparison between bat communities from ten selected caves in the Alto Ribeira karst area in the 1980s (Trajano 1985, 1996) and 25 years later (Arnone 2008) revealed differences in community structures, but not in total richness – Arnone recorded five rare species not found by Trajano (1985). However, he did not find four among those recorded by the latter author. This occurred despite increased touristic activities in several caves, including part of those studied by both authors (Tables S1a-b).

Due to the buffering properties of the soil and underlying rocks, cave temperatures tend to stabilize progressively and rapidly from the entrances inward (zone of variable temperature) around the regional mean annual temperature (zone of constant temperature); in the warm season, air temperature in the variable zone decreases with distance to the entrances, the opposite occurring in the cool season. Thus, measurements year-round and at different annual cycles are needed to characterize the speleoclimate of a cave. Moreover, the length of the variable zone may vary among caves according to the size and position of the entrances, but it is usually relatively short, some dozens of meters, except for caves and conduits with unidirectional air circulation (wind tubes) – subterranean spaces with two entrances at the opposite ends and with a significant difference in topographic level (Racovita 1975).

Some bats are regularly observed in the twilight zone, near or at cave entrances, such as emballonurids and *Chrotopterus auritus* throughout the country (E. Trajano pers. obs.), *Artibeus lituratus* and, occasionally, *Nyctinomops laticaudatus* in southern Brazil, and natalids and *F. horrens* in the Amazon region (S.M. Pacheco pers. comm.). However, most bats roost deeper in the subterranean realm. Therefore, cave air temperatures are unlikely to significantly differ among caves in the same area – differences around 0.5 are usually considered too small to influence bat distribution inside caves.

Some authors found a positive correlation between cave length and bat richness. However, in all cases, the studied caves were quite small. This is the case of Torquetti et al. (2017), who surveyed 66 caves, lengths from 3 to 60 m, in the Lagoa Santa karst area, Minas Gerais State. These authors did not explain the reason for selecting such small caves in a region with hundreds of caves, several more than 1 km long. Moreover, they excluded 32 caves without bats (at least during their visits) from the analyses, a methodological error that biased the results because zero bats may also be significant data. Likewise, Lizarro et al. (2020) analyzed 19 small caves from eastern Bolivia (in the Brazilian-Paranaense biogeographic region), 18 with 5 - 81 m of length, and one with 208 m. Vargas-Mena et al. (2020), studying 13 caves, also relatively small (12 up to 280 m, one with 740 m) in the Caatinga area of Rio Grande do Norte State, concluded that ca. 30% of the variance in bat richness could be attributed to cave length. However, they included in their analysis variables that are not totally independent – "horizontal development" (an unclear term, because cave length may be based on linear development or horizontal projection on maps), cave area, and volume, which are unreliable variables as aforementioned.

The present study points to the absence of a correlation between cave length and bat diversity in a large range of sizes and areas with relatively high availability of such shelters. Data from other authors point in the same direction: Campanhã and Fowler (1993) surveyed three caves in the Corumbataí sandstone area, Ipeúna/Itirapina municipalities, São Paulo State: Fazendão (267 m, five spp.); Paredão (60 m, seven spp.), Cachoeira (60 m, seven spp., differing from Paredão by one species). Silva et al. (2009) studied four caves in Indiara, Goiás State: Joel (316 m, 8 spp., 145 individuals), Lapa Grande (123 m, six spp., 123 ind.), Marimbondos (101 m, 5 spp., 30 ind.), and NH3 (65 m, six spp., 107 ind.).

The absence of correlation between cave size and bat diversity is in accordance with ob-

servations by experienced speleologists exploring caves throughout the country (including the first author, E.Trajano), in that: i) in carbonatic karst areas, where the majority of caves (and the largest ones) are located, number and types of bats are highly variable from time to time, being frequently difficult to predict which bats will be present and where they will be in the next visit to the cave; these anecdotal observations are consistent with the notion of significant temporal variations, some cyclic others not, in the composition and abundance of cave bat communities (Trajano 2013); ii) there is no correlation between cave size and bat diversity. The exception is caves from small, relatively isolated cave areas, such as sandstone areas, which frequently harbor rather stable bat colonies. Seasonal variations in the total abundance of bats have been reported for areas such as the Alto Ribeira, deconstructing the notion of the absence of migrations in tropical bats (Arnone et al. 2016).

Conclusions

Little is known about variables influencing the use of rock shelters by the rich Brazilian chiropterofauna. Special care must be taken when selecting and measuring such shelters because the use of spaces in rocks by bats and other subterranean animals is very different from the use by the much larger, terrestrial and mostly visual humans.

Under particular circumstances, such as small caves in isolated small cave areas, size may have some importance over bat diversity; however, this may not be generalized. On the contrary, the evidence so far available points to a minor, if any, importance of cave size as measured by human speleometry. As a general statement, at least in Brazil, cave size, as perceived and categorized by people, does not matter.

Authors' contributions

ET collected data on bats from the Alto Ribeira karst area, put together data from the literature, and prepared the manuscript. MFE carried out the statistical analysis and contributed to the interpretation of results. All the authors have read and approved the final version of the manuscript, and agreed to be held accountable for all aspects of the work.

Conflict of interest

The authors declare no potential conflict of interest.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article.

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Supplementary Material

Table S1a. Alto Ribeira karst area São Paulo-Paraná, **1978-1979** (Trajano 1985); caves ranked according to decreasing length.

