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Taxonomic distinctness and conservation of a new high biodiversity subterranean area in Brazil

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ABSTRACT

Subterranean environments, even though they do not possess a primary production (photosynthesis), may present high biodiversity, faunistic originality, endemism, phylogenetic isolations and unique ecological and/or evolution events, in addition to rare taxa. Studies investigating the biological diversity in Neotropical caves are relatively rare and recent, and most of them have been conducted in Brazil. We sampled caves from the state of Bahia, northeastern Brazil, and through sampling sufficiency tests and richness estimators, we demonstrate that the normatization for the Brazilian cave laws is not adequate for its conservation and that only α diversity index is not enough to verify faunistic patterns. We suggest that a phylogenetic diversity index be more robust and accurate for conservation purposes, particularly the Taxonomic Distinctness index. Moreover, we propose that the sandstone complex caves from Chapada Diamantina National Park need to be classified as being of high subterranean biodiversity in a global scope.

Key words: cave conservation, endemisms, faunistic singularity, speleological brazilian laws, troglobites.

INTRODUCTION

The subterranean environment comprises interconnected subsurface spaces that allow for the dispersion of species that inhabit there (Juberthie 2000). The hypogean realm presents faunistic originality and high endemism, as well as phylogenetic isolation (Gibert and Deharveng 2002) due to unique evolutionary events (Culver and Pipan 2009). Thus, some authors consider some subterranean systems as hotspots of biodiversity (*e.g.,* Culver and Sket 2000, Deharveng 2005).

Nevertheless, Myers (1990) proposed the term “hotspots” based on floristic diversity. The term is not used here due to its falsifiability in environments that lack primary producers, which may include subterranean systems. Therefore, here we used a new term: “High Biodiversity Subterranean Area (HBSA)”.

Cave populations can be divided into three ecological-evolutionary categories. Troglophiles (populations well established inside and outside of the caves); trogloxenes (populations inhabiting caves but must go out to complete their life cycles) and troglobites (exclusively and obligatory subterranean populations) (see Schiner 1854, Racovitza 1907, Barr 1968, Poulson and White 1969).

Troglobites generally present autapomorphic character states (troglomorphisms) related to the life in permanent darkness (Trajano 1993).

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The most known troglomorphisms are reduced or lack of eyes, elongated appendages and lighter coloration (Christiansen 1962). In general, troglobitic populations are specialized and fragile (Trajano and Bichuette 2006), and they need to be carefully considered in conservation programs.

Regarding the protection of Brazilian speleological patrimony, the current legislation (DECREE 6640 from November 7th 2008) regulates the use of natural subterranean cavities for environmental bids, classifying them by relevance level: maximum, high, medium and low. Only caves with maximum relevance are entirely protected from suppression.

To regulate this decree, Normative Instruction (NI) N. 2 from August 20th 2009 was published. In article 16 (paragraph 2) of this decree, some requirements of speleobiological studies were established, including the definition of the study period:

"**Art. 16**. The approval of speleological studies for classifying the relevance degree of natural subterranean caves is conditioned on the submission of sufficient information for the comprehension of the cave ecosystem. § 2º The biological surveys must be completed in at least an annual cycle with at least two samplings per year, one occurring during the rainy season and the other during the dry season, aiming to minimally reveal the characteristics resulting from climatic seasonality."

In addition to the proposal of only two samplings during one annual cycle, many biologists use only alpha diversity indexes such as Shannon (H') in the environmental impact reports to determine the amount of protection, or total destruction, of Brazilian caves (M.E. Bichuette and J.E. Gallão pers. obs.). Although these indexes are useful in some ecological studies, they must be used with extreme caution and parsimony (Trajano et al. 2012).

Considering these issues, we tested some ecological concepts applied to biological cave conservation. We chose a region in northeastern Brazil with sandstone caves and a high diversity of cave animals. We attempted to answer the following questions: (1) Are two samplings enough to access the minimum richness of subterranean fauna and to detect faunistic patterns? (2) Are α diversity indexes suitable for cave conservation purposes/decisions?

MATERIALS AND METHODS

We conducted the study in 11 sandstone caves from Chapada Diamantina, central Bahia northeastern Brazil, belonging to Serra do Espinhaço and cut by the Paraguaçu rivers basins (Fig. 1).

Because some localities have only recently been discovered, or because access to those localities is difficult, the following caves were sampled once: Cantinho cave (Cac), Criminoso cave (Crc), Canal da Fumaça cave (CFc), Morro de Alvo cave (Mac), Veio de Aurélio cave (VAc), Cobras cave (Coc), and Lava Pé cave (LPc).

Rio dos Pombos cave (RPc), Ressuegência do Morro de Alvo cave (RMAc), and Torras System (TS) were sampled five times, and Parede Vermelha cave (PVc) was sampled six times. The samples were collected through an extensive visual inspection in different substrates (humid places, walls and ceiling, soil, guano, under rocks and trunks), covering the maximum extension possible in all habitats.

