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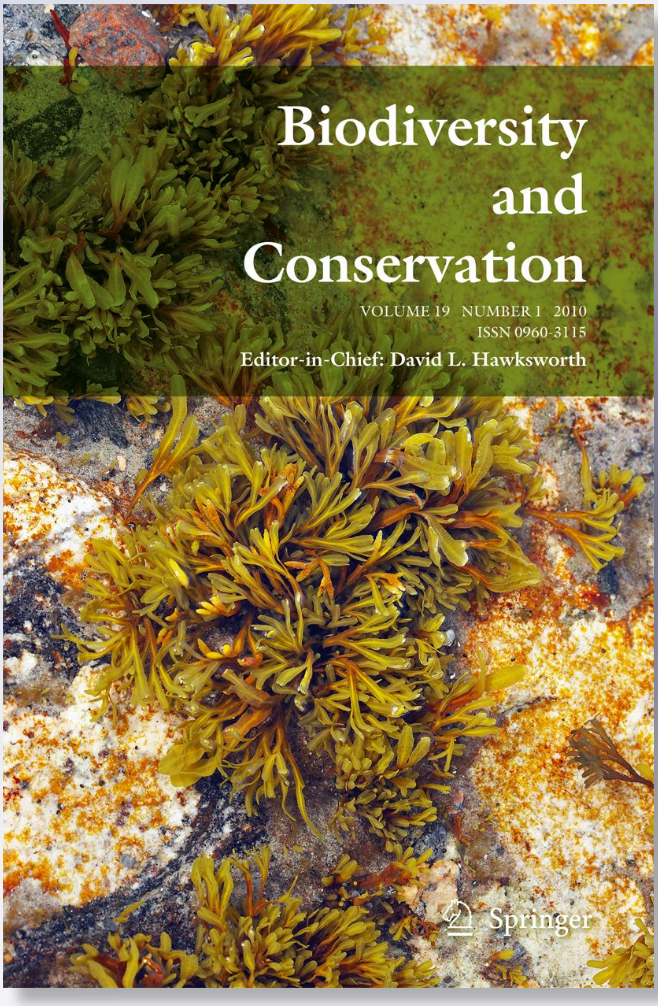

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ORIGINAL PAPER

Cave lithology determining the structure of the invertebrate communities in the Brazilian Atlantic Rain Forest

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Abstract In Brazil, only limestone caves and a few caves in sandstone, iron ore and granite rocks had their invertebrate communities evaluated. Being such, the present study aimed to promote a comparative analysis of the structure of the invertebrate communities in caves associated to carbonatic, magmatic, siliciclastic and ferruginous rocks of the Brazilian Atlantic forest. Significant differences in the relative richness, abundance and diversity were observed between lithologies. The average relative richness was higher in the ferruginous caves (0.53 spp). The total number of troglomorphic species was significantly different among caves and the highest average richness occurred at ferruginous caves (5.79 spp/cave). Siliciclastic, carbonatic and magmatic caves presented a higher quantitative similarity of the fauna. Ferruginous caves revealed communities with a fauna composition different from the other lithologies. The total richness of invertebrates correlated significantly and positively with the linear development in the siliciclastic caves ($R_s = 0.67$, $P < 0.05$), carbonatic ($R_s = 0.71$, $P < 0.05$) and ferruginous ($R_s = 0.74$, $P < 0.05$). The rock type in which the cave is inserted can determine differences in the richness of invertebrate troglophyles and troglobites. Therefore, on creating value attributes, the size of the caves should always come related to their lithology by the fact that same sized caves associated to different lithologies, possess communities with quite diverse structures.

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Introduction

The Brazilian Atlantic forest is one of the most threatened ecosystems on the planet mainly by the fact of more than 90% of its original area has been deforested and used for human activities (mining, pasture, agriculture, cities, etc.). More than 100 million people live in more than 300 cities that depend and exploite the components and environmental services of this biome (Morrelato and Haddad 2000). The degradation of the Brazilian Atlantic forest is one of the most alarming world conservationist problems, due to the consequent elimination of many populations and the potential erosion of the genetic diversity of many species (Terborgh 1992). In this scenario, the caves of the Atlantic forest are also susceptible to the same threats, since karst environments are extremely vulnerable to degradation and pollution, and the human activities in these places can generate impacts in the surface and underground ecosystems (Ford 2007; Van Beynen and Townsend 2005; Calo and Parise 2006).

Caves are subterranean environments inserted in rocky reliefs that present a wide diversity of habitats and shelter rich vertebrate fauna and micro and meso invertebrates (Culver and Sket 2000; Ferreira and Martins 2001; Ferreira 2005; Culver and Pipan 2009). Organisms that live in the subterranean environments can be accidental or use the caves as nighttime or daytime (trogloxene) shelters. They could also complete their whole life cycle inside or outside the caves (troglophilic). However, some species do not occur in epigean habitats, presenting behavioral, morphological and physiological specializations for exclusive survival within caves (troglobites). Frequently in these organisms there is the reduction of the ocular structures, depigmentation and the elongation of sensorial appendages (Desutter-Grandcolas 1997; Culver 2001; Christiansen 2005; Culver and Pipan 2009).

Most of the caves in the world are located in carbonatic rocks (limestones and dolomites), the most favorable to the dissolution process. The occurrence of caves in quartzite, sandstone, iron ore, granite, gneiss, micaschist, phyllite and even in soil are also registered, although on a smaller scale than in the carbonatic (Gillieson 1998; Ford 2007). In Brazil only 3,500 carbonatic caves are officially known. Furthermore, in the country are also known 1,000 ferruginous caves, 200 quartzite caves, 200 arenitic caves and 100 caves in other types of rocks (Auler 2006).

Most studies concerning cave fauna in Brazil and in the world have been carried out in limestone caves (Sharratt et al. 2000; Trajano 2000; Gunn 2005; Culver and Pipan 2009). Even knowning of the existence of cavities in non-carbonatic rocks in Brazil and in the world, their dimensions, in general reduced, has lead to a historical “indifference” and few speleolobiological studies have been conducted, with the exception of lava tubes, intensively studied in many parts of the world (Oromí et al. 1990; Culver et al. 2000; Howarth 2004; Deharveng 2005). In spite of this, a few caves in sandstone, iron ore and granite have had their invertebrate communities evaluated (Trajano and Moreira 1991; Gnaspini-Neto and Trajano 1994; Sharratt et al. 2000; Ferreira 2005).