Cave (development in m)	N. spp. cumul.	Rank cumul.	Abundance	Rank abund.
1 Santana (8,689)	3	15	27	5.5
2 Areias de Cima (5,680)	4	7.5	29	3
3 Água Suja (2,980)	4	7.5	27	5.5
4 Jeremias (1,930)	3	15	7	19
5 Areias de Baixo (1,850)	2	20.5	11	15.5
6 Ouro Grosso (1,820)	3	15	8	17.5
7 Córrego Fundo (1,800)	0	29.5	0	30.5
8 Gurutuva (1,760)	3	15	16	9
9 Alambari de Cima (1,580)	1	27	1	27
10 Hipotenuza (1,260)	3	15	11	15.5
11 Arataca (1,138)	0	29.5	0	30.5
12 Grilo (1,080)	3	15	3	23.5
13 Alambari de Baixo (890)	5	2.5	19	8
14 Morro Preto (830)	4	7.5	15	11
15 Passoca (700)	2	20.5	3	23.5
16 Lage Branca (650)	2	20.5	2	25,5
17 Couto (470)	2	20.5	15	11
18 Águas Quentes I (370)	4	7.5	12	13.5
19 Calcário Branco (300)	3	15	41	1.5
20.5 Chapéu (300)	2	20.5	8	17.5
20.5 Marreca (280)	0	29.5	0	30.5
22 Tira Prosa (250)	5	2.5	12	13.5
23 Betari (240)	5	2.5	41	1.5
24 Zezo (220)	2	20,5	5	21.5
25 Vieira (200)	4	7.5	22	7
26 Coruja (150)	0	29.5	0	30.5
27 Sítio Novo (145)	2	20.5	5	21.5
28 Araponga (95)	0	29.5	0	30.5
29 Córrego Seco (90)	4	7.5	15	11
30 São João (60)	4	7.5	28	4
31 Macaco (40)	0	29.5	0	30.5
32 Sumidouro do Davi (30)	2	20.5	2	25.5
33 Aberta Funda (40)	4	7.5	6	20

N. spp cumul., accumulative number of species; Rank cumul., cave rank according to number of species; Abundance, total number of individuals captured; Rank abund., cave rank according to total abundance.

Table S1b. Alto Ribeira karst area, São Paulo, **1979-1980** (Trajano 1985); ten selected caves ranked according to decreasing length.

Cave (development in m)	N. spp. cumul.	Rank cumul.	N. spp. max.	Rank max.
1. Santana (8,690)	6	6.5	3	9
2 Areias de Cima (5,680)	6	6.5	4	5.5
3 Água Suja (2,980)	6	6.5	4	5.5
4. Areias de Baixo (1,850)	3	10	3	9
5. Alambari de Baixo (890)	13	1	9	1
6. Morro Preto (830)	4	9	3	9
7. Couto (470)	6	6.5	5	3
8. Águas Quentes (370)	10	3	4	5.5
9. Betari (240)	11	2	7	2
10. Córrego Seco (85)	7	4	4	5.5

N. spp. cumul., cumulative number of species; Rank cumul., cave rank according to cumulative number of species; N. spp. max., maximum number of spp. recorded at one occasion; Rank max., cave rank according to maximum number of species.

Table S1c. Alto Ribeira karst area, São Paulo, **2006-2007** (Arnone 2008); caves ranked according to decreasing length.

Cave (development in m)	N. spp. cumul.	Rank cumul.	Abund.	Rank abund.
1 Santana (8,690)	10	5.5	292	2
2 Areias de Cima (5,680)	8	7	301	1
3 Água Suja (2,980)	6	10	105	4
4 Areias de Baixo (1,850)	7	8.5	52	9
5 Alambari de Baixo (890)	16	1	83	6
6 Morro Preto (830)	13	3	71	7
7 Couto (470)	7	8.5	29	10
8 Águas Quentes (370)	10	5.5	64	8
9 Betari (240)	11	4	153	3
10 Córrego Seco (85)	15	2	91	5

N. spp. cumul., cumulative number of species; Rank cumul., cave rank according to cumulative number of species; Abund., total number of individuals captured; Rank abund., cave rank according to total abundance.

Table S2. Rio Pardo karst area (Santos 2001); caves ranked according to decreasing length (linear development).

Cave (development in m)	N. spp. cumul.	Rank n. spp.	Abund.	Rank abund.
1 Caverna Milagrosa (286)	9	4	27	8
2 Toca dos Morcegos (250)	9	4	301	1
3 Gruta São Gotardo (245)	8	7	125	7
4 Gruta Califórnia (195)	9	4	175	5
5 Gruta Córrego Verde (180)	10	1	285	2
6 Gruta Pedra Suspensa (150)	9	4	280	4
7 Gruta Agachadinho (80)	6	8	162	6
8 Buraco do Galindo (45)	9	4	244	3

N. spp. cumul. cumulative number of species; Rank n. spp., cave rank according to cumulative number of species; Abundance, total number of individuals captured; Rank abund., cave rank according to total abundance.

Table S3. Distrito Federal karst area (Bredt et al. 1999); caves ranked according to decreasing length.