We did not use pitfall traps because we did not wish to impact the subterranean populations (Sharratt et al. 2000) and because in these sandstones caves, the rocks are exposed and do not allow for the installation of pitfall traps. Regarding the aquatic fauna, we used hand nets and *Surber* traps. The collection effort totaled approximately eight hours per cave, always in three or four sessions. Chiropteran fauna were not studied.

In order to determine if the sampling was enough in relation to the given access, i.e the minimum species richness, Mao Tao and Jackknife first order sampling rarefaction curves were calculated for those caves in which we had more than three samples. The analyses were performed using EstimateS version 9.1 software (Cowell 2013).

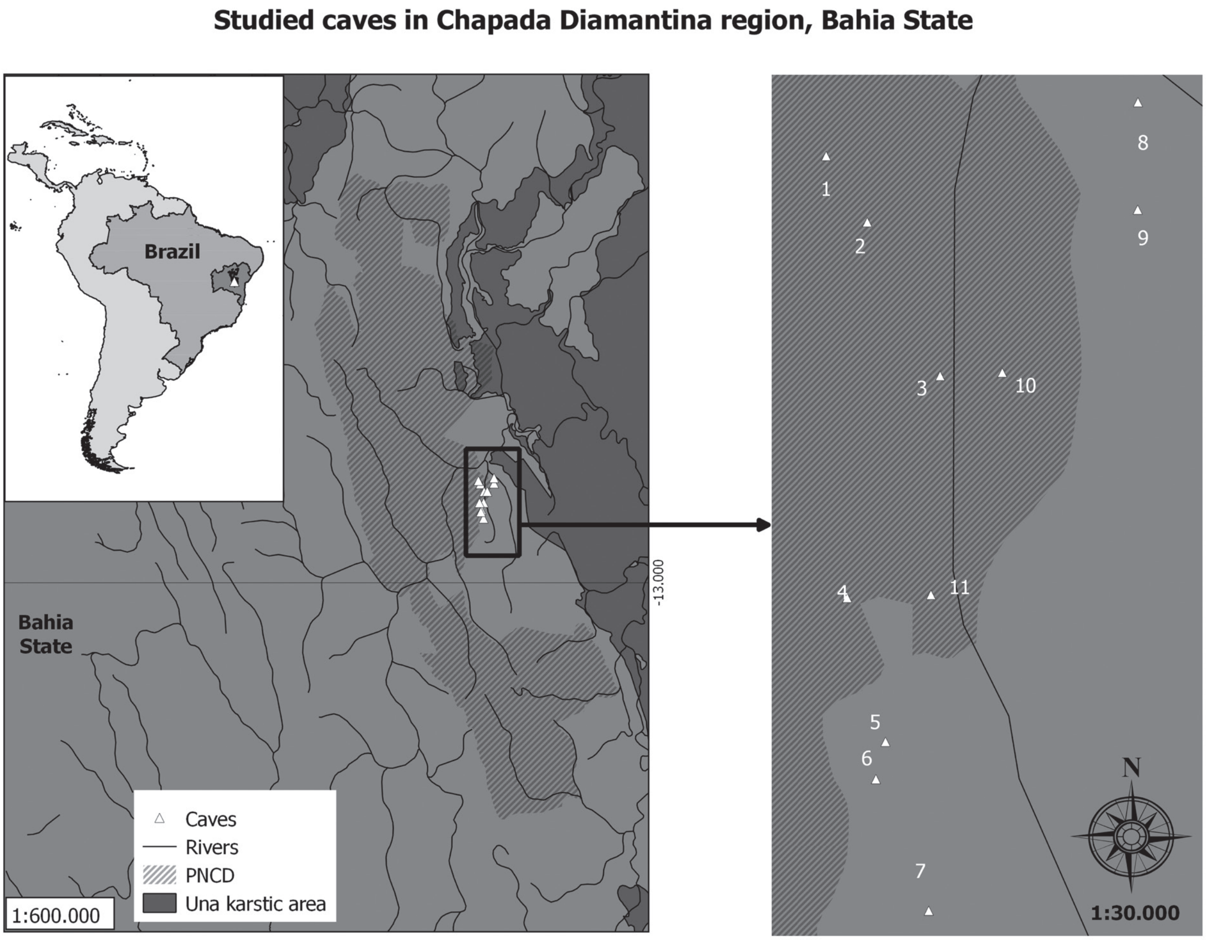

Figure 1 - Studied caves in the Chapada Diamantina region, state of Bahia. 1-Cantinho cave; 2-Criminoso cave; 3-Torras System; 4-Canal da Fumaça cave; 5-Rio dos Pombos cave; 6-Ressurgência do Morro de Alvo cave; 7-Morro de Alvo cave; 8-Veio de Aurélio cave; 9-Cobras cave; 10-Parede Vermelha cave; 11-Lava Pé cave. PNCD – Parque Nacional da Chapada Diamantina (National Park of Chapada Diamantina).

