RESEARCH ARTICLE

Invertebrates diversity in mountain Neotropical quartzite caves: which factors can influence the composition, richness, and distribution of the cave communities?

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Abstract

Twenty caves located in a high altitudinal quartzite area in Brazil were examined for invertebrate richness and composition and in terms of environmental factors that determine community structure. We evaluate how distance, altitude, cave extension, environmental stability, number and size of cave entrances and stream presence can act on species composition and richness. The caves presented a high richness of troglophilic (463 spp.) and troglobitic species (6 spp.) in relation to other siliciclastic caves around the world. The average richness was 39.55 species per cave (sd = 21.87), the quantitative similarity among caves was 41% and turnover was $\beta_{repl.} = 0.769$. Araneae (20% of the sampled species), Diptera (18%) and Coleoptera (14%) were the dominant orders regarding species richness. Only twenty percent of the caves were placed out of the confidence interval of the average taxonomic distinctness ($\Delta+$); however, the $\Delta+$ decreased with the increase of environmental stability. Cave extension and stream presence were the main factors determining the variation of species composition among caves. Cave extension also influenced species richness variations. Furthermore, the total richness and richness of troglobitic species increased with cave extension. The threats to these habitats further revealed that the fauna is at risk due to tourism, trampling and natural soil erosion that can promote microhabitat alterations. Therefore, quartzite caves also require special attention regarding conservation actions in order to keep their natural biological dynamics.

Introduction

Studies related to ecology and conservation of subterranean fauna have been receiving increasing attention in recent years (Mammola 2018, Mammola and Isaia 2018, Pellegrini et al. 2018, Moldovan et al. 2018). However, most of the knowledge regarding subterranean fauna has been historically focused on limestone caves so that other kinds of rocks, such as siliciclastic, have received less attention (Sharratt et al. 2000, Souza-Silva et al. 2011). Despite quartzite caves being less frequent than caves in other lithologies, studies with fauna from these habitats have been conducted in some regions of the world, as in Cape Peninsula in South Africa (Sharratt et al. 2000), in the Northwestern United States (Peck and Peck 1982), in the Amazon Tepuis in South America (Galán and Herrera 2006, Aubrecht et al. 2012), in the Brazilian Atlantic Rain Forest (Zeppelini et al. 2003, Gallão and Bichuette 2015) and in Brazilian Savannah (Guadanucci et al. 2015). Some of those studies have shown that quartzite and sandstone caves are important habitats for troglophilic and troglobitic fauna in Neotropics, thus deserving attention for conservation (Gallão and Bichuette 2015, Souza-Silva et al. 2015).

In Brazil, the cave fauna started to be systematically studied in the 1980s (Dessen et al. 1980), but only a few studies assessed ecological aspects of cave community structure. Furthermore, most of the knowledge on cave ecology in Brazil comes from works conducted in limestone caves (Bento et al. 2016, Pellegrini et al. 2016, Simões et al. 2015, Rabelo et al. 2018).

In Brazil, there are at least 2,300 known sandstone and quartzite caves, but they represent only 1% of the potential occurrence (Nascimento and Mantesso-Neto 2013, Cecav 2019). Only a small part of them have been sampled (about 50 caves), which revealed more than 500 invertebrate species. Furthermore, 20 caves presented at least two troglobitic species (Dessen et al. 1980, Trajano and Gnaspini-Netto 1991, Trajano and Moreira 1991, Gnaspini-Netto and Trajano 1994, Pinto-da-Rocha 1995, Lourenço et al. 2004, Zeppelini et al. 2003, Bichuette et al. 2008, Alves et al. 2011, Souza-Silva et al. 2011, Bertani et al. 2013, Fernandes and Bichuette 2013, Gallão and Bichuette 2015, Pellegrini et al. 2018).

Previous ecological studies conducted in 14 Brazilian quartzite caves in the South of Minas Gerais state found 400 species (44.85 species/cave, sd = 24.54), for an average cave extension of 231 m (sd = 219) (Souza-Silva et al. 2011). Gallão and Bichuette (2015) sampled 11 quartzite caves from Chapada Diamantina, a central region of the state of Bahia, Brazil, and found 160 morphotypes (29.72 species/cave, sd = 19.6). They did not present the extension of caves. Overall, 23 obligate cave species were mentioned (plus the other 14 species with some troglomorphisms) (Gallão and Bichuette 2015). Accordingly, the authors found 37 species with troglomorphic traits in 11 caves in the area, which represent 23% of the total invertebrates sampled (160 species).

Zeppelini et al. (2003) studied nine sandstone caves in the Northern region of the state of São Paulo, Brazil, and found 83 morphotypes (10 species/cave, sd= 10) for an average cave extension of 373 m (sd= 246).

However, a study performed on 33 temperate sandstone caves of the Cape Peninsula in South Africa (approximately 20–90 m long), found only 85 species (Sharratt et al. 2000). They did not present the number of species per caves, which also precludes further comparisons.

However, the previous studies did not present information on how composition, richness, and distribution cave communities are related to some cave attributes (distance between caves, cave size, number and size of entrances and altitudinal position among others). Such features were proven to be determinant for local and regional species richness and dissimilarity, mainly in the tropics (Souza-Silva et al. 2011, Simões et al. 2015, Jaffé et al. 2016). This study aimed to evaluate how some local environmental factors (distance, altitude, cave extension, environmental stability, number and size of entrances and stream presence) can act on invertebrate composition and richness. In addition, we described the human uses and alterations inside and surrounding the caves.

Material and methods

Study area

The study was conducted in the Ibitipoca mountain quartzite province, south of Minas Gerais state, Brazil. The caves in this region were formed and modeled by hierarchically organized drainages influenced by differences between the local water table and the regional base level. The Ibitipoca Mountain belongs to the Andrelândia geological group mainly composed of quartzite rocks of Mesoproterozoic lithostratigraphic age (Auler and Sauro 2019).

The mountain is located within a protected area, with 1,488 ha of extension and altitude ranging from 1,200 to 1,784 m asl. This reserve was created in 1973 and protects epigean fauna and flora and quartzite caves and their fauna (Nobre et al. 2013). The dominant vegetation is grasslands on hilltops and rainforest in the valleys (Figure 1). The climate is tropical (Cwb of Köppen) with mild summers, with dry (May to August) and rainy (August to January) well defined seasons (Alvares et al. 2013). The external temperatures range from 2 to 20 °C and internal caves temperatures range from 12 to 20 °C (Souza-Silva et al. 2013).

Environmental features of quartzite caves

Most of the caves in this study were mapped by Silva (2004) using a standardized mapping methodology with a British Cave Research Association (BCRA) – 4C survey grade. Additional information related to the cave extension (for those caves that were not mapped), number and area of entrances were determined during the fieldwork (as in Bento et al. 2016).
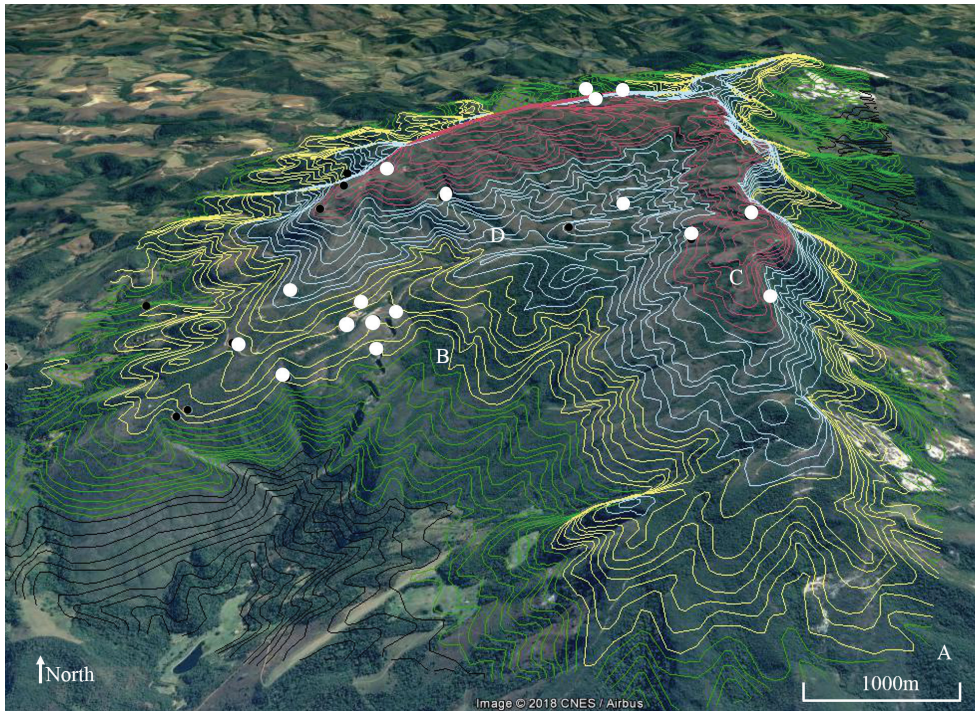
Figure 1. Borders of the Ibitipoca Estadual Park (**A**), sampled caves (white dots) and altitudinal layers (red lines 1610–1780, blue lines 1460–1600, yellow lines 1310–1450, green lines 1124–1450, black lines 950–1100 meters). Vegetation types vary from slope forest (**B**) to grasslands (**D** and **C**) on the top of the hills.