Cave (development in m)	N. spp cumul.	Rank cumul.	Abund.	Rank abund.
1 Gruta Fenda II (432)	8	6.5	242	5
2 Gruta do Sal (341)	8	6.5	160	8
3 Labirinto de Lama (260)/266	5	13.5	12	16
4 Gruta da Saúva (235)	7	10.5	280	4
5 Gruta Água Rasa* (101)/229	8	6.5	212	7
6 Dança dos Vampiros (223)	9	2.5	286	3
7 Gruta Dois Irmãos (90)	9	2.5	225	6
8 Gruta Volks Clube (84)	8	6.5	56	13
9 Gruta Morro (58)	13	1	617	1
10 Gruta da Barriguda (57)	8	6.5	19	15
11 Gruta Muralha (54)	2	16	20	14
12.5 Toca do Falcão (35)	6	12	109	11
12.5 Gruta das Orquídeas (35)	4	15	122	9
14 Gruta Mogi (34)	7	10.5	119	10
15.5 Toca da Gameleira (20)	8	6.5	82	12
15.5 Fenda do Barreiro (20)	5	13.5	416	2

N. spp. cumul., cumulative number of species; Rank cumul., cave rank according to cumulative number of species; Abund., total number of individuals captured; Rank abund., cave rank according to total abundance.

Table S4. Caatinga karst areas (Vargas-Menna et al., 2020); caves ranked according to decreasing length (development) and volume (rank vol. m^3).

Cave (development in m)	Rank vol. (m^3)	N. spp. cumul.	Rank cumul.
1 Furna Feia (740)	1	10	1
2 Furna do Urubu (283.5)	3	6	6.5
3 Gruta dos Trinta (272)	11	5	9.5
4 Caverna Boa (264.5)	2	6	6.5
5 Gruta da Carrapateira (242)	6	7	3
6 Furna Nova (239)	4	7	3
7 Caverna do Lajedo Grande (155)	5	4	11.5
8 Caverna da Pedra Lisa (150)	8	4	11.5
9 Caverna Porco do Mato1 (140)	7	6	6.5
10 Caverna do Arapuá (110)	9	2	13
11 Gruta dos Três Lagos (65)	12	7	3
12 Gruta Capoeira João Carlos (55)	10	6	6.5
13 Gruta Casa de Homens (31)	13	5	9.5

N. spp. cumul., cumulative number of species; Rank cumul., cave rank according to cumulative number of species.
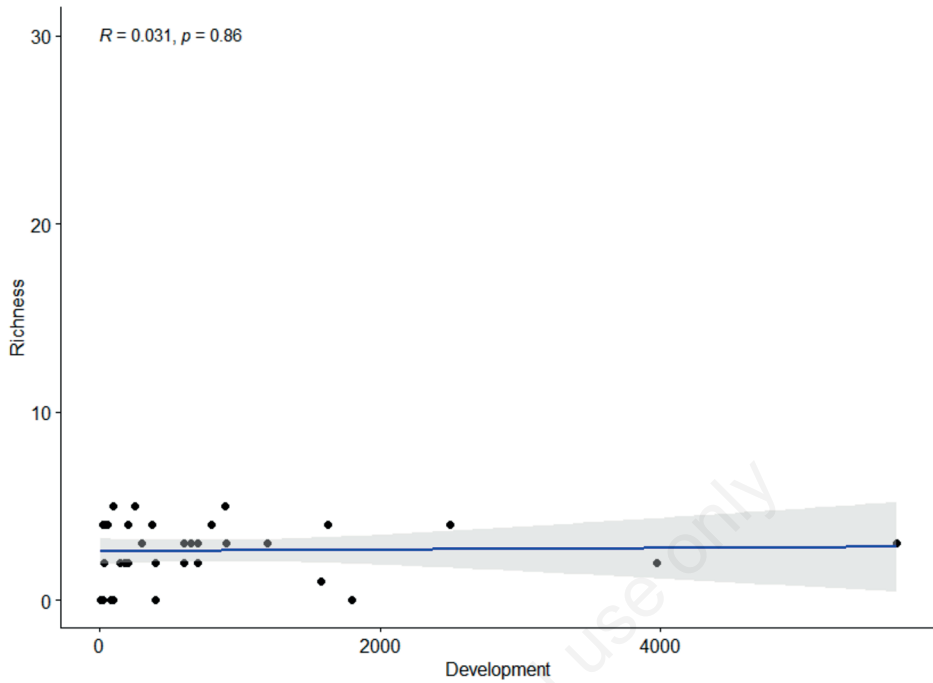
Figure S1. Correlation between cave length and bat richness in 1978-1979, in the Alto Ribeira, SP (data from Trajano 1985).
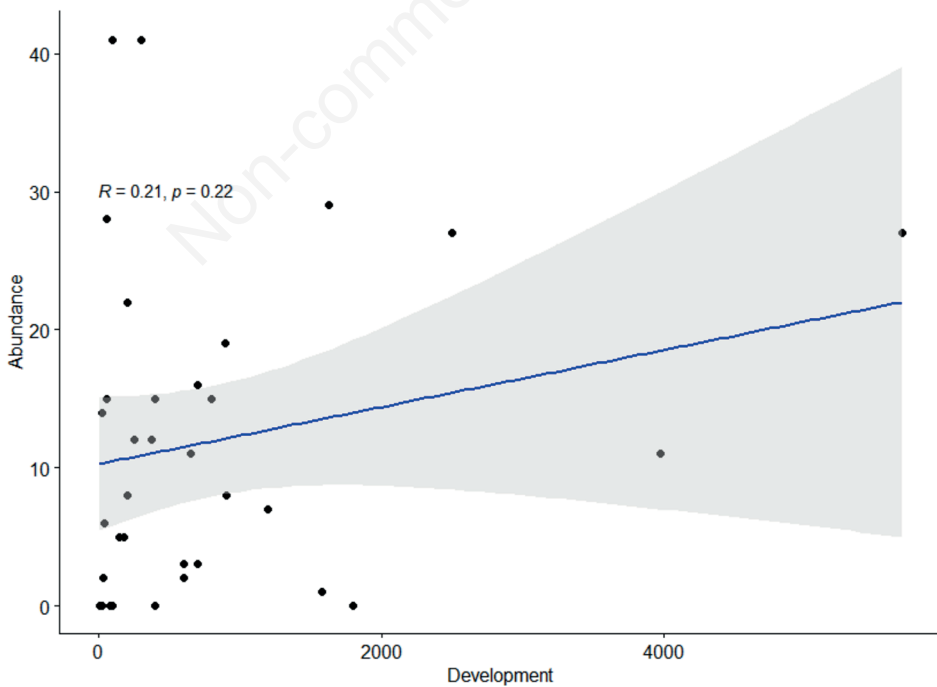