We also estimated the traditional Shannon (H') α diversity index, which is influenced by the sampling effort and requires the number of specimens (Clarke and Warwick 1998). These were calculated only for localities with more than three samples.

In addition, we calculated the Taxonomic Distinctness (TD) index and created a respective funnel graph for all sandstone caves because it is totally independent from the sampling effort (Warwick and Clarke 1998). All indexes were measured to determine which one would be the most robust in terms of cave conservation. The H' diversity index was calculated in Past version 2.13 (Hammer et al. 2001) and the TD index was calculated in R version 2.13.1 (2011).

Species that showed morphological troglomorphisms (mainly reduced or lack of eyes and/ or melanic pigmentation) but we were unsure as to whether they were real troglobites were left here only as troglomorphic species (TM in Appendix S1) (Supplementary Material). Of course, some of these troglomorphic species could change their status to troglobitic species, if we confirm its occurrence exclusive to caves.

RESULTS

We recorded an abundance of 1,307 individuals distributed in 162 taxa (Appendix 1). Among them, 23 were troglobites and another 14 species exhibited some type of morphological troglomorphism. Besides 20 new species confirmed already (Appendix S1). PVc was the richest cave, with 13 troglobites.

The lower relative proportion of collected species after the second collection occasion was 40.0% for TS and, for the other three caves, more than half of the species were collected after the second sampling (Table I). Shannon's index (H') ranged from 2.753 (TS) to 3.459 (RPc), and the richest cave (PVc) had the third lowest H' of 2.983 (Table I).

TABLE I

Number of species, number and percentage of species after second collection for the caves with five or more collections and H' index. PVc - Parede Vermelha cave; RPc - Rio dos Pombos cave; RMAc - Ressurgência do Morro de Alvo cave; TS - Torras System. n - number of total species in each cave; A - number of species after second collection; % - percentage of species after second collection; TM3 - number of troglobitic and troglomorphic species after second collection. H' - Shannon index.

Caves	n	A	%	TM3	H'
PVc	64	35	(54.6%)	10	2.983
RPc	54	42	(77.5%)	10	3.459
RMAc	41	24	(58.5%)	3	3.161
TS	20	8	(40.0%)	2	2.753

Furthermore, 25 troglobitic and troglomorphic species would have been neglected if the localities were sampled only twice (occasionally the same species occurred in different caves) (Table I).

Regarding the taxonomic distinctness, the expected Δ^+ was 67.985 (Fig. 2), and only two caves were below expectations; however, they were still inside the confidence interval. Six localities were above the expected Δ^+ and were in the funnel graph, and two caves were above the funnel graph: MAc (Δ^+ 85.286) and PVc (Δ^+ 72.062).

The addition of species at each collection was almost a constant (Fig. 3), including the addition of troglobitic species after the second sampling, which is the limit in the current Brazilian legislation regarding Environmental Impact Assessments/ Environmental Impact Reports (EIA/RIMA from Portuguese). In addition to these species, we noted that in none of the cases, even in those cases with six samples (such as in the case of PVc), was the asymptote reached, indicating that the sampling is far from adequate with only two collections.

DISCUSSION

Diversity in subterranean environments is better expressed regionally than locally because many passages are accessible only to fauna (Sket 1999). Considering Igatu, there are 162 registered species and 23 are troglobites, which are distributed in a small area of only 25 km^2. Among troglobites, this region is the type-locality of four troglobites (*Discocyrtus pedrosoi* Kury 2008. *Glaphyropoma spinosum* Bichuette, de Pinna and Trajano 2008. *Troglorhopalurus translucidus* Lourenço, Baptista and Giupponi 2004 and the first Brazilian troglobitic Mygalomorphae, *Tmesiphantes hypogeus* Bertani, Bichuette and Pedroso 2013), and it holds endemismics at a local, regional and zoogeographical scale as a new species of the troglobitic *Verhoeffiella* genus (Collembola), which previously only had a Paleartic distribution. However, the total number of troglobitic species may rise because some species exhibit some type of troglomorphic trait, which corroborates this hypothesis. The troglobitic catfish is already included on the IUCN Red List (Gallão and Bichuette 2012).