The altitude above sea level and geographic position of the caves were obtained with a Global Positioning System (GPS) in decimal degrees (Table 1). Moreover, the width of entrances and linear development of the caves were measured using a laser. The greatest horizontal length of an entrance was considered as width, while the greatest vertical length was considered as height. The cave linear development represented the linear development sampled in each cave since some caves were not sampled throughout their total length (Souza-Silva et al. 2011).

Faunal survey

Species richness and composition of the invertebrate communities were assessed in 20 caves (Table 1, Figure 1). Only one visit to each cave was conducted. Sampling was carried out only once by visual search within the accessible parts of each cave, prioritizing places with organic matter (such as plant debris, carcasses, and guano) and humid soils, cracks, speleothems, water bodies and spaces under rocks. Hand collections were made with the aid of tweezers, brushes and entomological nets (Bento et al. 2016, Wynne et al. 2019). Invertebrates were collected from water bodies with the aid of forceps. In the

Table 1. Biotic and abiotic characteristics of the 20 quartzite caves in southeastern Brazil. Cave with stream (S) or dry caves (D), total richness (TS); relative richness (RS), abundance (A), altitude (ALT in meters), geographic coordinates (Lat and Long in decimal degrees), Sampled extension of the caves (SE in meters), Number of morphotypes with troglomorphic traits (ST), entrance number (NE) extension of the entrances (EE) and results of the environmental stability index (IEA). *Caves open to tourist visitation. Numbers above cave names are the morphotypes with troglomorphic traits; 1 – Blattodea, 2 – *Brasilomma enigmatica,* 3 – Hypogastruridae, 4 – Projapygidae, 5 – Palpigradi, 6 – Pselaphidae.

Cave names	S/D	TS	RS	A	ALT	Latitude, Longitude	SE	ST	NE	EE	IEA
Catedral III	S	22	0.13	145	1634	-21.701486, -43.872046	170	0	5	60	9.28
Bichana II	D	19	0.63	580	1350	-21.171357, -43.389859	30	0	1	4	2.01
Bichana I	D	31	1.55	132	1360	-21.712851, -43.898126	20	0	1	1	1.61
Catedral I	S	14	0.54	89	1646	-21.701486, -43.872046	26	0	5	1	1.65
Manequinho	S	61	0.1	940	1270	-21.719923, -43.903194	160	0	4	40	8.76
*Cruz	D	61	1.45	344	1632	-21.694923, -43.896249	50	0	3	20	10.93
Dobras[1]	D	26	0.19	220	1600	-21.696294, -43.896608	138	1	2	15	8.32
*Ponte de Pedra	S	30	0.44	103	1283	-21.171659, -43.898472	54	0	2	20	7.68
*Gnomos	S	23	0.38	137	1363	-21.171159, -43.389486	32	0	2	15	6.46
Lagarto Teiú	S	40	0.4	266	1349	-21.712168, -43.893929	40	0	1	10	1.40
*Monjolinhos	D	22	1.05	39	1428	-21.169659, -43.880138	21	0	1	5	1.44
Martiniano	D	35	0.16	270	1360	-21.715316, -43.900316	240	0	4	40	2.3
Martiniano II	D	18	0.36	96	1340	-21.710917, -43.894719	50	0	4	50	2.53
*Viajantes	D	33	0.2	333	1660	-21.704646, -43.876249	166	0	2	50	9.5
Fugitivos	D	33	0.08	842	1669	-21.677731, -43.883096	440	0	4	80	7.45
*Pião[1]	D	34	0.27	270	1643	-21.701868, -43.874027	126	1	1	4	3.45
*Coelhos	D	67	0.84	488	1358	-21.709646, -43.895972	80	0	2	10	9.46
Bromélias[2]	D	96	0.19	2869	1450	-21.704923, -43.899583	500	1	3	10	5.11
Moreiras[3,4]	D	75	0.13	3735	1651	-21.676595, -43.388241	600	2	6	80	9.33
Casas[1,4,5,6]	S	47	0.07	249	1340	-21.700479, -43.883749	650	4	1	7	4.53

laboratory, invertebrates were separated into morphotypes (Oliver and Beattie 1996). The sampling time spent in each cave was dependent on the extension of the cave.

The determination of potentially obligate cave species was conducted by identifying the specimens with troglomorphic traits (Christiansen 2012). However, for some specific groups (e.g., Palpigradi, Diplura), other traits were considered, such as the increased number of sensory receptors (lateral organs) (Souza and Ferreira 2012) and an increased number of antennomeres and cercal articles (Sendra et al. 2012). Furthermore, experts on Diplura, Blattodea, and Collembola were consulted to evaluate the degree of troglomorphisms.

Descriptions of human uses and impacts

Human modifications were determined in relation to uses and impacts. Tourist and religious activities were considered uses while real impacts were trampling, illumination and construction resulting from these activities (Souza-Silva et al. 2015). Impacts were determined for each cave as a function of the presence or absence of visual modifications inside the cave.

Data analyses

The components of beta diversity were calculated using the BAT package developed by Cardoso et al. (2015) in the software R to assess βtotal (overall beta diversity), βrepl (the replacement component) and βrich (the richness differences component) (R Development Core Team 2008).

The average taxonomic distinctness ($\Delta+$) analysis was conducted with the software Primer 7 using 297 from the 463 morphotypes because they were identified up to family level (Anderson et al. 2008). We used Phyla (weight 100), Class (weight 80), Order (weight 60), Family (weight 40) and morphotypes (weight 20) as variables for a matrix of morphotypes distribution among caves (Anderson et al. 2008). Previous analysis comparing the group of sampled morphotypes and the above mentioned 297 morphotypes were carried out using a Spearman Rank Order Correlations to test the representativeness of this sub-sample (of species identified until the family level), which revealed regression Rs = 0.93 and p ≤ 0.05.

The Environmental stability of each cave was determined using the Environmental Stability Index (IEA) proposed by Ferreira (2004) (Pellegrini et al. 2016, Bento et al. 2016), which considers the degree of isolation between the cave and epigean environments through a mathematical ratio, calculated as follows. For caves having just one entrance: IEA = ln(AT/EE) and for caves having more than one entrance: IEA= ln((AT/∑EE)/((NE)*(x̄ DEE)/AT))), in which: AT (total size of each cave), EE (sum of the highest and longest measurements of cave entrances using perpendicular lines), NE (number of entrances), DEE (average distance between entrances, taken from one reference entrance).