Figure S2. Correlation between cave length and bat abundance in 1978-1979, in the Alto Ribeira, SP (data from Trajano 1985).
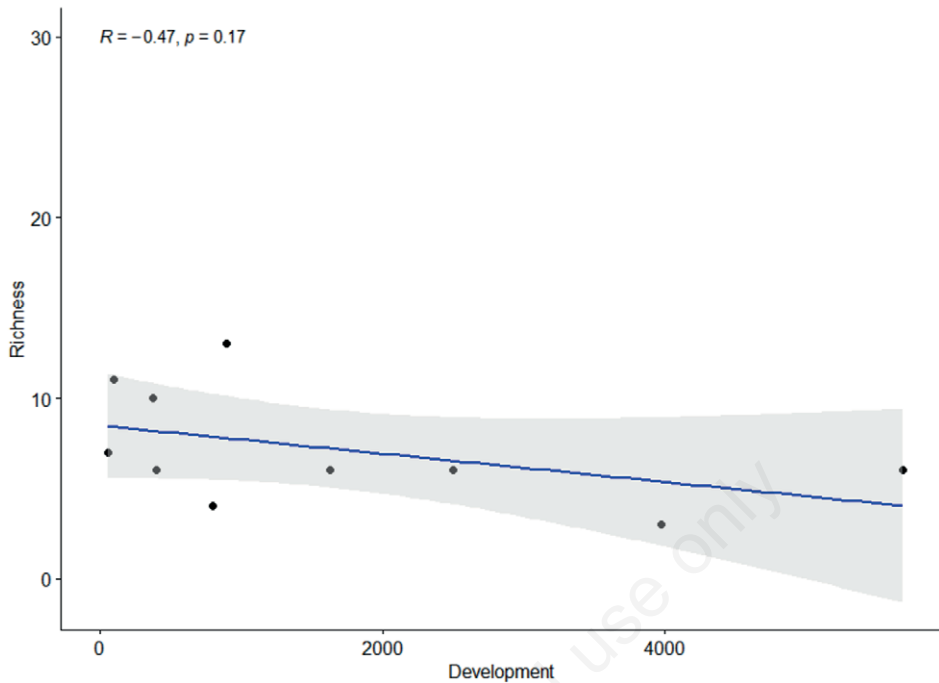
Figure S3. Correlation between length of 10 selected caves and bat richness in 1978-1979, in the Alto Ribeira, SP (data from Trajano 1985).
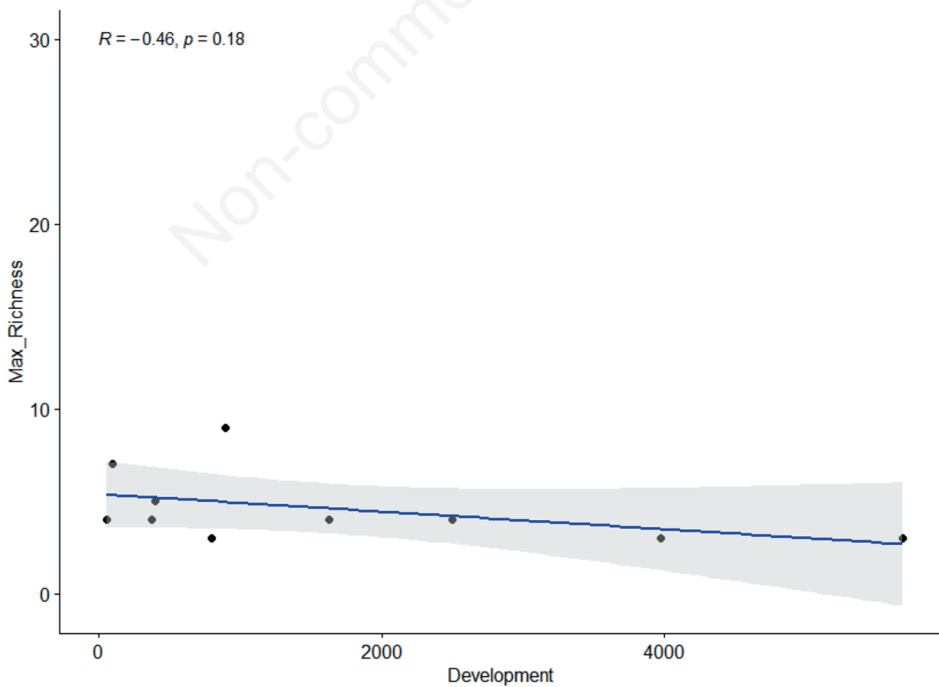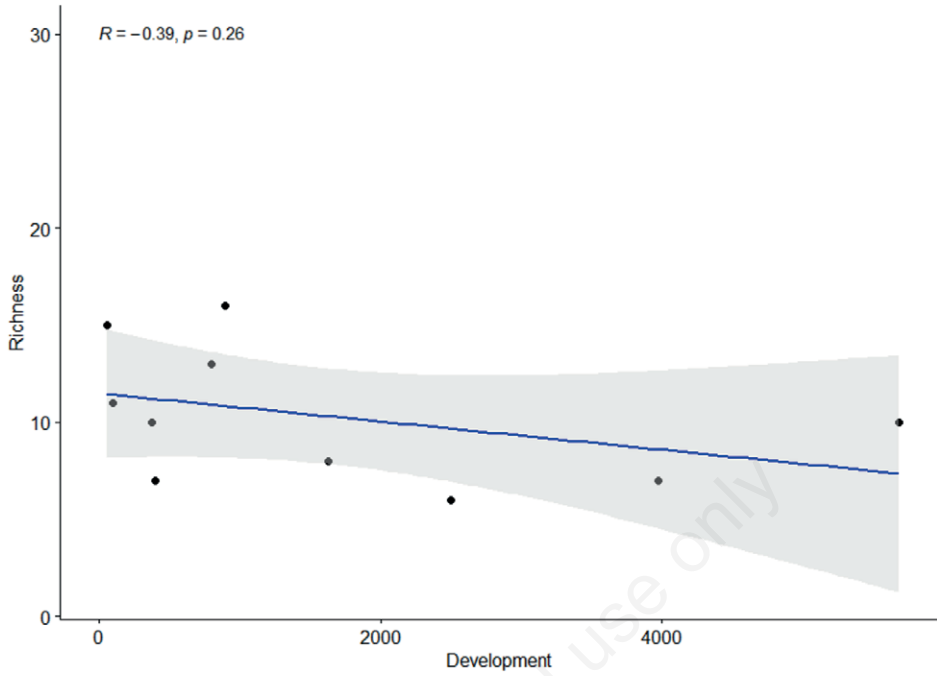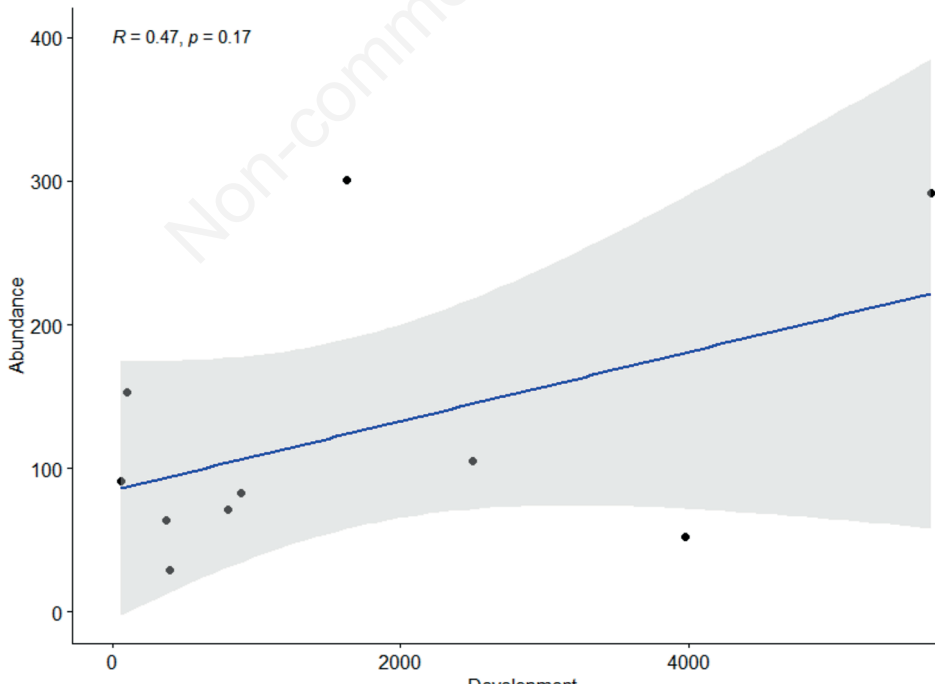