If we consider a local approach, PVc presented 13 troglobitic species, and there is a great possibility that this number will increase, which renders this cave of extreme importance for the Brazilian subterranean fauna because the Areias System, Alambari de Cima and Olhos d'Água caves

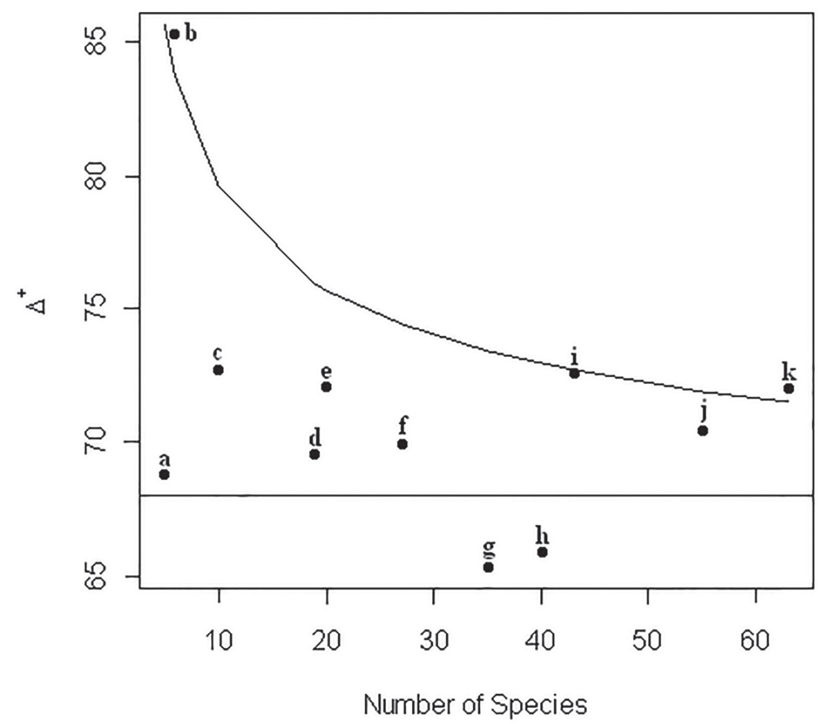

Figure 2 - Taxonomic distinctness of sandstone caves in Igatu and Lencóis. a-Cobras cave; b-Morro de Alvo cave; c-Criminoso cave; d-Veio de Aurélio cave; e-Torras System; f-Cantinho cave; g-Canal da Fumaça cave; h-Ressurgência do Morro de Alvo cave; i-Lava Pé cave; j-Rio dos Pombos cave; k-Parede Vermelha cave. Δ^+ means Taxonomic Distinctness. Funnel graph means 95% confidence limits.

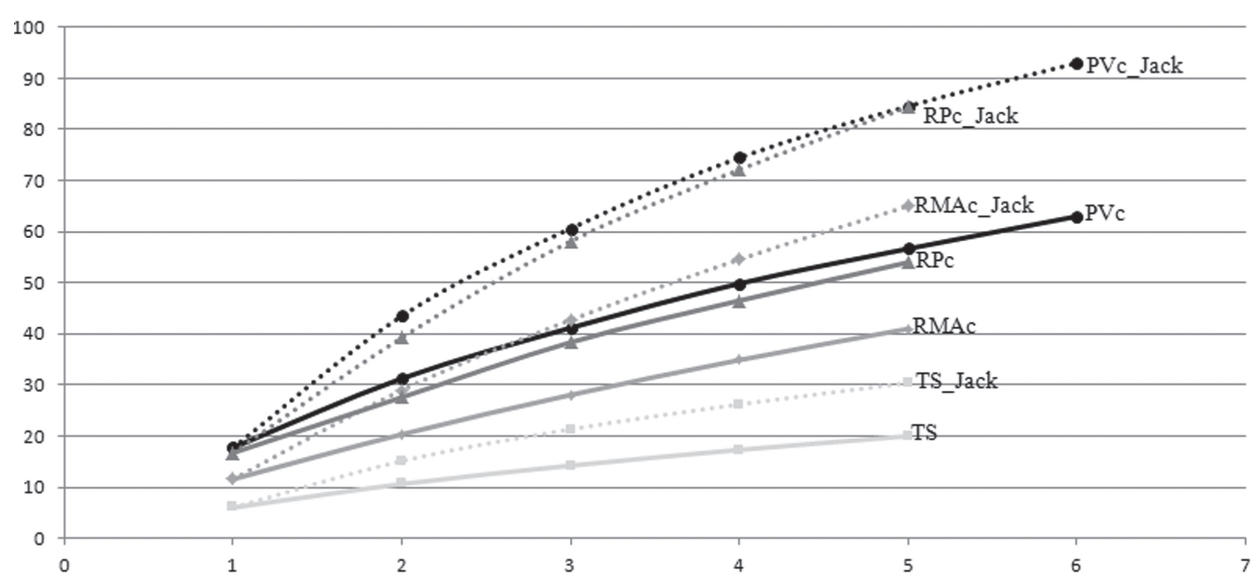

Figure 3 - Sampling rarefaction curves from caves with five or more collections and Jackknife first order estimator. PVc - Parede Vermelha cave; RPc - Rio dos Pombos cave; RMAc - Ressurgência do Morro de Alvo cave; TS - Torras System. For each cave, solid lines are Mao Tau sampling rarefaction curves and dashed lines are Jackknife first order richness estimator. Horizontal numbers means samples and vertical numbers means species.

comprise 20, 10 and eight troglobites, respectively, and are considered Neotropical caves of high biodiversity relevance (Deharveng 2005, Trajano and Bichuette 2010).