A non-parametric multivariate analysis (DistLM – Distance-based Linear Model) was used to evaluate the influences of the distance between caves (dist), the extension of the sampled cave (SE), environmental stability (IEA), number (NE) and size of entrances (EE) and altitude (Alt) over invertebrate composition, total richness and average taxonomic distinctness with AICc as selection criteria and Forward as selection procedure (Anderson et al. 2008). The similarity measure based on Bray-Curtis Index was used for fauna composition and Euclidean distance was used for total richness and average taxonomic distinctness in DistLM analysis (Anderson et al. 2008). Jaccard similarity based on presence/absence, specifically as a measure of ß diversity and tested against predictors variables (dist, SE, IEA, NE, EE, Alt) using DistLM analysis. Once the definition of ß-diversity is based on variation in the identities of species (Whittaker 1972), the similarity measures with abundance do not provide a ß diversity measure (Anderson et al. 2008).

The distance-based redundancy analysis (dbRDA) was performed to determine the strength and direction (- or +) of the predictor variables relationship selected by the DistLM routine. A metric multidimensional scaling (MDS) using bootstrap-average analysis was performed to determine the level of variation in species composition within sampled caves with and without stream and to produce two 95% bootstrap regions (Clarke et al. 2014).

Similarity analysis(ANOSIM) one-way layout with pairwise analysis was used to select faunal group formation based on Bray-Curtis similarity using caves with and without streams, frequency classes of cave sampled extension (SE), environmental stability (IEA), number (NE) and extension of entrances (EE) and altitude (Alt) as selected factors. The Similarity Percentages analysis (SIMPER) was used to determining species responsible for sample groupingsrs using Bray-Curtis dissimilarities (Clarke 1993). These analyses were performed in the Plymouth routine in Multivariate ecological research – Primer 7 (http://www.primer-e.com). We also used the Spearman correlation test (R_s) (Zar 1984) to evaluate the relationship between cave physical attributes (SE, IEA, NE, EE, and Alt) and total richness and average taxonomic distinctness. Significant differences of average richness, diversity and taxonomic distinctness among caves with and without stream were evaluated using Mann-Whitney U Test (Sprent and Smeeton 2000).

Results

Environmental factors of the caves

Caves are located at altitudes between 1270 and 1669 m asl (sd = 150 m). Sampled cave extension varied from 20 to 650 m in length (sd = 202 m), presenting one to six entrances. Surface of entrances varied from 1 to 80 m² (sd = 26 m). Environmental stability varied from 1.4 to 10.93 (Table 1).

Faunal composition, abundance, and richness

We found a total of 12,123 individuals distributed in 463 morphotypes and at least 117 families. The composition considering higher taxa is presented in Figure 2A and Table 2.

The richest higher taxa in the sampled caves were the orders Araneae (100 spp., 21.6% of the total richness) and Diptera (85 spp., 18.35% of the total richness), while Dermaptera, Neuroptera, Gastropoda, and Nematomorpha presented a single species each (0.2% of the total richness). The most abundant higher taxa were the orders Diptera (3,322 individuals, 27% of the total abundance), Araneae (2,164 individuals, 18% of the total abundance), Opiliones (1,462 individuals, 12% of the total abundance) and Coleoptera (1,396 individuals, 11% of the total abundance). The less abundant higher taxa were Odonata, Megaloptera, Dermaptera, Diplura, Ephemeroptera, Zygentoma, Mollusca and Nematomorpha with less than 10 individuals each (0.3% of the total abundance) (Figure 2A).

The average richness of the caves was 39.55 spp. (sd= 21.87). The Bromélias (95 spp.) and Moreiras (75 spp.) caves presented the highest invertebrate richness, contrasting with Martiniano II (18 spp.) and Catedral I (14 spp.) caves, which presented the lowest richness values (Table 1).

Table 2. Invertebrate taxa, richness and distribution in the 20 studied caves of the Ibitipoca quartzite speleological province, Brazil. Gruta Catedral III (1), Gruta Beira de Estrada II (2), Gruta Beira de Estrada I (3), Gruta Catedral I (4), Gruta Manequinho (5), Gruta da Cruz (6), Gruta das Dobras (7), Ponte de Pedra (8), Gruta dos Gnomos (9), Gruta do Lagarto Teiú (10), Gruta do Monjolinhos (11), Gruta do Martiniano (12), Gruta do Martiniano II (13), Gruta dos Viajantes (14), Gruta dos Fugitivos (15), Gruta do Pião (16), Gruta Coelhos (17), Gruta das Bromélias (18), Gruta dos Moreiras (19), Gruta das Casas (20). Total Richness (TS).

Order	Family	TS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Tricladida	Dugesiidae	4															+		+	+	+	+
	Not identified	1								+												
Gordioidea	Gordiidae	1																		+		
Haplotaxida	**Not identified**	9					+	+		+							+	+		+	+	+
Pulmonata	**Not identified**	1					+															
Opiliones	Gonyleptidae	7	+	+	+		+	+				+	+	+	+	+	+	+	+	+	+	+
	Not identified	6	+				+		+		+			+			+					
Palpigradi	Eukoeneniidae	2													+		+		+			
Pseudoscorpiones	Chernetidae	3		+	+		+					+	+	+			+	+	+			
Acari	Anoetidae	1																		+		
	Anystidae	2													+							+
	Ascidae	1																		+		
	Calyptostomatidae	1																			+	
	Ixodidae	2									+					+						
	Ixodorhynchidae	1																				+
	Laelapidae	3																		+		+
	Macrochelidae	1																		+	+	
	Macronyssidae	1																		+		
	Rhagidiidae	3								+								+				+
	Trombidiidae	2																			+	+
	Not identified	5			+			+				+		+								
	Uropodidae	1																		+		
	Veigaiidae	1																		+		+
Araneae	Amaurobiidae	1	+	+					+													
	Araneidae	3				+				+										+		
	Clubionidae	2																			+	
	Corinnidae	1		+				+								+						
	Ctenidae	8		+	+		+	+				+		+	+				+	+	+	+
	Dipluridae	2											+			+	+	+			+	
	Gnaphosidae	1																		+		
	Lycosidae	1						+														
	Mimetidae	1		+								+	+			+			+	+		
	Nemesiidae	2	+						+					+						+	+	+
	Ochyroceratidae	5	+		+	+	+	+				+	+	+	+	+	+	+	+	+	+	+
	Oonopidae	2	+																	+		
	Pholcidae	6		+	+	+	+	+				+		+	+	+	+		+	+	+	
	Prodidomidae	1																		+		
	Salticidae	3						+	+	+	+					+						
	Scytodidae	1						+		+											+	
	Segestriidae	1														+						
	Tetrablemmidae	1					+						+									
	Theraphosidae	1						+														
	Theridiidae	17		+	+	+	+	+	+	+	+	+			+	+			+	+	+	+
	Theridiosomatidae	6		+	+		+				+				+	+	+			+		+
	Trechaleidae	2							+	+	+											
	Not identified	22		+			+			+		+	+	+	+	+				+	+	+
Isopoda	Philosciidae	3						+	+				+	+			+			+	+	+
Blattodea	**Not identified**	10						+	+	+					+	+			+	+		+
Coleoptera	Carabidae	5		+				+									+			+	+	
	Chrysomelidae	4						+												+		
	Curculionidae	3						+													+	+
	Dermestidae	2																		+	+	
	Dytiscidae	1								+												