Cavities associated to different lithological types frequently possess completely differentiated genesis (Ford and Williams 2007). Besides, the compaction level (or, on the other hand, discontinuity) of a rock defines different configurations and even dimensions for the subterranean environments of smaller volume (micro- and meso-caverns and their contact with the soil-MSS and epikarst), conected to the macro-caves (Juberthie and Decu 1998; Brancelj 2005; Culver and Pipan 2009).

Although those differences in the rock structure have been known for decades, some authors had assumed that the type of rock would not determine differences in the cave communities (Gnaspini-Neto and Trajano 1994). In that case, the differences observed would be only the product of biogeographical variations, being not related to the lithology of the cave, at least for Brazilian caves (Gnaspini-Neto and Trajano 1994).

However, understanding the environmental and community particularities associated to the different cave lithologies, is crucial to preserve the cave communities in a country with a megabiodiversity. It is not actually possible to propose cave preservation actions if we do not know the influence of the rock matrix variations upon the composition and structure of the subterranean communities. As such, the present work has as its main objective, to promote a comparative analysis of the abundance, richness, diversity and similarity of the invertebrate cave fauna in different lithologies in the Brazilian Atlantic forest.

Methodology

Study area

The study was conducted in a total of 91 caves: granite (34%), iron ore (19%), limestone (14%), quartzite (14%), sandstone (8%), calcarenite (4), marble (2%), gneiss (2%) and conglomerate (2%), all of them within the domain of the Brazilian Atlantic Rain Forest (Table 1 and Fig. 1). For purposes of analysis, such caves were grouped in four lithological groups, that encompased carbonatic caves (limestone, marble, calcarenite and conglomerated carbonatic), magmatic (and derived metamorphic—granite and gneiss), siliciclastic (quartzite and sandstone) and ferruginous (iron ore: caprock “canga”, itabirite and hematite). The average length of the caves associated to each group was variable. The siliciclastic caves possessed an average length of 240 m, the carbonatic 200 m, the magmatic 53.5 m and the ferruginous 34 m (Table 1). The average altitude was 1,404.6 m for ferruginous caves, 1,080.8 m for the siliciclastic, 508.7 m for the magmatic and 269.1 m for the carbonatic.

Procedures

All the invertebrates species found on each cave had some of their specimens collected. The organisms observed during the collections were counted and plotted on schematic maps of each cave, according to the methodology proposed by Ferreira (2004). Extensive visual searching and manual collections were made with the aid of tweezers, brushes and entomological nets. All microhabitats such as vegetable debris, guano deposits, spaces under stones and humid places were inspected (Sharratt et al. 2000). In the water collections, flowing or still, the organisms were collected with the aid of tweezers and hand nets. The collection team was always composed by five biologists (always the same team) with experience in caving and manual collection of invertebrates.

Pitfall traps with bait were not used to determine taxon abundances because trapping was not considered an appropriate census technique. Pitfall trapping is notorious for causing population disturbances in caves (Weinstein and Slaney 1995; Sharratt et al. 2000). For invertebrate faunal survey, direct searching is very effective, but is dependent on the presence of a surveyor with previous experience (Weinstein and Slaney 1995).

Table 1 List of all studied caves, location in UTM (X, Y, Z) in different Brazilian states (BS), lithologies (L), size in meters (E), troglomorphic species (T), total number of species (S), total number of individuals (A), Shannon diversity (H), Berker–Parker dominance (D), equitability (J), realative number of species (SR), relative number of individuals (AR) and relative diversity (HR). Carbonatic (Ca) Ferruginous (Fe), Magmatic (Ma), Siliciclastic (Si)

CAVE NAME	X	Y	Z	BS	L	E (m)	T	S	A	H	D	J	SR	AR	HR
Archimides Panssini	285168	7711062	24	ES	Ca1	300	1	66	760	2.987	0.082	0.713	0.073	0.844	0.003
California	420374	8296354	24	BA	Ca2	195	3	63	5364	1.835	0.336	0.441	0.162	13.754	0.005
Córrego Verde	427602	8289937	24	BA	Ca3	100		50	2705	1.940	0.243	0.496	0.050	2.705	0.002
Cova da Onca I	493234	8514476	24	BA	Ca4	7		38	640	2.269	0.164	0.624	1.086	18.286	0.065
Cova da Onça II	493234	8514476	24	BA	Ca5	25		28	182	2.333	0.175	0.700	0.747	4.853	0.062
Gruta das Furnas	194227	7612291	25	RJ	Ca6	100	1	71	899	3.044	0.073	0.714	0.118	1.498	0.005
Gruta de Ubajara	289164	9576252	24	CE	Ca7	1120	2	74	3711	2.649	0.098	0.615	0.013	0.663	0.000
Gruta do Morcego Branco	291347	9579450	24	CE	Ca8	274		54	552	3.146	0.064	0.789	0.099	1.007	0.006
Gruta dos Mocós	291347	9579450	24	CE	Ca9	116		24	320	1.950	0.222	0.606	0.103	1.379	0.008
Lapão de Santa Luzia	461229	8292277	24	BA	Ca10	500	1	107	4353	2.294	0.200	0.491	0.014	0.580	0.000
Limoeiro	273406	7733590	24	ES	Ca11	600	1	78	4074	2.376	0.204	0.545	0.013	0.679	0.000
Milagrosa	420012	8296903	24	BA	Ca12	305	1	65	1714	2.393	0.182	0.573	0.018	0.468	0.001
Mirante	285168	7711062	24	ES	Ca13	30		45	1920	2.107	0.197	0.547	0.188	8.000	0.009
Pedra Branca	705979	8815882	24	SE	Ca14	100		24	4335	1.750	0.193	0.551	0.080	14.450	0.006
Pedra do Sino	466472	8293253	24	BA	Ca15	100	2	74	609	3.079	0.082	0.718	0.247	2.030	0.010
Pedra Santa	783587	7566048	23	RJ	Ca16	150		31	1200	2.137	0.187	0.622	0.103	4.000	0.007
Pedra Suspensa	420756	8298168	24	BA	Ca17	113	3	76	7146	1.913	0.234	0.442	0.112	10.540	0.003
Praia da Cueira I	493234	8514476	24	BA	Ca18	8		19	3757	0.958	0.526	0.325	2.375	469.625	0.120
Praia da Cueira II	493234	8514476	24	BA	Ca19	8		7	524	1.432	0.275	0.736	0.875	65.500	0.179
Tião Lima	201849	8028311	24	MG	Ca20	15		22	242	1.992	0.228	0.644	0.147	1.613	0.013
Toca dos Morcegos	420638	8295919	24	BA	Ca21	200	1	81	3607	2.537	0.154	0.577	0.081	3.607	0.003
Mina do pico 01	619370	7765026	23	MG	Fe1	8		11	39	1.696	0.302	0.707	0.917	3.250	0.141
Mina do pico 02	619251	7762602	23	MG	Fe2	20	2	20	144	2.037	0.223	0.680	0.500	3.600	0.051
Mina do pico 03	619287	7762606	23	MG	Fe3	14	3	18	781	1.286	0.440	0.437	0.257	11.157	0.018