Therefore, the sandstone caves from Chapada Diamantina represent a new Neotropical HBSA, under a local and regional focus.

As a consequence of incomplete sampling, species may be neglected, leading to erroneous estimations and resulting in incorrect decisions for management and conservation plans (Conroy and Noon 1996, Nichols et al. 1998). Two samples in an annual cycle, as proposed by Normative Instruction N. 2 for environmental bids, are absolutely insufficient to demonstrate faunistic patterns or even to determine the minimum species richness.

Corroborating this inadequacy, the rarefaction Mao Tau curves reveal that the asymptote is far from being achieved and that the addition of species in each collection event is a constant, including troglobitic or troglomorphic representatives (Fig. 3). This is in addition to the fact that at least 40% of species were registered starting from the third sampling occasion, as occurred in TS. However, it is worth noting that this cave is a huge duct tunnel-shaped cave and is entirely washed out during each rainy season. For the other three tested caves, the percentage of species collected starting from the third sampling occasion was higher than 50%.

Jackknife first order richness estimators were elevated, even for PVc, the only cave with six samples (Fig. 3). Thus, the survey of the Igatu caves is still not completely inclusive and two samplings are insufficient to assess the richness of a cave and to consequently classify its relevance levels.

Despite being elevated, these indeces, as Jackknife first order used here, may underestimate the real diversity. Any estimation that involves time and space does not reveal the differences in species composition in relation to time, collection period and different localities in the same habitat (Novotny 1993). Furthermore, propositions for habitat conservation must include both the observed richness and the number of species still undiscovered (Santos 2003).

According to the new Brazilian laws, troglobitic species are crucial to cave preservation or suppression. In this study, 25 troglobitic plus troglomorphic species would have been neglected (Table I) if only two samplings were used for environmental bids, which would certainly result in a decrease in the relevance of the sampled caves. Consequently, in this hypothetical situation, these caves could be suppressed. Trajano (2010) states that at least 10 samplings would be necessary, in distinct annual cycles, to begin to characterize subterranean environments; even after 20 samplings, new troglobitic species may still be found. To illustrate this requirement, in six karstic European regions, 190 samples were collected on average, and even after 100 samplings, troglobitic fauna was still being found (Culver and Pipan 2009).

The alpha diversity indeces were similar for the four localities (Table I), which do not reveal a faunistic singularity. Additionally, PVc had the third lowest H' of the four caves. If we took only this index as a basis for conservation purposes, PVc would most likely be neglected. This cave had a higher number of total and troglomorphic species, and its singularity was not reflected in the H' alpha diversity index.

Studies based only on alpha indeces that may or may not be mandatory for cave conservation must be used with extreme caution. Information about the identity of species, their phylogenetic relationships and other characteristics are lost due to the species' abundance and richness as well as their faunistic singularities, which are the main justification for the conservation of subterranean environments; these factors are minimized in numerical diversity values (Trajano et al. 2012).

Cianciaruso et al. (2009) affirm that the traditional indeces hide more than they reveal due to a great loss of information, and that such indeces are not sufficient for selecting locations, in this case caves, for conservation purposes (Sarkar 2006). Thus, it is inadvisable to use only α diversity indeces for biodiversity purposes, as occurs in advisory studies for cave suppression, which are not published because confidential contracts (M.E. Bichuette and J.E. Gallão pers. obs.).

We verify the high dispersion of points on the funnel graph (Fig. 2), which corroborates the faunistic singularity and the great phylogenetic diversity that exists in the Igatu caves.

Environments that are too degraded or polluted present a low TD, which may produce points below the 95% trust interval on the funnel graph (Warwick and Clarke 1998). Many caves of Chapada Diamantina were subjected in the past to heavy diamond mining, which continues in a residual, clandestine fashion at present (Bichuette et al. 2008). This activity could explain why the results were below expectations for some caves (Fig. 2).

Both caves that had points outside of the trust intervals were MAc and PVc, with six and 63 species, respectively. Despite its low richness in a single sample, MAc presented high phylogenetic diversity because all six species were distributed in four distinct classes, which explains the point outside of the trust interval. On the other hand, PVc presented a higher richness and a higher number of troglobites, items that also corroborate the presence of this cave outside the trust interval. All of the other caves are in the funnel graph and above expectations and corroborate the faunistic singularities found in the cave's biodiversity.

In conclusion, the Igatu region of central Bahia represents a HBSA for Brazil, as well as a Neotropical region and must be protected.