Order	Family	TS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Coleoptera	Elmidae	2								+										+		
	Eucnemidae	1						+														
	Gyrinidae	1																		+		
	Lampyridae	1				+																
	Leiodidae	1		+	+		+	+									+			+		
	Melyridae	1						+														
	Noteridae	1																+				
	Phengodidae	1						+														
	Ptilodactylidae	1									+											
	Scarabeidae	3						+											+	+		+
	Staphylinidae	15	+	+	+	+	+	+	+			+		+		+	+	+	+	+	+	+
	Tenebrionidae	5						+				+		+			+		+	+		+
	Torrindicolidae	1								+												
	Not identified	17					+	+				+		+		+	+	+	+	+	+	
Collembola	Arrhopalitidae	1											+									
	Hypogastruridae	1																			+	
	Not identified	19	+	+	+		+	+	+	+		+	+	+		+	+	+	+	+	+	+
Dermaptera	Anisolabididae	1																+	+			
Diplura	Campodeidae	1																			+	+
	Japygidae	1				+																
Diptera	Agromyzidae	1																			+	
	Bibionidae	1																+				
	Calliphoridae	1																			+	
	Cecidomyidae	2						+		+												
	Ceratopogonidae	4					+				+								+	+	+	
	Chironomidae	8	+				+			+	+									+		
	Culicidae	2		+		+				+	+											
	Dolychopodidae	1											+								+	
	Drosophilidae	3								+											+	
	Empididae	2						+													+	
	Hybotidae	1							+													
	Keroplatidae	3																		+	+	
	Limoniidae	1						+														
	Lonchaeidae	1															+					
	Lugistrorrhidae	1									+											
	Milichiidae	1		+	+		+					+										
	Muscidae	6				+	+										+	+			+	
	Mycetophilidae	5	+	+	+		+			+											+	
	Phoridae	8			+		+	+	+			+	+						+	+	+	
	Psychodidae	3								+	+						+					
	Sarcophagidae	1																			+	
	Sciaridae	4									+	+							+			
	Stratyiomidae	1					+															
	Tipulidae	3	+			+	+	+	+	+							+		+	+	+	
	Not identified	21	+		+	+	+	+	+			+	+				+	+	+	+	+	+
Ensifera	Phalangopsidae	4		+		+						+		+	+		+	+	+	+	+	+
	Not identified	5	+			+	+	+	+				+	+	+	+	+	+	+	+	+	
Ephemeroptera	Leptohyphidae	1										+										
	Not identified	1							+													
Hemiptera	Cicadellidae	1						+														
	Cixidae	3					+					+	+					+	+	+		+
	Cydnidae	2										+	+							+		
	Enichocephalidae	3		+	+			+		+											+	
	Hebridae	1																	+		+	
	Orthezidae	1										+										
	Emesinae	3	+			+								+					+		+	+
Hemiptera	Reduviidae	3	+	+	+	+	+		+	+		+	+	+	+	+		+	+	+	+	+
	Not identified	2						+														+
	Veliidae	1	+																			
Hymenoptera	Formicidae	19						+	+	+	+	+		+			+		+	+	+	+
	Not identified	11					+	+	+					+	+	+		+		+	+	+
Isoptera	Nasutitermitidae	2		+			+				+								+			+

Order	Family	TS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Lepidoptera	Noctuidae	5		+	+	+			+			+	+						+			
	Pyralidae	1		+	+		+							+								
	Tineidae	10		+			+								+	+		+	+	+	+	
	Not identified	2			+	+												+				
Megaloptera	Corydalidae	2	+				+															
Neuroptera	Myrmeleontidae	1						+	+									+				
Odonata	**Not identified**	2	+																		+	
Psocoptera	Pseudocaeciliidae	3												+		+				+		+
	Psyllipsocidae	1																				+
	Ptiloneuridae	3	+		+	+				+	+											
	Not identified	8		+				+	+				+	+	+	+					+	
Trichoptera	Hydropsychidae	7	+		+		+			+	+	+					+			+	+	+
Zygentoma	Nicoletiidae	2						+				+										
Geophilomorpha	Geophilidae	2												+							+	
	Not identified	1																				+
Lithobiomorpha	**Not identified**	5							+						+	+	+	+	+		+	
Scolopendromorpha	**Not identified**	1																			+	
Polydesmida	Chelodesmidae	1										+							+			
	Cryptodesmidae	1																		+		
	Pyrgodesmidae	1												+								
	Not identified	1															+		+	+		
Spirostreptida	Pseudonannolenidae	2		+	+		+					+	+	+		+			+	+	+	+
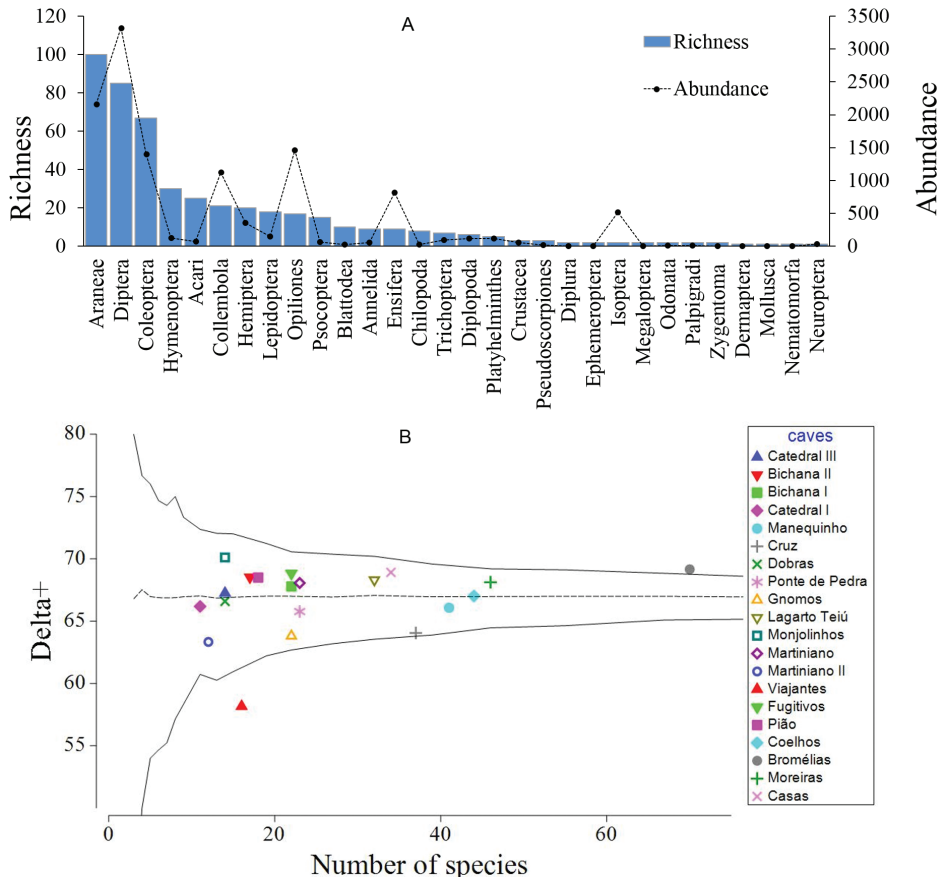
Figure 2. Higher taxa invertebrate abundance, taxonomic diversity (richness) (**A**) and average taxonomic distinctness (Δ+) (**B**) in all 20 quartzite caves placed above 1200 m high in Minas Gerais (Brazil).

Obligate cave species richness

Six invertebrate species, distributed in five caves, presented troglomorphic traits. Casas cave had four troglobitic species ((Blattodea (Figure 3B), Projapygidae (Diplura) (Figure 3D), Pselaphinae (Coleoptera: Staphylinidae), and *Eukoenenia ibitipoca* Souza & Ferreira, 2019 (Palpigradi: Eukoeneniidae) (Figure 3E)), Moreiras cave had two species ((Hypogastruridae (Collembola) species (Figure 3A) and one Projapygidae species (Diplura)). Three other caves had each only one troglomorphic species. Pião and Dobras caves had the same Blattodea species that occurred in Casas cave. Bromélias cave had the Prodidomidae spider *Brasilomma enigmatica* Brescovit, Ferreira & Rheims, 2012 (Figure 3C).

Invertebrate diversity and distribution and their relationships with abiotic factors

The quantitative similarity among cave communities was low (< 41%) and the β_{total} was 0.952, β_{repl} = 0.769 and β_{rich} = 0.178.

Average taxonomic distinctness Δ+ varied between 58 to 70, and 18 caves were placed within the 95% confidence interval of the average taxonomic distinctness (Δ+) (Figure 2, Table 3). However, Δ+ decreased with environmental stability (R_S = -0.46, $p ≤ 0.05$).