Table 1 continued

CAVE NAME	X	Y	Z	BS	L	E (m)	T	S	A	H	D	J	SR	AR	HR
Mina do pico 04	619754	7763446	23	MG	Fe4	60	4	43	2441	0.888	0.708	0.236	0.239	13.561	0.005
Mina do pico 07	619800	7764722	23	MG	Fe5	39	1	26	126	2.612	0.106	0.802	0.133	0.646	0.013
Mina do pico 08	619795	7764761	23	MG	Fe6	128	14	78	735	3.139	0.088	0.716	0.030	0.287	0.001
Mina do pico 09	619727	7764759	23	MG	Fe7	21	7	37	267	2.432	0.141	0.664	0.587	4.238	0.039
Mina do pico 10	616173	7758696	23	MG	Fe8	64	8	39	780	1.990	0.232	0.543	0.152	3.047	0.008
Mina do pico 11	619404	7764005	23	MG	Fe9	30	8	46	427	2.736	0.109	0.711	0.613	5.693	0.036
Mina do pico 12	618942	7763240	23	MG	Fe10	37	4	37	312	2.218	0.272	0.614	0.500	4.216	0.030
Mina do pico 13	618914	7763214	23	MG	Fe11	13	1	17	146	1.715	0.312	0.606	0.654	5.615	0.066
Mina do pico 16	618273	7761166	23	MG	Fe12	16		15	103	2.044	0.193	0.737	0.469	3.219	0.064
Mina do pico 17	619424	7763990	23	MG	Fe13	10		12	162	1.575	0.330	0.614	0.800	10.800	0.105
Serra da Moeda Sul-04	607457	7767894	23	MG	Fe14	34	3	58	1437	2.119	0.231	0.522	0.853	21.132	0.031
Serra da Moeda Sul-25	607996	7760803	23	MG	Fe15	58	10	57	414	3.106	0.075	0.772	0.246	1.784	0.013
Serra da Moeda Sul-29	607912	7765887	23	MG	Fe16	23	11	75	492	3.266	0.066	0.756	0.652	4.278	0.028
Serra da Moeda Sul-31	607918	7765858	23	MG	Fe17	15	5	40	205	2.887	0.101	0.777	1.333	6.833	0.096
Boa Vista	235465	8110493	24	MG	Ma1	80		48	1725	0.785	0.757	0.203	0.050	1.797	0.001
Buraco do Cão	182967	8975832	25	AL	Ma2	20		31	365	2.374	0.151	0.691	0.310	3.650	0.024
Cabeceira do americaninha	267413	8104793	24	MG	Ma3	70		32	113	2.974	0.072	0.858	0.057	0.202	0.005
Cachoeira do Reinaldo 1	306727	8154136	24	MG	Ma4	15		23	95	2.200	0.201	0.702	0.307	1.267	0.029
Cachoeira do Reinaldo 2	306727	8154136	24	MG	Ma5	8		5	68	0.908	0.567	0.507	0.208	2.833	0.038
Casa Branca	305381	7830778	24	ES	Ma6	15		41	183	2.361	0.197	0.636	0.182	0.813	0.010
Caverna do Didi Vieira	284809	7766144	24	ES	Ma7	79		64	231	3.515	0.059	0.845	0.101	0.366	0.006
Córrego dos Vieira	240564	240564	24	MG	Ma8	90	1	48	325	1.961	0.357	0.507	0.053	0.361	0.002
Gruta da Lavra do Cristal	228366	8028692	24	MG	Ma9	10		23	320	1.597	0.327	0.509	0.288	4.000	0.020
Gruta da Manga da Pedra	797307	7972939	23	MG	Ma10	20		10	54	1.425	0.366	0.619	0.050	0.270	0.007
Gruta da Michele	311940	7872453	24	ES	Ma11	60		73	245	3.481	0.062	0.811	0.122	0.408	0.006