Two samplings, as stated in Brazilian laws for environmental bids, are insufficient for accessing the minimum richness of subterranean species and for predicting any pattern for subterranean fauna.

The traditional diversity index alone is not sufficient for conservation purposes, and we suggest other indeces, including those used for phylogenetic and functional diversity (Cianciaruso et al. 2009, Winter et al. 2013), as well as dark diversity (Partel et al. 2011).

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RESUMO

Os ambientes subterrâneos, embora não possuam uma produção primária (fotossíntese), podem apresentar elevada biodiversidade, originalidade faunística, endemismos, isolamentos filogenéticos e eventos ecológicos e/ou evolutivos únicos, além de táxons raros. Estudos investigando a diversidade biológica em cavernas neotropicais são relativamente raros e recentes e, a maioria destes têm sido conduzidos no Brasil. Amostramos cavernas no estado da Bahia,

nordeste do Brasil e, através de testes de suficiência amostral e estimadores de riqueza, demonstramos que a regulação das leis para cavernas brasileiras não é aplicável para conservação destas e que apenas índices de diversidade α não são suficientes para verificar padrões faunísticos. Sugerimos que um índice de diversidade filogenética é mais robusto e acurado para propostas de conservação, particularmente o índice de Distinção Taxonômica. Adicionalmente, propomos que o complexo de cavernas areníticas localizadas no Parque Nacional da Chapada Diamantina devem ser consideradas como de elevada biodiversidade subterrânea, em uma escala global.

Palavras-chave: conservação de cavernas, endemismos, singularidade faunística, Leis espeleológicas brasileira, troglóbios.

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SUPPLEMENTARY MATERIAL

APPENDIX S1

Faunistic composition from Igatu/Andaraí, Chapada Diamantina, central Bahia, northeastern Brazil. Coc - Cobras cave; TS - Torras System; Crc - Criminoso cave; LPc - Lava Pé cave; Mac - Morro de Alvo cave; PVc - Parede Vermelha cave; RMAc - Ressurgência do Morro de Alvo cave; RPc - Rio dos Pombos cave; CFc – Canal da Fumaça cave; Cac – Cantinho cave; VAc - Veio de Aurélio cave; Troglobite taxa are outlined in bold; TM Troglomorphic. See main text for number off collections in each cave.

Supplementary Material

APPENDIX S1

Faunistic composition from Igatu/Andaraí, Chapada Diamantina, central Bahia, northeastern Brazil. Coc - Cobras cave; TS - Torras System; Crc - Criminoso cave; LPc - Lava Pé cave; Mac - Morro de Alvo cave; PVc - Parede Vermelha cave; RMAc - Ressurgência do Morro de Alvo cave; RPc - Rio dos Pombos cave; CFc – Canal da Fumaça cave; Cac – Cantinho cave; VAc - Veio de Aurélio cave; Troglobite taxa are outlined in bold; TM Troglomorphic. See main text for number off collections in each cave.

Taxa/Caves	Coc	TS	Crc	LPc	MAc	PVc	RMAc	RPc	CFc	Cac	VAc
C. Secernentea				X		X					
C. Turbellaria											
O. Tricladida											
Geoplanidae gen. 1 sp. 1				X							
Geoplanidae gen. 1 sp. 2				X							
Geoplanidae gen. 2 sp. 1						X					
C. Annelida											
Sc. Oligochaeta											
O. Haplotaxida											
Haplotaxidae gen. 1 sp. 1					X	X		X			
C. Arachnida											
Sc. Acari gen. 1 sp. 1 [TM]						X				X	
Sc. Acari gen. 2 sp. 1 [TM]								X			
Sc. Acari gen. 3 sp. 1								X			
O. Mesostigmata gen. 1 sp. 1				X							
O. Parasitiformes											
Opilioacaridae gen. 1 sp. 1				X		X					
O. Araneae											
Mygalomorphae											
Guyruita atlantica Guadanucci et al. 2007						X					
Tmesiphantes hypogeus Bertani et al. 2013	X					X					
Araneomorphae											
Amaurobiidae gen. 1 sp. 1							X				
Anapidae gen. 1 sp. 1						X					
Pseudanops sp.								X			
Araneidae											
Alpaida sp.									X		
Corinnidae gen. 1 sp. 1						X	X				
Creugas sp.								X		X	
Ctenidae											
Ctenus sp.		X						X			
Ctenus gr. *ornatus*									X		
***Isoctenus* sp. n. 1**						X			X		
Ochyroceratidae gen. 1 sp. n. 1											X
Ochyroceratidae gen. 2 sp. n. 1										X	
Theotima sp.				X						X	
Oonopidae gen. 1 sp. 1										X	
Neotrops sp.								X	X		
Palpimanidae gen. 1 sp. 1				X							
Philodromidae gen. 1 sp. 1			X		X						
Pholcidae gen. 1 sp. 1							X				
Mesabolivar sp. n. 1				X		X		X	X		