The Distance-based linear models (DistLM) revealed in marginal tests that the sampled extension (SE) of the caves (R^2 = 0.08, AICc = 168.7, Pseudo-F = 1.5071; p = 0.01) was the only predictor determining the similarity of cave communities, both for Bray-Curtis and Jaccard similarities. The two axes of the distance-based redundancy analysis (dbRDA) graphic model captured nearly 52.6% of the variability in the fitted

Figure 3. Obligate cave species found in the Ibitipoca Estadual Park, Brazil. **A** Hypogastruridae **B** Blattodea **C** *Brasilomma enigmatica* (Prodidomidae) **D** Projapygidae **E** *Eukoenenia ibitipoca* (Palpigradi).

Table 3. Average taxonomic distinctness with respective lambda and significance values (% sig) of the 20 mountain quartzite caves in southeastern Brazil and the 297 morphotypes that were identified to family level.

Cave names	Richness	Delta+	Delta+ Sig %	Lambda+	Lambda+ Sig %
Catedral III	14	67.25	94.1	197.95	57.1
Bichana II	17	68.53	47	215.48	77.1
Bichana I	22	67.79	67.1	233.65	91.5
Catedral I	11	66.18	75.9	187.24	56.1
Manequinho	41	66.07	45	249.46	57.3
Cruz	37	64.05	5.8	280.86	12.2
Dobras	14	66.59	84.9	255.43	53.3
Ponte de Pedra	23	65.77	52.3	271.84	30.2
Gnomos	22	63.81	15.4	317.96	5.6
Lagarto Teiú	32	68.31	36	208.42	39.4
Monjolinhos	14	70.11	21.8	240.65	72.3
Martiniano	23	68.06	55.9	279.65	22
Martiniano II	12	63.33	24.2	261.62	50.5
Viajantes	16	58.17	1	333.31	6.6
Fugitivos	22	68.83	31.4	233.7	93.3
Pião	18	68.5	49.8	191.86	34.4
Coelhos	44	67.02	99.5	238.26	84.9
Bromélias	70	69.16	1	234.78	96.9
Moreiras	46	68.12	35.2	228.62	85.7
Casas	34	68.91	17	210.05	36.4

model and 16.4% of the total variation in the data cloud. The first overlay showed that the first dbRDA axis is strongly related to cave sampled extension (SE) (Figure 4). The Distance-based linear models (DistLM) revealed that the sampled cave extension (SE) was also the only predictor influencing variations over species richness (R^2 = 0.335, AICc = 117.45, Pseudo-F = 9.1066, p = 0.009) of the cave communities. Furthermore, only total richness (R_S = 0.58, $p ≤ 0.05$) and richness of obligate cave species (R_S = 0.58, $p ≤ 0.05$) increased with cave extension.

Finally, Figure 5 shows the two groups formed in ANOSIM between caves with and without a stream (R = 0.262, p = 0.02) and the bootstrap data variation within the 95% confidence interval. Araneae (*Mesabolivar* sp., Ochyroceratidae spp., Theridiidae sp.), Opiliones (*Mitogoniella indistincta* Mello-Leitão, 1936), Diplopoda (*Pseudonan-nolene* sp.), Ensifera (*Endecous* sp.), Psocoptera (Ptiloneuridae sp.), Collembola sp., Diptera (Tipulidade sp.), Isopoda sp., Hemiptera (Emesinae sp.) andTrichoptera sp., were the taxa that most contributed for disimilarity between the two types of caves.

Trophic resources for the cave invertebrates

Organic resources were composed of plant debris deposited close to vertical or horizontal entrances, as well as sparse roots, root stalagmites, termite galleries, guano of carnivorous bats (*Chrotopteus auritus* Peters, 1856), hematophagous bats (*Desmodus rotundus* (É. Geoffroy, 1810)) and swifts (*Streptoprocne biscutata* (Sclater, 1865)), a very abundant bird in these caves. In some caves, bacterial and fungal biofilms were
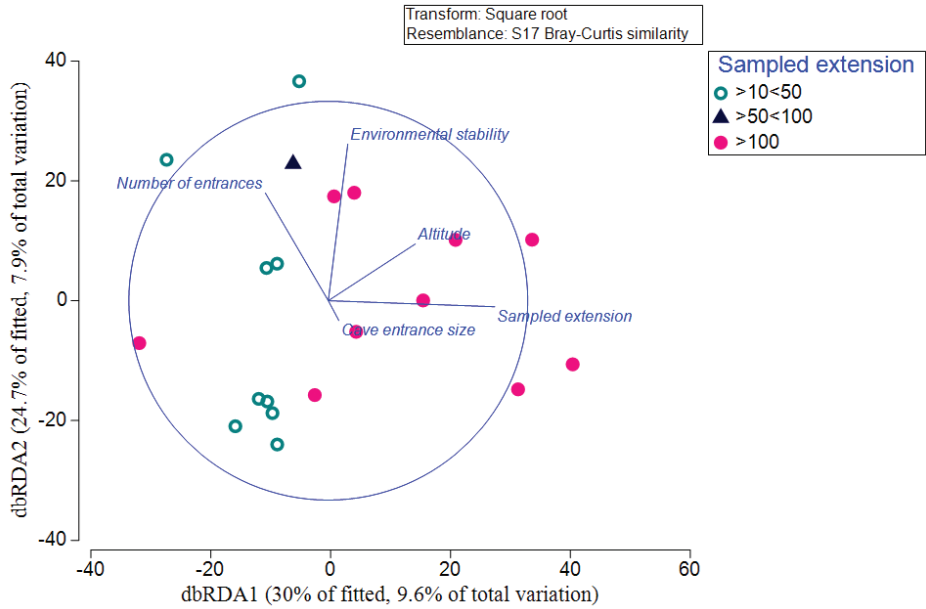
Figure 4. Distance-based redundancy analysis (dbRDA) showing the influences of the environmental factors on cave fauna composition in the 20 studied caves. The two axes explained nearly 55% of the variability in the fitted model and nearly 17% of the total variation in the data cloud. The first overlay shows how the first dbRDA axis is strongly related to cave sampled extension.
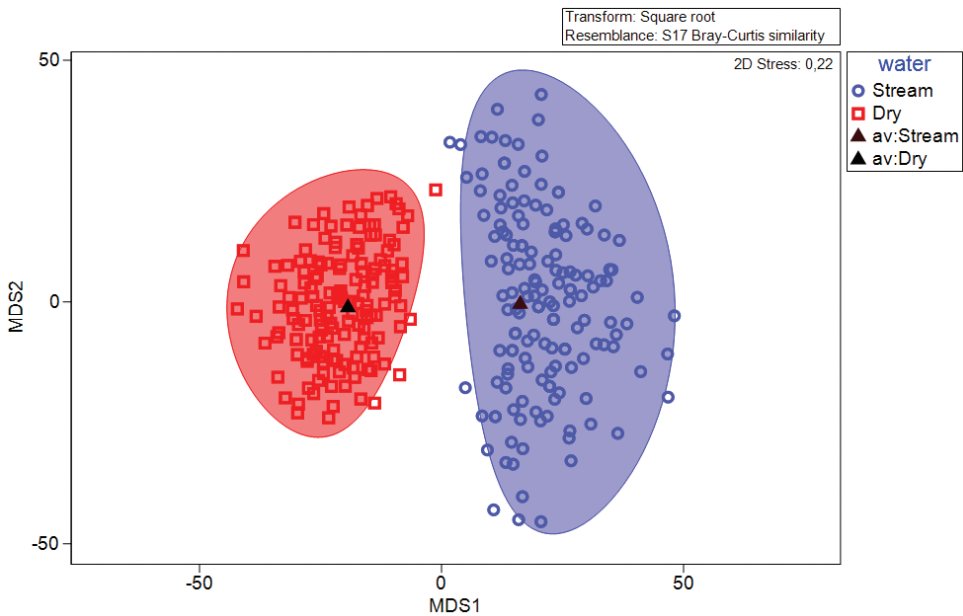
Figure 5. Metric multidimensional scaling (MDS) ordination plot of the 20 quartzite caves with and without a stream using bootstrap regions for group means around their centroids (triangles). Average (Av).

seen on different substrates, which were identified as an alternative organic resource for invertebrates.