Table 1 continued

CAVE NAME	X	Y	Z	BS	L	E (m)	T	S	A	H	D	J	SR	AR	HR
Gruta da Pedra Riscada	779553	7524950	23	RJ	Ma12	40	1	35	147	2.808	0.100	0.790	0.109	0.459	0.009
Gruta da Represa	322639	7808340	24	ES	Ma13	25		43	297	2.859	0.098	0.760	0.096	0.660	0.006
Gruta da Santa Bárbara	275936	7747596	24	ES	Ma14	80		61	617	2.955	0.080	0.719	0.191	1.928	0.009
Gruta da Serraria	475907	7366598	23	SP	Ma15	190		29	476	2.384	0.133	0.708	0.015	0.251	0.001
Gruta da Vaca Parida	264939	8019188	24	MG	Ma16	12		39	275	2.214	0.241	0.609	0.120	0.849	0.007
Gruta do evald	320007	7747606	24	ES	Ma17	23		17	50	2.232	0.191	0.788	0.246	0.725	0.032
Gruta do Huschi	339370	7791692	24	ES	Ma18	30	2	79	462	3.130	0.095	0.716	0.878	5.133	0.035
Gruta do João Buteco	308438	7974280	24	ES	Ma19	25		17	646	2.168	0.156	0.765	0.340	12.920	0.043
Gruta do João Matias	290537	7994379	24	MG	Ma20	180		19	601	0.620	0.791	0.211	0.018	0.556	0.001
Gruta do Rio Itaúnas	395452	7977430	24	ES	Ma21	41	1	49	9029	2.284	0.125	0.587	0.120	22.022	0.006
Gruta do Rio Suaçui	797307	7972939	23	MG	Ma22	100		36	1108	2.324	0.146	0.648	0.045	1.385	0.003
Gruta dos Pirozzi	266037	7689921	24	RJ	Ma23	35		56	462	3.055	0.073	0.759	0.267	2.200	0.015
Henrique Altoé	289929	7709392	24	ES	Ma24	90		50	854	2.442	0.145	0.628	0.139	2.372	0.007
Lapa do Dr. Saulo	302473	79699408	24	ES	Ma25	60	2	46	1162	2.606	0.112	0.681	0.077	1.937	0.004
Lapa Fazenda Paraiso	306636	7957526	24	ES	Ma26	13		40	797	2.116	0.177	0.574	1.026	20.436	0.054
Quarto Patamar 1	367407	7368938	23	SP	Ma27	30		81	518	2.589	0.245	0.591	0.540	3.453	0.017
Quarto Patamar 2	367407	7368938	23	SP	Ma28	150	4	56	1407	1.545	0.427	0.382	0.124	3.127	0.003
Ribeirão do Anastácio	263501	8084168	24	MG	Ma29	10		22	132	1.478	0.451	0.478	0.440	2.640	0.030
Serra do Jardim	268693	7994094	24	MG	Ma30	90		23	442	2.039	0.194	0.650	0.051	0.982	0.005
Toca da Raposa	179908	8978784	25	AL	Ma31	10		51	443	3.037	0.086	0.772	1.020	8.860	0.061
Toca da Raposa 2	179870	8978720	25	AL	Ma32	15		30	187	2.831	0.085	0.832	0.250	1.558	0.024
Zé Branco	256446	8085205	24	MG	Ma33	50		30	282	1.415	0.512	0.416	0.020	0.188	0.001
Baixada dos Crioulos I	677160	7849887	23	MG	Si1	50		26	92	2.605	0.134	0.800	0.017	0.061	0.002
Baixada dos Crioulos II	677160	7849887	23	MG	Si2	200		79	2087	2.784	0.130	0.639	0.013	0.348	0.000
Bromélias	614813	7599005	23	MG	Si3	500	2	96	2868	2.385	0.207	0.524	0.019	0.574	0.000

Table 1 continued

CAVE NAME	X	Y	Z	BS	L	E (m)	T	S	A	H	D	J	SR	AR	HR
Cavernas das Casas	614323	7598762	23	MG	Si4	650	4	47	249	2.577	0.186	0.669	0.010	0.055	0.001
Coelhos	614208	7598763	23	MG	Si5	80		66	487	3.247	0.065	0.775	0.083	0.609	0.004
Fugitivos	615614	7602474	23	MG	Si6	166		34	842	2.001	0.190	0.572	0.003	0.063	0.000
Gruta da Fonte Samuel	296307	7685239	23	MG	Si7	80		57	1891	1.659	0.353	0.410	0.089	2.955	0.003
Gruta da Toca	216647	75442614	23	SP	Si8	345	1	27	2420	1.599	0.279	0.485	0.004	0.351	0.000
Gruta do Edgar	248621	7668354	23	SP	Si9	30		26	161	1.553	0.443	0.477	0.058	0.358	0.003
Gruta do Pião	614991	7599772	23	MG	Si10	126	1	34	270	2.564	0.144	0.727	0.067	0.536	0.005
Gruta dos Palhares	244663	7807417	23	MG	Si11	50		21	978	1.420	0.390	0.466	0.021	0.978	0.001
Gruta Itambé	248621	7668354	23	SP	Si12	355		59	1242	2.829	0.086	0.694	0.008	0.175	0.000
Gruta Olho de Cabra	297106	7685772	23	SP	Si13	721	1	58	1598	2.245	0.188	0.553	0.005	0.148	0.000
Gruta Paraná	248688	7670137	23	SP	Si14	150	2	49	987	2.578	0.116	0.662	0.033	0.658	0.002
Martiniano I	614323	7598762	23	MG	Si15	40		22	104	2.201	0.189	0.712	0.138	0.650	0.014
Martiniano II	614323	7598762	23	MG	Si16	50		18	96	2.396	0.123	0.829	0.090	0.480	0.012
Monjolinho	614991	7599772	23	MG	Si17	21		22	39	2.810	0.081	0.909	0.210	0.371	0.027
Moreiras	615614	7602474	23	MG	Si18	600	2	75	3735	2.573	0.130	0.596	0.002	0.078	0.000
Sete Salões	757272	757272	23	MG	Si19	150		49	1701	2.224	0.168	0.572	0.047	1.620	0.002
Viajantes	614815	7599282	23	MG	Si20	440		33	333	2.504	0.128	0.716	0.002	0.015	0.000