Taxa/Caves	**Coc**	**TS**	**Crc**	**LPc**	**MAc**	**PVc**	**RMAc**	**RPc**	**CFc**	**Cac**	**VAc**
Mesabolivar sp. 2							X		X		
***Metagonia* sp. n. 1**								X		X	
Prodidomidae gen. 1 sp. 1™								X			
Scytodidae gen. 1 sp. 1						X					
Scytodes sincora Rheims & Brescovit 2009				X		X					
Scytodes sp. 1									X		
Sicariidae											
Loxosceles sp. n. 1				X					X		
Loxosceles sp. 2				X		X	X		X		
Sicarius sp.								X			
Tetragnathidae gen. 1 sp. 1									X		
Theridiidae gen. 1 sp. 1											X
Latrodectus sp.						X		X			
Theridion sp.						X		X			X
Theridiosomatidae gen. 1 sp. 1						X	X				
Naatlo sp.								X			
Plato sp. 1		X	X	X	X	X	X	X	X	X	
Plato sp. 2								X			
O. Amblypygi											
Charinidae											
***Charinus* sp. 1**											X
Charinus sp. 2	X	X		X		X				X	
O. Scorpiones											
Buthidae											
Troglorhopalurus translucidus Lourenço et al. 2004						X					
O. Palpigradi											
Eukoenenidae gen. 1 sp. n. 1				X						X	
O. Pseudoscorpiones											
Chernetidae											
Spelaeochernes sp. n.						X					
Syarinidae gen. 1 sp. 1				X		X				X	
Chtoniidae gen. 1 sp. 1						X				X	
O. Opiliones											
Gonyleptidae											
Pachylinae gen. n. 1 sp. n. 1		X	X	X		X	X	X	X		
Pachylinae gen. n. 1 sp. n. 2	X		X			X	X	X	X		X
Discocyrtus pedrosoi Kury 2008	X	X	X	X		X	X	X	X		X
Tricommatinae gen. 1 sp. n. 1										X	
C. Symphyla											
Scolopendrellidae											
Symphyllela sp.™										X	
C. Chilopoda											
O. Scutigeromorpha											
Pselliodidae											
Sphendenonema guildingii (Newport 1845)		X		X		X			X		
O. Scolopendromorpha											
Cryptopidae											
Cryptopinae											
***Cryptops* sp. n. 1**						X					
Scolopendridae gen. 1 sp. 1							X				
Scolopendridae gen. 2 sp. 1™						X				X	

Taxa/Caves	**Coc**	**TS**	**Crc**	**LPc**	**MAc**	**PVc**	**RMAc**	**RPc**	**CFc**	**Cac**	**VAc**
Scolopocryptopidae											
Scolopocryptopinae											
***Scolopocryptops* sp. n. 1**				X				X		X	
Scolopocryptops ferrugineus macrodon Kraepelin 1903						X					
O. Geophilomorpha											
Geophilidae gen. 1 sp. 1						X					
C. Diplopoda											
O. Spirostreptida											
Pseudonannolenidae gen. 1 sp. 1		X		X		X	X	X	X	X	X
Pseudonannolenidae gen. 2 sp. 1™						X	X				
O. Polydesmida											
Oniscodesmidae gen. 1 sp. 1						X					
Oniscodesmidae gen. 1 sp. 2										X	
Pyrgodesmidae gen. 1 sp. 1		X						X			
C. Malacostraca											
O. Isopoda											
Philosciidae gen. 1 sp. 1				X					X	X	
Philosciidae gen. 1 sp. 2™						X					
Philosciidae gen. 1 sp. 3™											X
Philosciidae gen. 2 sp. 1™						X					
Plathyartridae gen. 1 sp. 1						X		X			
Trichorhina sp.™				X				X			
C. Entognatha											
O. Collembola											
Dycirtomidae											
Dycirtoma sp.							X	X			
Entomobryidae											
***Verhoeffiella* sp. n. 1**						X	X				
***Heteromurus* sp. 1**							X	X		X	X
Paronellidae											
***Troglopedetes* sp. 1**						X	X			X	X
Troglopedetes sp. 2		X				X		X	X		
Tomoceridae indet.				X							
O. Diplura											
Projapygidae gen. 1 sp. 1™								X			
C. Insecta											
O. Zygentoma											
Nicoletiidae gen. 1 sp. 1									X		
O. Odonata											
So. Zygoptera gen. 1 sp. 1		X				X			X		
O. Orthoptera											
Gryllidae gen. 1 sp. 1			X			X					
Phalangopsidae gen. 1 sp. 1								X			
Endecous sp. n. 1		X		X	X	X			X		
Endecous sp. 2		X		X			X	X	X	X	
Eidmanacris sp.							X				
O. Blattaria											
Blattellidae gen. 1 sp. 1™			X			X				X	X
Blattellidae gen. 2 sp. 1								X			
Blattellidae gen. 2 sp. 2					X						
O. Psocoptera gen. 1 sp. 1						X					