Figure S4. Correlation between length of 10 selected and maximum number of bat spp. recorded at one occasion in 1978-1979, in the Alto Ribeira, SP (data from Trajano 1985).

Figure S5. Correlation between cave length and bat richness in 2006-2007, in the Alto Ribeira, SP (data from Arnone 2008)

Figure S6. Correlation between cave length and bat abundance in 2006-2007, in the Alto Ribeira, SP (data from Arnone 2008).
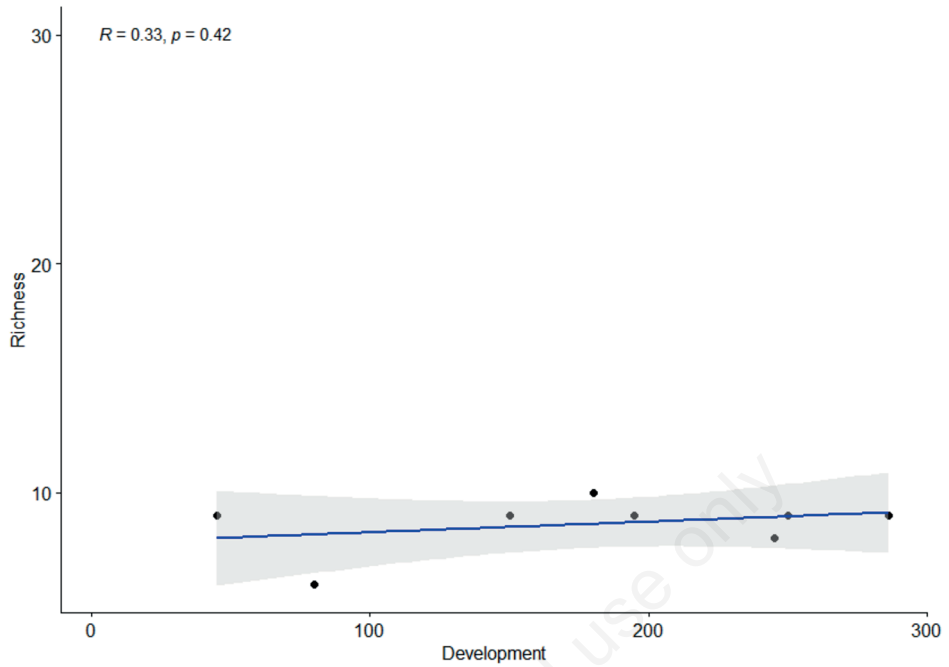