The bat guano piles were always small and scarce, but were colonized by Diptera larvae (1500 specimens in total), Collembola (300 specimens in total), Staphylinidae (250 specimens) and Leiodidae (300 specimens), while guano deposits of swifts harbored Acari (50 specimens), Diptera larvae (300 specimens, crickets and spiders. The bat species *Desmodus rotundus* was the most frequent in caves on the park periphery, quite close to cattles. A high diversity of invertebrates, such as Ensifera, Acari, Coleoptera and Diptera larvae, Annelida (Haplotaxida) were found in the guano of these bat. In Casas cave, Collembola, Acari, and Blattodea were observed associated with termite galleries or abandoned nests, the only macroscopic organic matter observed inside this cave. Top predator taxa were Opiliones (about 1000 counted *Mitogoniela* sp.), Reduviidae (about 200 counted *Zelurus* sp.), Pholcidae (about 500 counted *Mesabolivar* sp.) among others.

Description of human uses and impacts

All impacts observed in the caves were the consequences of tourism. Impacts like graffiti on the cave walls, trails and trampled soil were the most common, which were observed in almost all the studied caves. In some caves, the entrances located near the touristic trails garbage (organic and plastics) was found. In the Cruz cave, a wooden ladder was installed to facilitate the access of visitors. Currently, only three caves in the Park are open to tourist visitation: Pião, Coelhos and Monjolinhos caves. Other caves, like Bichana I and II, showed no signs of visitation, although they are located near the access road. Although few impacts were found inside the Park boundaries, the surrounding forests were removed for pastures and monocultures (such as *Eucalyptus*).

Discussion

Besides the influence of potential epigean colonizers, the higher average richness found in the present work (39.55 spp., SD = 21.87 spp.) may have been influenced by the size of the studied caves (average: 180 m in length), which can promote a greater heterogeneity of habitats and support richer fauna. Furthermore, the dissimilarity and turnover may also have been determined by a higher variation in the heterogeneity of caves in terms of number and size of entrances, microhabitats and trophic conditions, which can promote diverse and heterogeneous communities (Howarth 1993, Souza-Silva et al. 2011, Lunghi et al. 2014, Simões et al. 2015). The environmental structural complexity by habitat variation and resource amount may increase the niche availability and thus allow more species to coexist (Tews et al. 2004, Schneider et al. 2011, Stein et al. 2014, Busse et al. 2018).

Many troglophilic species do not occur randomly in caves, being preferentially found in humid, deep and dark areas (Lunghi et al. 2014). Furthermore, some studies

in limestone Brazilian caves have suggested that factors such as cave extension, number, size and position of entrances, besides their trophic conditions and human impacts, may influence the invertebrate species richness and replacement (Ferreira and Horta 2001, Souza-Silva et al. 2011, Simões et al. 2015, Rabelo et al. 2018).

It is known that cave extension represents an important environmental component determining species richness, since it can eventually provide more habitat heterogeneity (Culver and Pipan 2009, Lunghi et al. 2014, Manenti et al. 2015) and availability of organic resources (specially guano), since larger caves may support larger bats colonies (Brunet and Medellín 2001, Souza-Silva et al. 2011).

The influence of big cave entrances is well known since cave entrances act as ecotones between epigean and hypogean sites, sheltering rich communities, with representatives of both epigean and hypogean fauna (Prous et al. 2015).

The presence of streams increase humidity and bring organic matter inside caves, and can also transport epigean species inside caves (Waters 1981, Souza Silva et al. 2011a and 2013). All these characteristics provided by the presence of streams can lead to distinct community compositions in wet and dry quartzite caves, as found by Simões et al. (2015) for some limestone caves in Brazil.

Obligate cave species diversity

In Brazil, with exception of the iron ore cavities (Souza-Silva et al. 2015; Ferreira et al. 2018), non-carbonate caves usually have a low richness of obligate cave species (one to three species) in comparison to limestone (Souza-Silva et al. 2011). However, for the Ibitipoca quartzite landscape, a higher number of obligate cave species was found. Two factors may be determinant for this richness. It is known that variations in environmental conditions associated with a complex geological history are leading causes for the colonization of the subterranean environment in some areas of the world, *e. g.* western Balkans (Deharveng et al. 2012, Mammola 2017), which can be also the cause of cave colonization in Ibitipoca caves.

However the 37 species with troglomorphic traits sampled by Gallão and Bichuette (2015) in 11 caves from Chapada Diamantina, This constitutes an extremely atypical scenario for Neotropical caves. It is important to highlight that, from this total, only 5 species were described and considered as true troglobites (*Tmesiphantes hypogeus* Bertani et al., 2013*, Scolopocryptops troglocaudatus* Chagas-Jr & Bichuette, 2015, *Troglorhopalurus translucidus,* Baptista & Giupponi, 2004 *Discocyrtus pedrosoi* Kury 2008*, Glaphyropoma spinosum* Bichuette, Pinna & Trajano, 2008).

Sharratt et al. (2000) reviewed the fauna of 31 sandstone caves placed between 450–750 m asl on the Cape Peninsula, South Africa, and found 85 invertebrate morphotypes (13 of them troglobites). Peck and Peck (1982) observed 15 troglophiles and 2 obligate cave species in Devils Den cave, USA. Although these studies used different sampling methodologies, these caves showed a lower average richness when compared to the quartzite caves from this study. The smaller size, lower number of entrances

might play a role in the richness in siliciclastic caves. To these features, the latitude of caves can be added possibly influencing the richness, since tropical regions have greater species richness (and diversity) compared to temperate regions (Gaston and Blackburn 2000) and thus, the pool of potential cave colonizers is richer.

Threats to the cave fauna

The use of caves for tourism is not uncommon and can be extremely important for the local economy worldwide (Bočić et al. 2006, Polak and Pipan 2011). This practice can be conducted with direct alterations to the cave structure, with the installation of stairs, railings and lighting equipment or without such modifications, characterizing an option for sporting nature (Polak and Pipan 2011). In fact, such modifications can cause intense instantaneous or cumulative pressures to the fauna (Gillienson 2011), directly influencing the species richness and abundance. In some cases, the touristic impact may focus on alterations in entrance zones, affecting both the flow of animals to the environment (*e.g.* bats) and the availability of organic resources (Polak and Pipan 2011). However, it is important to emphasize that depending on the cave structure (like the size of the chambers), the impacts can be different for the cave biodiversity (Faille et al. 2015).

Ibitipoca is a State Park and represents one of the most visited areas in the state of Minas Gerais. Nevertheless, its caves are not arranged for tourists. The management plan of the Park included caves, but cave species were not considered for planning conservation strategies (Trajano et al. 2007).

Areas deforested for cattle ranching were observed in the surroundings of Ibitipoca Mountain and may have directly influenced the abundance of *Desmodus rotundus* (hematophagous bat) in peripheral caves. Therefore, further attention to the preservation of forests surrounding the Park is also required for the conservation of cave invertebrates because obligate cave species depends on the bat and swift guano.

Final considerations

The present study revealed a rich and diverse invertebrate community sheltered in Ibitipoca quartzite caves, influenced mainly by the extension of the caves and presence of streams. This relationship has been recurrent in several other studies conducted with caves associated with different lithologies in Brazil and can be considered a keystone element for the maintenance of cave biodiversity.

Acknowledgments

References

Anderson MJ, Gorley RN, Clarke KR (2008) Permanova + for primer: a guide to software and statistical methods. PRIMER-E, Plymouth.