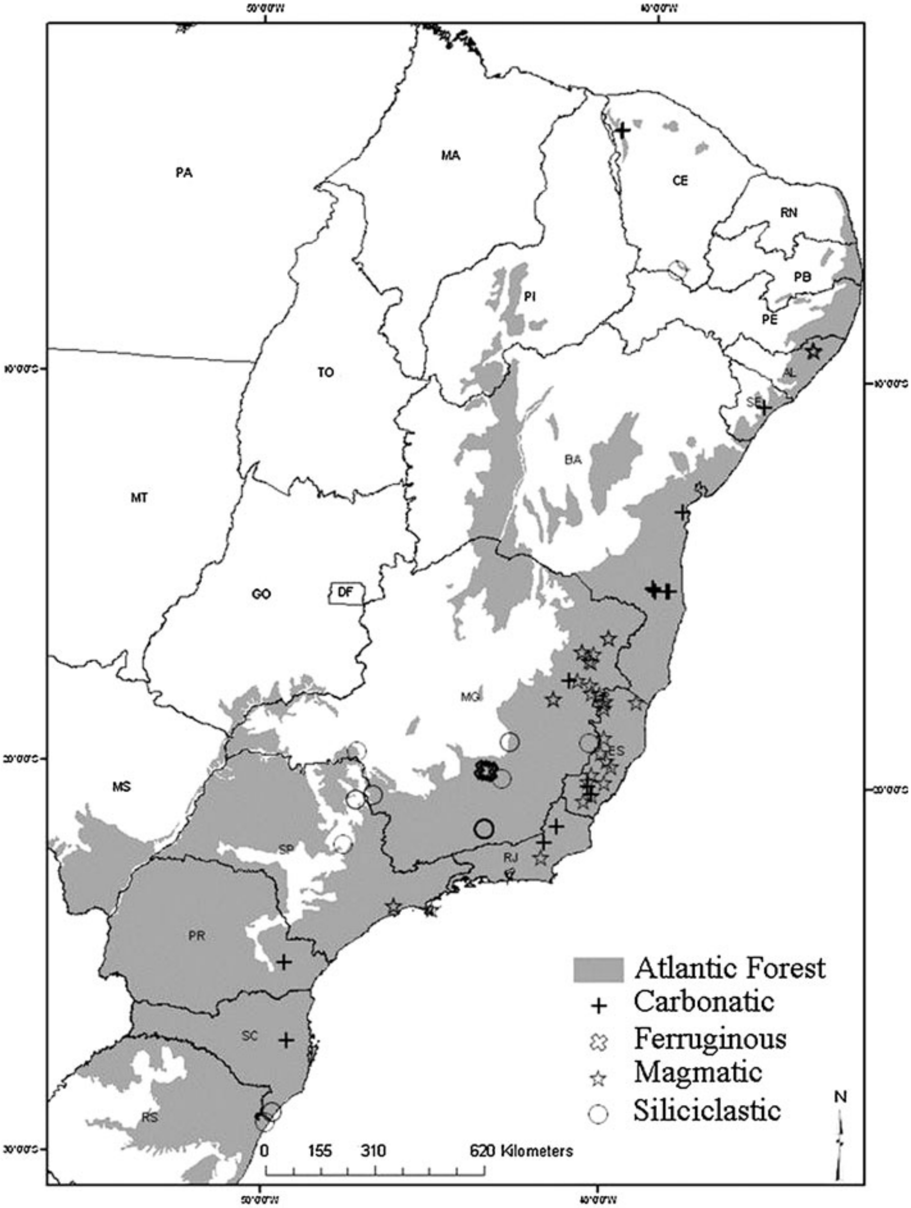

Fig. 1 Areas of Brazilian Atlantic Forest and the caves sampled (www.conservation.org.br/). Obs: some points represent more than one cave due to the low detail level of scale

In the laboratory all of the organisms were identified to the best possible taxonomic level and grouped in morphospecies according to the field references (Oliver and Beattie 1996; Sharratt et al. 2000). The general abundance of each species was acquired through the recounting of individuals in each schematic map.

The determination of potentially troglobitic species was conducted through the identification of “troglomorphisms” in the specimens. Troglomorphisms are frequently used for the definition of potentially troglobitic groups, since they result from evolutionary processes occurring after the isolation of populations in caves (Desutter-Grandcolas 1997; Culver and Pipan 2009). So, for this study, we have only considered as troglobites, those species with obvious troglomorphic trais, usually found in the advanced troglobites.

Data analysis

To standardize the abundance, richness and diversity values used in the analyses, they were relativized in function of the linear development and horizontal extension of the entrances of each cave ((biological variable/linear development of the cave)/$\sum$width of the entrances)) (Ferreira 2004). Such procedure aimed to reduce the effect of huge caves or huge entrances in the analysis. The diversity was calculated through the Shannon index (Magurran 2004). To evaluate the differences among the total richness, total diversity, total troglomorphic richness, relative abundance, relative richness and relative diversity in relation to the lithology, the nonparametric Kruskal–Walis test was used (Zar 1984).

Beta diversity (turnover or β) was calculated using data of presence and absence, through the index of Harrison (1992), modified by Whittaker (1960), in order to compare samples of different sizes. $\beta\text{Harrison} = \{[(S/\alpha) - 1]/(N - 1)\} \times 100)$. Where $S =$ total species richness values, $\alpha =$ average richness values and $N =$ number of samples. This measure ranges from 0 (no turnover) to 100 (each sample has a unique set of species) (Koleff et al. 2003).

For the obtaining of the quantitative similarity relationship between the caves and their respective lithologies, a non-metric Multidimensional Scaling was used (n-MDS), built based on the quantitative composition of the invertebrate fauna using the Jaccard index (Magurran 2004). Spearman correlations (R_s) were used to detect possible relationships among the richness and diversity with the linear development of the caves in the different lithologies (Zar 1984). The program used for the analyses was PAST (Hammer et al. 2001).

Results

The highest average richness occurred in the carbonatic caves (691spp/21 caves − 32.9 species *per* cave) followed by the siliciclastic (518spp/20 caves − 25.9 species *per* cave), the the magmatic (795spp/33 caves − 24 species *per* cave) and ferruginous (311spp/17 caves − 18.29 species *per* cave). The average richness was 53 spp (SD = 26.35) in carbonatic caves, 45.4 spp (SD = 22.7) in siliciclastic caves, 39.88 ss (SD = 19.27) in magmatic caves and 37.5 spp (SD = 20.96) in ferruginous caves. It is reiterated that the average extension of the caves associated to each lithology was variable, the ferruginous being considerably smaller than that present in the other lithologies. The β-diversity (turnover) was found to be 60.19 in carbonatic caves, 59.17 in magmatic caves, 54.74 in siliciclastic caves and 45.58 in ferruginous caves.

The total richness of invertebrates related significantly and positively with the linear development in the siliciclastic caves ($R_s = 0.67$, $P < 0.05$), carbonatic ($R_s = 0.71$, $P < 0.05$) and ferruginous ($R_s = 0.74$, $P < 0.05$). Furthermore, the higher inclination of the straight line in this relationship for ferruginous caves reveals that a much higher number of species in caves of this lithology can be found, than in carbonatic, siliciclastic and magmatic caves of the same extension (Fig. 2).