Figure S7. Correlation between cave length and bat richness in Rio Pardo karst area, BA (data from Santos 2001).
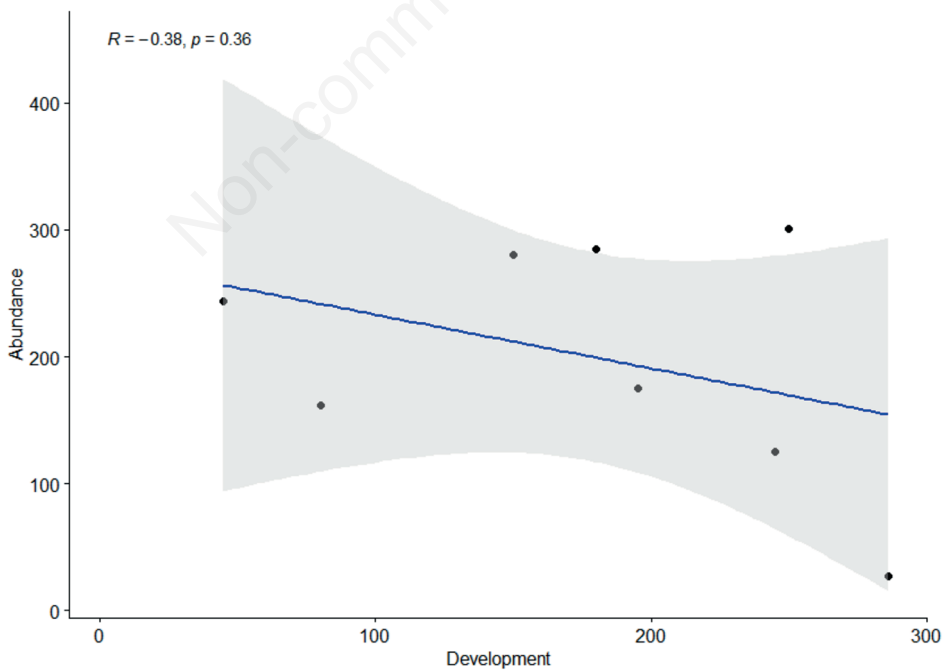
Figure S8. Correlation between cave length and bat abundance in Rio Pardo karst area, BA (data from Santos 2001).
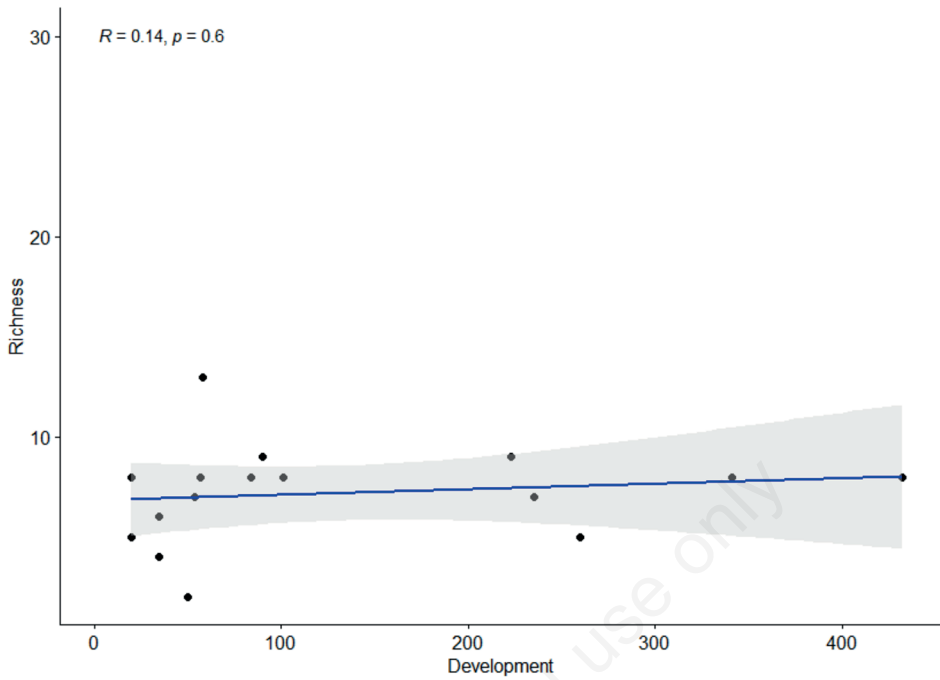
Figure S9. Correlation between cave length and bat richness in Distrito Federal karst area (data from Bredt et al. 1999).
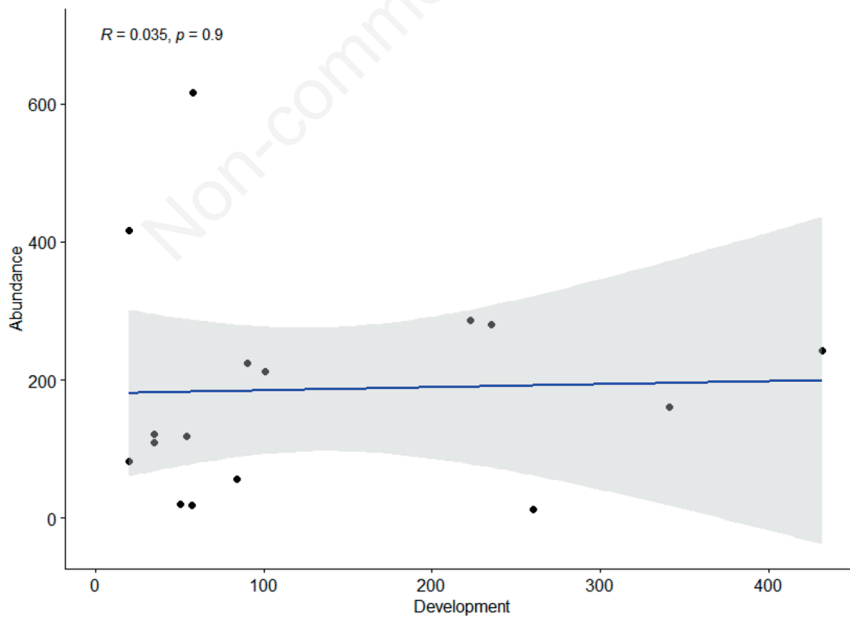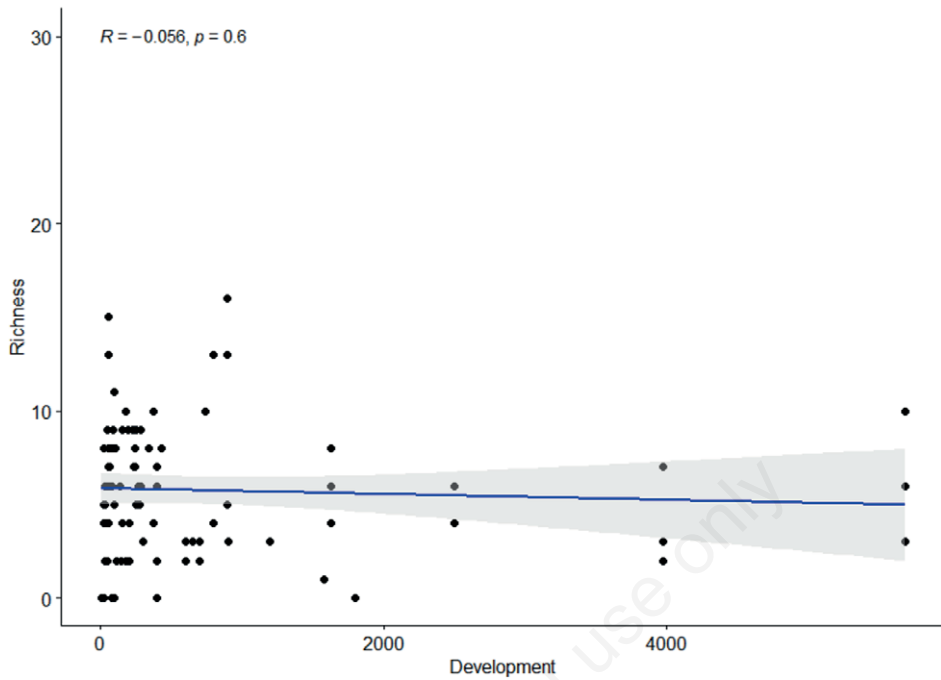