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Alves VR, Freitas RAD, Santos FL, Barrett TV (2011) Diversity of sandflies (Psychodidae: Phlebotominae) captured in sandstone caves from Central Amazonia, Brazil. Memórias do Instituto Oswaldo Cruz 106(3): 353–359. https://doi.org/10.1590/S0074-02762011000300016

Astorga A, Death R, Death F, Paavola R, Chakraborty M, Muotka T (2014) Habitat heterogeneity drives the geographical distribution of beta diversity: the case of New Zealand stream invertebrates. Ecology and Evolution 4(13): 2693–2702. https://doi.org/10.1002/ece3.1124

Aubrecht R, Barrio-Amorós CL, Breure ASH, Brewer-Carías C, Derka T, Fuentes-Ramos OA, Gregor M, Kodada J, Kováčik Ľ, Lánczos T, Lee NM, Liščák P, Schlögl J, Šmída B, Viček L (2012) Venezuelan tepuis: their caves and biota. Acta Geologica Slovaca – Monograph, Comenius University, Bratislava, 168 pp.

Auler AS, Sauro F (2019) Quartzite and quartz sandstone caves of South America. In: White W, Culver D, Pipan T (Eds) Encyclopedia of Caves. Academic Press, 850–860. https://doi.org/10.1016/B978-0-12-814124-3.00102-3

Bento DM, Ferreira RL, Prous X, Souza-Silva M, Bellini BC, Vasconcellos A (2016) Seasonal variations in cave invertebrate communities in the semiarid Caatinga, Brazil. Journal of Cave and Karst Studies 78(2): 61–71. https://doi.org/10.4311/2015LSC0111

Bertani R, Bichuette ME, Pedroso DR (2013) *Tmesiphantes hypogeus* sp. nov. (Araneae, Theraphosidae), the first troglobitic tarantula from Brazil: Anais da Academia Brasileira de Ciências (85): 235–243. https://doi.org/10.1590/S0001-37652013005000007

BCRA (2017) British Cave Research Association Survey-Grade. http://bcra.org.uk/surveying

Bichuette ME, de Pinna MCC, Trajano E (2008) A new species of *Glaphyropoma*: The first subterranean Copionodontine catfish and the first occurrence of opercular Odontodes in the subfamily (Siluriformes: Trichomycteridae): Neotropical Ichthyology (6): 301–306. https://doi.org/10.1590/S1679-62252008000300002

Bočić N, Lukic A, Opacic VT (2006) Management models and development of show caves as tourist destinations in Croatia: Acta Carsologica 2(35): 13–21. https://doi.org/10.3986/ac.v35i2-3.224

Brunet AK, Medellín RA (2001) The Species-Area Relationship in Bat Assemblages of Tropical Caves: Journal of Mammalogy 82: 1114–1122. https://doi.org/10.1644/1545-1542(2001)082<1114:TSARIB>2.0.CO;2

Busse A, Antiqueira PAP, Neutzling AS, Wolf AM, Romero GQ, Petermann JS (2018) Different in the dark: The effect of habitat characteristics on community composition and beta diversity in bromeliad microfauna. PLoS ONE 13(2): e0191426. https://doi.org/10.1371/journal.pone.0191426

Cardoso P, Rigal F, Carvalho JC (2015) BAT – Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods in Ecology and Evolution 6: 232–236. https://doi.org/10.1111/2041-210X.12310

Christiansen K (2012) Morphological adaptations. In: White W, Culver D (Eds) Encyclopedia of Caves (2nd edn). Academic Press, 517–528. https://doi.org/10.1016/B978-0-12-383832-2.00075-X

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2014) Change in marine communities: an approach to statistical analysis and interpretation, 3rd edn. PRIMER-E, Plymouth.

Corrêa-Neto AV, Filho JB (1997) Espeleogênese em quartzito da Serra de Ibitipoca, Sudeste de Minas Gerais: Anuário do Instituto de Geociências 20: 75–87.

Culver DC, Pipan T (2009) The Biology of Caves and Other Subterranean Habitats. Oxford University Press, UK, 256 pp.

Deharveng L, Gibert J, Culver DC (2012) Diversity patterns in Europe. In: White WB, Culver DC (Eds) Encyclopedia of Caves (2nd edn). Elsevier Inc, UK, 219–228. https://doi.org/10.1016/B978-0-12-383832-2.00030-X

Dessen EMB, Eston VR, Silva MS, Temperini-Beck M T, Trajano E (1980) Levantamento preliminar da fauna de cavernas de algumas regiões do Brasil: Ciência e Cultura 6(32): 714–725.

Faille A, Bourdeau C, Deharveng L (2015) Weak impact of tourism activities on biodiversity in a subterranean hotspot of endemism and its implications for the conservation of cave fauna: Insect Conservation and Diversity 8: 205–215. https://doi.org/10.1111/icad.12097

Fernandes CS, Bichuette ME (2013) Levantamento preliminar de invertebrados em três cavernas areníticas do Rio Grande do Sul, Brasil. Espeleo-Tema 1(24): 41–47.

Ferreira RL, Oliveira MPA, Souza-Silva M (2018) Subterranean Biodiversity in Ferruginous Landscapes. Cave Ecology. Springer, Cham, 435–447. https://doi.org/10.1007/978-3-319-98852-8_21

Ferreira RL (2004) A medida da complexidade ecológica e suas aplicações na conservação e manejo de ecossistemas subterrâneos. PhD Thesis, Belo Horizonte, Universidade Federal de Minas Gerais, 158 pp.

Ferreira RL, Horta LCS (2001) Natural and human impacts on invertebrate communities in Brazilian caves: Revista Brasileira de Biologia 7(61): 7–17. https://doi.org/10.1590/S0034-71082001000100003

Galán C, Herrera FF (2006) Fauna cavernícola de Venezuela: una revisión, Boletín de la Sociedad Venezolana de Espeleología 40: 39–57.

Gallão JE, Bichuette ME (2015) Taxonomic distinctness and conservation of a new high biodiversity subterranean area in Brazil: Anais da Academia Brasileira de Ciências 1(87): 209–217. https://doi.org/10.1590/0001-3765201520140312

Gaston KJ, Blackburn TM (2000) Pattern and Process in Macroecology. Blackwell Science Ltd, Oxford, 377 pp. https://doi.org/10.1002/9780470999592

Gaston KJ (2000) Global patterns in Biodiversity. Nature 403: 220–227. https://doi.org/10.1038/35012228

Gillienson DS (2011) Management of caves. In: van Beynen PE (Ed.) Karst Management. Springer Dordrecht Heidelberg London, 141–158. https://doi.org/10.1007/978-94-007-1207-2_6

Gnaspini-Netto P, Trajano E (1994) Brazilian cave invertebrates, with a checklist of troglomorphic taxa: Revista Brasileira de Entomologia 38: 549–584.

Guadanucci JPL, Braga PLM, Sá FDS (2015) Aspects of the activity rhythm and population size of troglophilic mygalomorph spiders (*Trechona* sp., Dipluridae) in a quartzite cave in Minas Gerais, Brazil. Journal of Natural History 49(15–16): 889–903. https://doi.org/10.1080/00222933.2014.946108

Howarth FG (1993) High-stress subterranean habitats and evolutionary change in cave-inhabiting arthropods. American Naturalist 142: S65–S77. https://doi.org/10.1086/285523

Jaffé R, Prous X, Zampaulo R, Giannini TC, Imperatriz-Fonseca VL, Maurity C, Siqueira, JO (2016) Reconciling Mining with the Conservation of Cave Biodiversity: A Quantitative Baseline to Help Establish Conservation Priorities. PLoS ONE 11(12): e0168348. https://doi.org/10.1371/journal.pone.0168348

Lourenço WR, Baptista RLC, Giupponi APDL (2004) Troglobitic scorpions: A new genus and species from Brazil. Comptes Rendus – Biologies 327: 1151–1156. https://doi.org/10.1016/j.crvi.2004.09.001

Lunghi E, Manenti R, Ficetola GF (2014) Do cave features affect underground habitat exploitation by non-troglobite species? Acta Oecologica 55: 29–35. https://doi.org/10.1016/j.actao.2013.11.003

Magurran AE (2004) Measuring Biological Diversity. Blackwell Science, 256 pp.