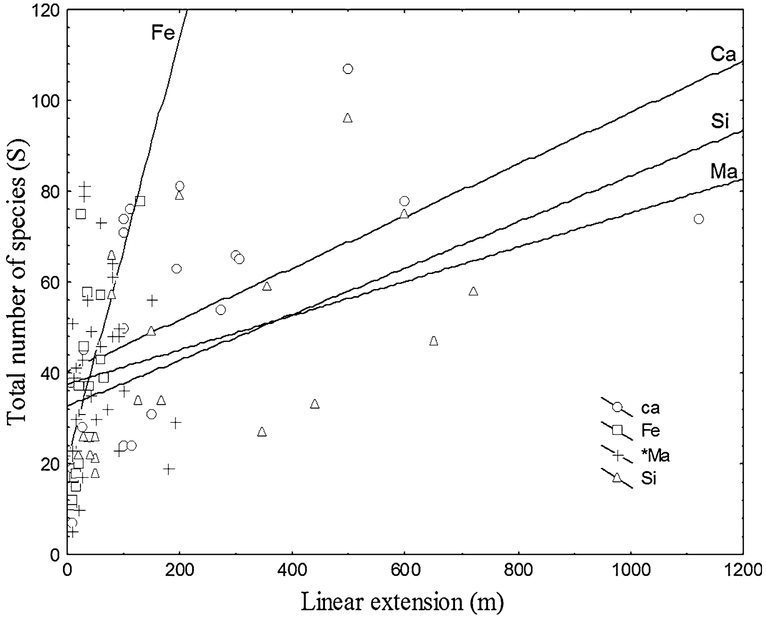

Fig. 2 Positive significant and non significant (*) relation of the total number of species (*S*) with the increasing linear development of caves of different lithologies in the Brazilian Atlantic Forest. Carbonatic (*Ca*) ferruginous (*Fe*), magmatic (*Ma*), siliciclastic (*Si*)

Significant differences were not observed in the total richness and diversities among the studied lithologies. The average total diversities was higher in the siliciclastic ($H' = 2.34$), magmatic ($H' = 2.26$), carbonatic ($H' = 2.24$) and ferruginous ($H' = 2.22$).

Significant differences in the relative richness were observed between caves associated to siliciclastic and carbonatic rocks (KW-H(1;41) = 10.98; $P < 0.05$), ferruginous and siliciclastic (KW-H(1;37) = 23.19; $P < 0.05$), magmatic and siliciclastic (KW-H(1;53) = 17.97; $P < 0.05$), magmatic and ferruginous (KW-H(1;50) = 9.95; $P < 0.05$) and carbonatic and ferruginous (KW-H(1;38) = 7.86; $P < 0.05$).The average relative richness was higher in the ferruginous rock caves (0.53 spp) followed by the carbonatic (0.32 spp), magmatic (0.24 spp) and siliciclastic (0.05 spp).

Significant differences among the average relative abundances were observed between caves associated to ferruginous and siliciclastic rocks (KW-H(1;37) = 21.,18; $P < 0.05$) and magmatic and siliciclastic (KW-H(1;53) = 14.29; $P < 0.05$), Carbonatic and magmatic (KW-H(1;54) = 3.60; $P < 0.05$), Carbonatic and siliciclastic (KW-H(1;41) = 21.07; $P < 0.05$), ferruginous and magmatic (KW-H(1;50) = 8.64; $P < 0.05$). The average relative abundance was higher in the caves present in carbonatic rocks (29.81 ind.), followed by the ferruginous (6.08 ind.), magmatic (3.35 ind.) and siliciclastic (0.55 ind.).

Significant differences among the average relative diversities were observed between caves associated to carbonatic and ferruginous rocks (KW-H(1;38) = 7.71; $P < 0.05$) carbonatic and siliciclastic (KW-H(1;41) = 6.,62; $P < 0.05$), ferruginous and magmatic (KW-H(1;50) = 8.59; $P < 0.05$), ferruginous and siliciclastic (KW-H(1;37) = 20.44; $P < 0.05$) and mamatic and siliciclastic (KW-H(1;53) = 16.25; $P < 0.05$). The average

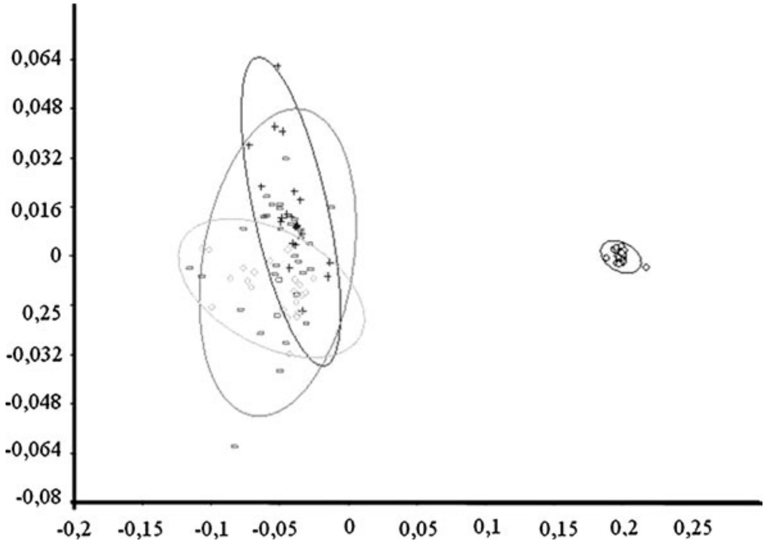

Fig. 3 Non-metric multidimensional scaling (*MDS*) of caves with carbonatic (*plus*), siliciclastic (*diamond*), ferruginous (*circle*) and magmatic (*square*) lithological standards

relative diversity being higher in the ferruginous (Hr = 0.04), carbonatic (Hr = 0.02), magmatic (Hr = 0.02), and siliciclastic (Hr = 0.0038).

A total of 70 troglomorphic invertebrates were found. Such species were distributed in 38 caves, and they included the following taxa: Araneae (17 spp), Collembola (8 spp), Diplopoda (6 spp), Chilopoda (5 spp), Coleoptera (5 spp), Isopoda (5 spp), Opiliones (4 spp), Acari (3 spp), Diplura (3 spp), Thysanura (2 spp), Blattodea (2 spp), Homoptera (2 spp), Nematomorpha (2 spp), Amphipoda (2 spp), Pseudoscorpiones (2 sp.) and Palpigradi (2 sp.).