Taxa/Caves	**Coc**	**TS**	**Crc**	**LPc**	**MAc**	**PVc**	**RMAc**	**RPc**	**CFc**	**Cac**	**VAc**
O. Thysanoptera gen. 1 sp. 1								X			
O. Hemiptera											
Cixiidae gen. 1 sp. 1				X		X	X	X	X	X	X
Cydnidae gen. 1 sp. 1		X				X			X		
Pyrrhocoridae gen. 1 sp. 1				X							
Reduviidae											
Emesinae gen. 1 sp. 1		X						X	X		
Emesinae gen. 2 sp. 1				X							
Reduviinae gen. 1 sp. 1								X			
Veliidae gen. 1 sp. 1						X			X	X	
Paravelia sp. n. 1		X		X							X
O. Hymenoptera											
Diapriidae											
Diapriinae gen. 1 sp. 1				X							
Formicidae											
Atta sexdens						X					
Cephalotes bruchi (Forel 1912)			X								
Pheidole sp. 1							X				
Solenopsis sp. 1						X					
Solenopsis sp. 2							X	X	X		
Solenopsis sp. 3				X		X	X		X		X
Solenopsis sp. 4							X				X
Scelionidae											
Scelioninae gen. 1 sp. 1										X	
O. Coleoptera											
Alleculidae gen. 1 sp. 1.						X					
Carabidae gen. 1 sp. 1								X			
Carabidae gen. 1 sp. 2								X			
Carabidae gen. 2 sp. 1								X			
Carabidae gen. 3 sp. 1				X							
Curculionidae gen. 1 sp. 1						X		X		X	
Curculionidae gen. 1 sp. 2										X	
Curculionidae gen. 2 sp. 1								X			
Elateridae gen. 1 sp. 1								X			
Elmidae											
Macrelmis sp. 1							X				
Macrelmis sp. 2							X				
Eucnemidae gen. 1 sp. 1		X									
Dytiscidae gen. 1 sp. 1								X	X		
Ptilodactylidae gen. 1 sp. 1						X					
Scarabaeidae gen. 1 sp. 1							X				
Scarabaeidae gen. 1 sp. 2				X							
Scarabaeinae gen. 1 sp. 1				X							
Scarabaeinae gen. 2 sp. 1								X			
Scirtidae											
Scirtes sp.							X			X	
Scydmaenidae gen. 1 sp. 1[TM]										X	
Staphylinidae gen. 1 sp. 1				X			X				
Staphylinidae gen. 1 sp. 2								X	X		
Aleocharinae gen. 1 sp. 1				X			X				
Paederinae gen. 1 sp. 1							X				

Taxa/Caves	**Coc**	**TS**	**Crc**	**LPc**	**MAc**	**PVc**	**RMAc**	**RPc**	**CFc**	**Cac**	**VAc**
Paederinae gen. 1 sp. 2											X
Paederinae gen. 1 sp. 3							X				
Homaeotarsus sp.						X	X				
Pselaphinae gen. 1 sp. 1™						X					
Pselaphinae gen. 2 sp. 1						X					
Pselaphinae gen. 2 sp. 2									X		
Pselaphinae gen. 3 sp. 1™									X		
O. Diptera											
Cecidomyiidae gen. 1 sp. 1						X					X
Chaoboridae gen. 1 sp. 1							X				
Chironomidae gen. 1 sp. 1						X	X				
Hippoboscidae gen. 1 sp. 1		X									
Keroplatidae											
Keroplatinae gen. 1 sp. n. 1				X			X		X	X	
Limoniidae gen. 1 sp. 1		X					X	X			X
Muscidae gen. 1 sp. 1				X							
Psychodidae											
Phlebotominae gen. 1 sp. 1				X							
Sciaridae gen. 1 sp. 1						X	X	X			
Simuliidae gen. 1 sp. 1								X			
Tipulidae gen. 1 sp. 1							X				
O. Lepidoptera											
Tineidae gen. 1 sp. 1				X		X		X	X		
O. Trichoptera											
Hidropsychidae gen. 1 sp. 1								X			
C. Gastropoda											
O. Pulmonata											
Subulinidae											
Obeliscinae gen. 1 sp. 1				X				X			
Systrophiidae											
***Happia* sp. n. 1**				X		X		X	X		
***Happia* sp. n. 2**										X	
C. Actinopterygii											
O. Siluriformes											
Trichomycteridae											
***Copionodon* sp. n.**	X	X	X		X	X	X	X			X
Glaphyropoma spinosum Bichuette et al. 2008		X	X			X	X	X			