Moldovan OT, Kováč Ľ, Halse S (2018) Cave Ecology. Ecological Studies 235, Springer, Cham. https://doi.org/10.1007/978-3-319-98852-8

Mammola S, Isaia M (2018) Day-night and seasonal variations of a subterranean invertebrate community in the twilight zone. Subterranean Biology 27: 31–51. https://doi.org/10.3897/subtbiol.27.28909

Mammola S (2017) Modelling the future spread of native and alien congeneric species in subterranean habitats – the case of Meta cave-dwelling spiders in Great Britain. International Journal of Speleology 46(3): 427–437. https://doi.org/10.5038/1827-806X.46.3.2134

Mammola S (2018) Finding answers in the dark: caves as models in ecology fifty years after Poulson and White. Ecography 41: 1–21. https://doi.org/10.1111/ecog.03905

Manenti R, Lunghi E, Ficetola GF (2015) The distribution of cave twilight-zone spiders depends on microclimatic features and trophic supply. Invertebrate Biology 134(3): 242–251. https://doi.org/10.1111/ivb.12092

Nascimento MAL, Mantesso-Neto V (2013) Speleological heritage in Brazil's proposed geoparks, as presented in the book "Geoparques do Brasil: "propostas" Tourism and Karst Areas 6(1): 27–42.

Nobre PH, Mello RM, Manhães MA, Rezende AC (2013) Morcegos (Chiroptera, Mammalia) do Parque Estadual do Ibitipoca, Minas Gerais – Brasil: MG. Biota 2(6): 4–29.

Oliver I, Beattie AJ (1996) Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 1(10): 99–109. https://doi.org/10.1046/j.1523-1739.1996.10010099.x

Peck SB, Peck JH (1982) Invertebrate fauna of Devils Den, a sandstone cave in northwestern Arkansas: Arkansas Academy of Science Proceedings 36: 46–48.

Pellegrini TG, Pompeu PS, Ferreira RL (2018) Cave benthic invertebrates in south-eastern Brazil: are there 'key' factors structuring such communities? Marine and Freshwater Research 69(11): 1762–1770. https://doi.org/10.1071/MF18025

Pellegrini TG, Sales LP, Aguiar P, Ferreira RL (2016) Linking spatial scale dependence of land-use descriptors and invertebrate cave community composition. Subterranean Biology 18: 17–38. https://doi.org/10.3897/subtbiol.18.8335

Pinto-da-Rocha R (1995) Sinopse da fauna cavernícola do Brasil (1907–1994): Papéis Avulsos de Zoologia 6(39): 61–173.

Polak S, Pipan T (2011) Subterranean habitats and fauna, their threats and conservation. In: Prelovšek M, Hajna NZ (Eds) Pressures and Protection of the Underground Karst – Cases from Slovenia and Croatia. Postojna, Karst Research Institute ZRC SAZU, 23–32.

Prous X, Ferreira RL, Jacobi CM (2015) The entrance as a complex ecotone in a Neotropical cave: International Journal of Speleology 944: 177–189. https://doi.org/10.5038/1827-806X.44.2.7

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Rabelo LM, Souza-Silva M, Ferreira RL (2018) Priority caves for biodiversity conservation in a key karst area of Brazil: comparing the applicability of cave conservation indices. Biodiversity and Conservation 9(27): 2097–2129. https://doi.org/10.1007/s10531-018-1554-6

Schneider K, Christman MC, Fagan WF (2011) The influence of resource subsidies on cave invertebrates: results from an ecosystem-level manipulation experiment: Ecology 3(92): 765–776. https://doi.org/10.1890/10-0157.1

Sendra A, Arnedo MA, Ribera C, Teruel S, Bidegaray-Batista L, Conde B (2012) Revision of *Cestocampa* Condé (Diplura, Campodeidae), with description of a new species from caves in the eastern Iberian Peninsula. Zootaxa 3252: 43–56. https://doi.org/10.11646/zootaxa.3252.1.2

Sharratt NJ, Picker M, Samways M (2000) The invertebrate fauna of the sandstone of the caves of the Cape Peninsula (South Africa): patterns of endemism and conservation priorities. Biodiversity and Conservation 9: 107–143. https://doi.org/10.1023/A:1008968518058

Silva SM (2004) Carstificação em rochas siliciclásticas: estudo de caso na Serra do Ibitipoca, Minas Gerais. Tese de Doutorado. Dissertação de Mestrado. Instituto de Geociências, Universidade Federal de Minas Gerais, 142 pp.

Simões MH, Souza-Silva M, Ferreira RL (2015) Cave physical attributes influencing the structure of terrestrial invertebrate communities in Neotropics: Subterranean Biology 16: 103–121. https://doi.org/10.3897/subtbiol.16.5470

Souza-Silva M, Martins RP, Ferreira RL (2011a) Trophic Dynamics in a Neotropical Limestone Cave. Subterranean Biology (9): 127–138. https://doi.org/10.3897/subtbiol.9.2515

Souza MFVR, Ferreira RL (2012) A new highly troglomorphic species of *Eukoenenia* (Palpigradi: Eukoeneniidae) from tropical Brazil. The Journal of Arachnology 40: 151–158. https://doi.org/10.1636/Ha11-26.1

Souza-Silva M, Júnior AS, Ferreira RL (2013) Food resource availability in a quartzite cave in the Brazilian montane Atlantic Forest. Journal of Cave and Karst Studies 75(3): 177–188. https://doi.org/10.4311/2010JCKS0158

Souza-Silva M, Martins RP, Ferreira RL (2011b) Cave lithology determining the structure of the invertebrate communities in the Brazilian Atlantic Rain Forest: Biodiversity Conservation 20: 1713–1729. https://doi.org/10.1007/s10531-011-0057-5

Souza-Silva M, Martins RP, Ferreira RL (2015) Cave conservation priority index to adopt a rapid protection strategy: A case study in brazilian atlantic rain forest. Environmental Management 55: 279–295. https://doi.org/10.1007/s00267-014-0414-8

Sprent P, Smeeton NC (2000) Applied nonparametric statistical methods. Chapman and Hall/ CRC, 480 pp. https://doi.org/10.1201/9781420057713

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17(7): 866–880. https://doi.org/10.1111/ele.12277

Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31: 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Trajano E, Bichuette ME, Franco FP (2007) Bioespeleologia. In: Instituto Estadual de Florestas, ed., Plano de Manejo do Parque Estadual de Ibitipoca, Belo Horizonte, Governo de Minas Gerais, 46–52.

Trajano E, Gnaspini-Netto P (1991) Composição da fauna cavernícola brasileira, com uma análise preliminar da distribuição dos táxons. Revista Brasileira de Zoologia 3(7): 383–407. https://doi.org/10.1590/S0101-81751990000300017

Trajano E, Moreira JRA (1991) Estudo da fauna de cavernas da província espeleológica arenítica Altamira-Itaituba, Pará. Revista Brasileira de Biologia 51(1): 13–25.

Waters TF (1981) Drift of stream invertebrates below a cave source. Hydrobiologia 78: 169–175. https://doi.org/10.1007/BF00007592

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon, 21, 213–251. https://doi.org/10.2307/1218190

Wynne JJ, Howarth FG, Sommer S, Dickson BG (2019) Fifty years of cave arthropod sampling: techniques and best practices. International Journal of Speleology 48: 33–48. https://doi.org/10.5038/1827-806X.48.1.2231

Zar JH (1984) Biostatistical analysis (2nd edn). New Jersey, Prentice-Hall, 718 pp.

Zeppelini D, Ribeiro AC, Ribeiro GC, Fracasso MPA, Pavani MM, Oliveira, OMP, Oliveira SA, Marques AC (2003) Faunistic survey of sandstone caves from Altinópolis region, São Paulo State, Brazil. Papéis Avulsos de Zoologia 5(43): 93–99. https://doi.org/10.1590/S0031-10492003000500001