Figure S10. Correlation between cave length and bat abundance in Distrito Federal karst area (data from Bredt et al. 1999).

Figure S11. Correlation between cave length and bat richness in the Alto Ribeira, Rio Pardo and Distrito Federal karst areas (Group 1).
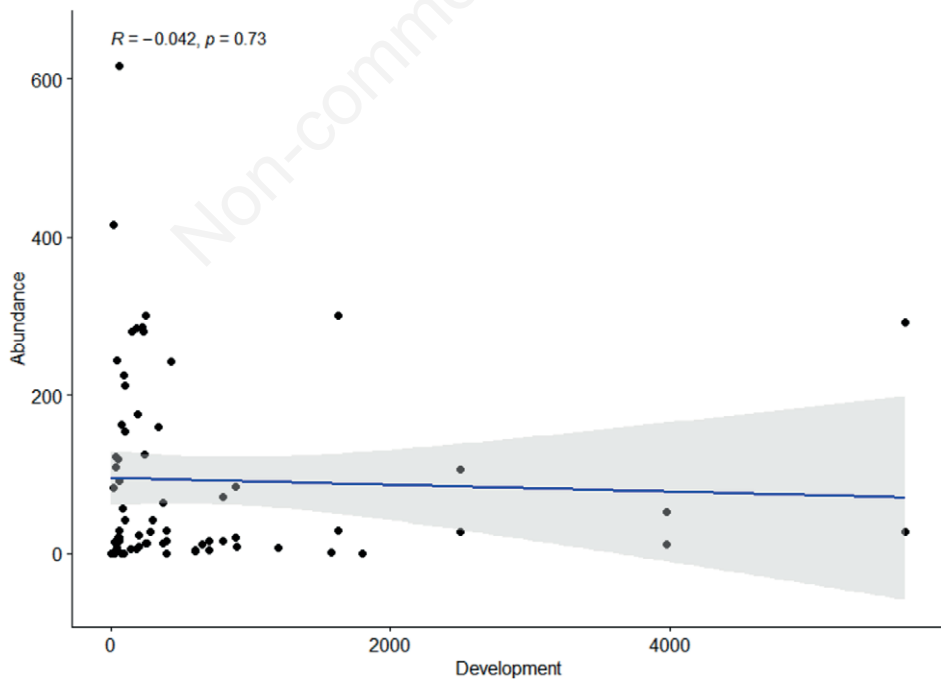