The total number of troglomorphic species was significantly different between carbonatic and ferruginous caves (KW-H(1;24) = 9.32; $P < 0.05$), ferruginous and magmatic (KW-H(1;20) = 5.46; $P < 0.05$) and ferruginous and siliciclastic (KW-H(1;21) = 6.02; $P < 0.05$). The ferruginous caves presented the highest average richness of troglomorphic invertebrates (5.79 spp/cave), followed by the carbonatic (1.60 sp/cave), siliciclastic (1.86 sp/cave) and magmatic (1.83 sp/cave).

Siliciclastic, carbonatic and magmatic caves presented a higher quantitative similarity of invertebrate fauna (Fig. 3).

Discussion

Most part of the research accomplished in Brazil and in the world regarding the subterranean fauna, is limited to caves inserted in a single rock type, usually limestone. As such, few studies have been conducted in the world with cave fauna in basalt, silicates, granite, laterites, among others (Gnaspini-Neto and Trajano 1994; Ruzicka and Zacharda 1994; Arechavaleta et al. 1999; Sharratt et al. 2000; Culver et al. 2004; Ferreira 2005; Howarth et al. 2007).

The most comprehensive study of fauna conducted in Brazil in caves of different lithologies, describes the invertebrate fauna of 50 carbonatic, 2 arenitic, 1 quartzitic and 4 granitic caves (Gnaspini-Neto and Trajano 1994). However, this study presents only data on the composition of some hypogean taxa, without a concern with the richness, abundance, diversity and similarity among the communities.

Distinct traits of each cave lithology

The singularity of the ferruginous caves in relation to the high relative richness and low similarity when compared to caves associated to the other lithologies had been already related by Ferreira (2005). The 'canga' is a ferruginous rock formed by fragments containing compact itabirite and hematite besides lesser components, cemented by limonite. In some places the cement completely fills in the interstices of the 'canga' but, when the fragments are large, the limonite partially fills in the gaps resulting in a porous rock (Simmons 1963; Piló and Auler 2005). According to Maurity and Kotschoubey (1995) the 'canga' cuirass possesses centimetric cavities, anastomosed tubule systems, fissures and pockets.

The existence of this great amount of canaliculi that make up an extensive network of interstitial spaces (meso and micro-caves) connected to the macro-caves, makes for ferruginous subterranean system habitats with great extensions. The extension and the number of subterranean systems can be a direct measure of the availability and variety of habitats for the maintenance of a rich fauna (Christman and Culver 2001; Ferreira 2005; Culver 2006). According to Ferreira (2005), the micro-caves are used by countless organisms that transit from the surface to more interior areas, frequently accessing macro-caves. Such macro-caves are sustained by the primary productivity of roots originating from external trees, beyond guano patches and some organic vegetable matter deposits (Ferreira 2005). As such, the microhabitat and food resource availability act on the "concentration" of the subterranean diversity in the ferruginous macro-caves (Ferreira 2005). Thus, in the ferruginous systems, the occurrence of extensive shallow sub-surface compartments probably acts allowing a migration of the fauna through interstitial spaces to macro-caves, increasing the richness of these systems.

The relationships of the total richness increase to the size increase of the cavities in different lithologies are probably related to the increase of the supply of microhabitats and food resources for the invertebrate fauna (Ferreira 2004). Communities of bats are richer and more abundant in larger caves, producing large guano deposits (Brunet and Medelin 2001). Large deposits, in turn, provide food and microhabitats for a larger number of invertebrate species (Ferreira et al. 2007). It stands out that the productivity in cave environments is an important predictor of a richness increase in invertebrate communities (Culver 2006).

However, caves in different types of rocks showed a distinct richness increase pattern in relation to the increase of their linear extensions. Ferruginous caves showed a stronger species increase tendency with the increase of the linear projection. Such a fact can be due to the heterogeneous micro-environmental characteristics of these caves associated to the intricate canaliculi mesh present in the ferruginous rock. The ferruginous macro-caves potentially enhance their connectivity to a larger amount of canaliculi by the increase of their volume. Such condition causes the macro-caves to work as fauna 'receptors' (especially from the "shallow" subterranean habitats, connected to the canaliculi). Many species that are living especially in those habitats can eventually reach some macro-cave, by chance or attracted by some food resource, as bat guano. Such "attraction" can happen in an exponential way, that is, small increases in the linear development of the macro-cave can lead to an exponential increase of attractiveness (by the increase of the connection with the canaliculi), surprisingly elevating the amount of species present, different from what occurs for other lithologies, where such canaliculi are not abundant.

Being such, the cave extension, as a parameter of invertebrate richness prediction, depends directly on the lithology to which the cave is associated. Thus, contradicting the postulate by Gnaspini-Neto and Trajano (1994), caves associated to different lithologies present communities with clearly different composition and structure, keeping in mind the differentiated potentiality of species absorption that each lithology presents.

The lowest relative richness relative abundances and relative diversity in the siliciclastic caves can be due to a lower availability of food resources for invertebrates. The arenitic caves of Altamira-Itaituba (Pará state) present abundant populations of invertebrates associated to enormous guano deposits (Trajano and Moreira 1991, Gnaspini-Neto and Trajano 1994). Large guano deposits were not observed in the siliciclastic caves in this study. Like this, the oligotrophic condition prevalent in the siliciclastic caves inventoried in this work does not make the presence of rich invertebrate communities possible. However, another factor that should be considered as a possible richness reducer is the predominance of tourist activities in many of the siliciclastic caves sampled. The visitor presence can probably alter microhabitats and drive off trogloxene importers of food (e.g., bats, swifts), culminating with the establishment of an oligotrophic condition. As an example, we have the tourist quartzitic caves in the Serra de Ibitipoca (South of Minas Gerais) that has already presented large guano deposits produced by swift populations (Pinto 1939). Currently, swift guano deposits were only observed in the caves distant from the visitation center. Furthermore, trampling impact can aggravate the fauna depletion situation even more, through microhabitat alteration.

Troglomorphic species

The high number of troglomorphic species found in the ferruginous caves is an uncommon occurrence for the Brazilian caves (Ferreira 2005). According to this author, the superficiality of many ferruginous caves can make up one of the important factors that lead to the speciation of subterranean groups, as occurs in many lava tubes (Howarth 1980). Such superficiality contributes to the access of root, which on reaching ample subterranean spaces, develop, forming extensive root systems that act as trophic resources for several invertebrate species. Furthermore, they allow an "indirect" continuous primary productivity (via root growth) that leads to the maintenance of a considerable volume of nutrients within these caves.

In way similar to the ferruginous systems, a rich troglobiotic fauna associated to superficial volcanic caves (lava tubes) are also distributed along a network of channels formed by small spaces. Many of those species depends directly or indirectly on the roots of the epigean vegetation (Juberthie et al. 1980; Medina and Oromi 1990; Hoch and Asche 1993, Ashmole, 1994).

Howarth (1972) argues that the colonization of lava tubes would be a consequence of an adaptative shift. According to this author, the introgression in the subterranean environment for a given species would take place due to an attraction to an available alimentary resource and one unused by other species, instead of a reaction to the unfavorable conditions of the epigean environment. Thus, terrestrial troglobiotic species can occur in tropical areas where there are extensive caves with stable humidity supply conditions and available alimentary resources for colonization over a long period (Howarth 1980). The adaptative shift hypothesis for the evolution of specialized taxa to tropical lava tubes is based on the distribution of phytophagous troglobiotic species (Homoptera: Cixiidae) that are found distributed in a parapatric manner with their ancestral epigeans (Howarth 2005).

The importance of altitude as a determinant of the evolution of some troglobiotic groups (Picker and Samways 1996; Ferreira 2006) also deserves attention. Caves associated to high altitudes occur in places where external adversity is still more intense, due to the higher temperature ranges and more intense winds than in places of lower altitudes. Such a fact is perceptible when observing that in ferruginous caves situated at higher altitudes, there concentrates a larger amount of troglomorphic species (Ferreira 2005).

The caves of the Atlantic Forest possess a high richness of troglomorphic species, with 214 species present in almost 300 caves already sampled in this biome (0.71 spp/cave). Among these, the invertebrates stand out (97.7% of the total).

Ferreira (2004) relates the occurrence of 43 troglomorphic species in 113 Brazillian calcareous caves (0.4 spp/cave). However, this fauna is not as representative when compared to that present in temperate area caves (Culver and Pipan 2009). As examples, Peck (1992) relates the presence of 250 species in 54 limestone caves of Alabama, USA (4.6 spp/cave) and Sharratt et al. (2000) tell of the occurrence of 85 troglobitic species in 80 quartzite caves located in the south of Africa (1.06 spp/cave). In France, Juberthie and Ginet (1994) relate 639 troglobitic species in 911 limestone caves (0.7 spp/cave).

Culver and Sket (2000) enumerated 18 caves with 20 or more obligate subterranean species and revealed that fourteen are in Europe, three from North America and one from southeast Asia. The sites tended to have high primary productivity or rich organic input from the surface, they are large caves, or have permanent groundwater phreatic water (Culver and Sket 2000). However, the caves of our study are of small extension, and in a general way, do not present permanent groundwater (phreatic water).

Culver et al. (2003) compared the obligate cave faunas of nine karstic regions of the United States (Florida Lime Sinks, Appalachians, Interior Low Plateaus, Ozarks, Driftless Area, Edwards Aquifer/Balcones Escarpment, Guadalupe Mountains, Black Hills, and Mother Lode), and showed that terrestrial (troglobitic) species ranged from zero (Florida Lime Sinks) to 256 species (Interior Low Plateau).

In Brazil, However, it should be considered that the identification of troglobitic species in tropical areas is hindered by the fact that the epigean invertebrate fauna is practically unknown. Therefore, more recent troglobites, that do not present morphologic modifications (such as eyes reduction, depigmentation and prolongation of appendages), will rarely be identified due to the lack of certainty as to their exclusiveness in the subterranean environment (Andrade 2003).

On the other hand, the low richness of troglobiotic species in magmatic caves can be probably due to the reduced extension of superficial subterranean systems (MSS), which compromises the colonization and isolation of the hypogean species. In granitic talus caves, the contact of the large blocks of rock with the soil can produce intense spaces characterized as MSS. However, in Tafoni and dissolution caves (that make up the most inventoried types in this work), the compact nature of the rock greatly reduces the possibilities of the existence of well developed superficial subterranean environments.

Differences in species composition

The few studies conducted at non-carbonatic caves conclude that the communities are comparable to those of limestone caves located in the same geographical area, independent of the rock type in which the cave is formed (Trajano and Moreira 1991; Dessen et al.

1980; Trajano 2000). The present work, however, presents important information on the structure and composition of the invertebrate communities in caves with different lithologies which invalidates those conclusions. The rock types where the caves are inserted determine clear differences in the richness, abundance and diversity of the invertebrate communities.

Ferruginous caves reveal invertebrate communities with a high relative richness, besides a distinct fauna composition from the other lithologies. Such distinctiveness can be related not only to the physical structure of those caves, but also to the great amount of troglobiotic species observed. Since most part of the Brazilian troglobiotic species are endemic, one would expect that the richer the cave is in troglobiotic species, the more distinct will be its community.

As a result, this study demonstrates that the differences in the composition and structure of the invertebrate communities in caves are not only the product of biogeographical variations, as postulated by Gnaspini-Neto and Trajano (1994). In addition, the linear development of the caves in different lithologies imposes differences in the amount of species found.

Cave conservation

Until 2008, all of the Brazilian caves were protected by law. However, unfortunately, the legislation was altered, and the Brazilian caves now can be destroyed by different anthropogenic activities (especially mining activities). With the intention of defining which caves can be suppressed and which should be preserved, categories were created (based on biological and geological parameters) that define the “status” of each cave. Within the biological parameters, are: the presence of endemic troglobiotic species, as well as richness of each cave.

However, differences in cave lithologies were not considered within the biological criteria. Thus, for the establishment of value attributes, the size of the caves should always come related to their lithology, by the fact that same size caves associated to distinct lithologies possess communities with quite diverse richness values. As such, the cave lithology and extension are important parameters to be considered in plans and action for the conservation of cave invertebrate fauna.

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