Figure S12. Correlation between cave length and bat abundance in the Alto Ribeira, Rio Pardo and Distrito Federal karst areas (Group 2).
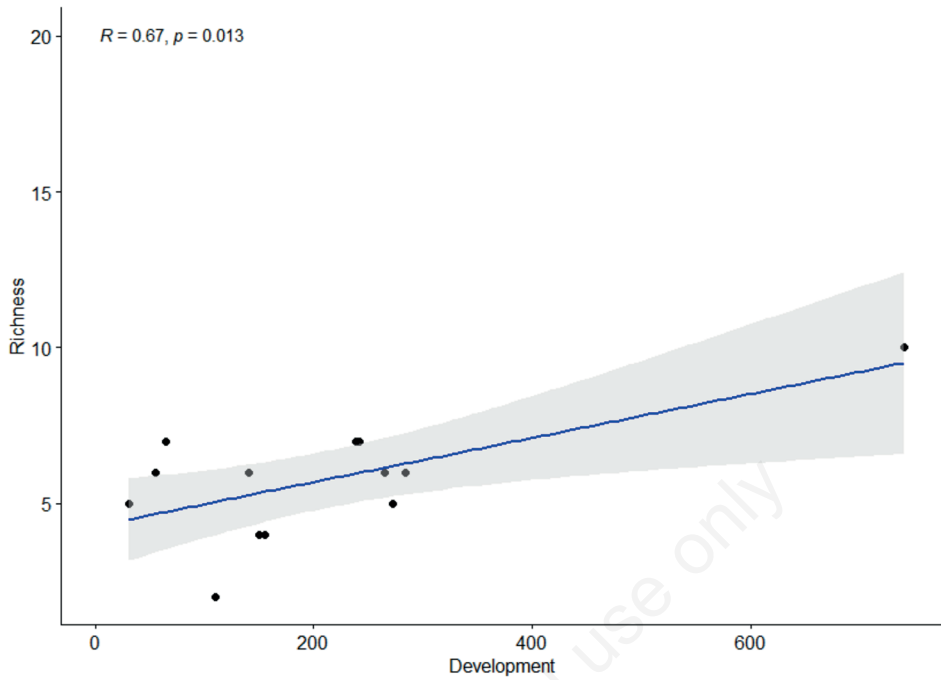
Figure S13. Correlation between cave length and bat richness in Caatinga karst areas (Vargas-Menna et al. 2020).
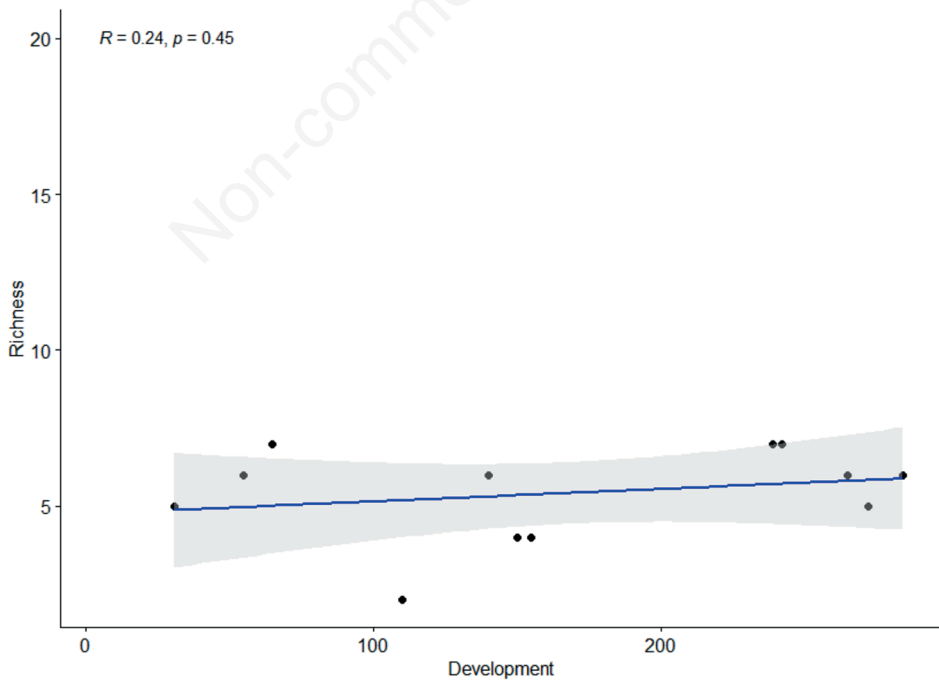

Figure S14. Correlation between cave length and bat richness in Caatinga karst areas, possible outliers excluded (Vargas-Menna et al. 2020).