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RESEARCH PAPER

Multi-spatial analysis on cave ecosystems to predict the diversity of subterranean invertebrates

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Abstract

Subterranean habitats around the world can shelter diversified and threatened faunal communities. However, issues related to alterations in the landscape and structure of subterranean habitats still need to be better understood. Therefore, we used a multi-spatial scale analysis of land cover, land use, and cave habitats to predict the diversity of communities of subterranean invertebrates. We hypothesized that changes in land cover promote alterations in both faunal richness and composition and microhabitat diversity and that microhabitat features determined subterranean biodiversity. Sixteen limestone caves were sampled in Brazil at micro, meso, and macro scales using quadrats ($1m^2$), transects (100 meters) as sample units inside caves and buffers with the radius of 100 and 250 meters in the surroundings of the cave entrances. Models performed showed that land cover and land use influenced cave environments, regarding both microhabitats traits and terrestrial invertebrate richness and composition. We also observed a relationship between microhabitat structure and terrestrial invertebrate richness and composition. Our results showed that deforested areas had negative effects on species richness and changed their composition, while natural areas had positive effects on microhabitat diversity. The same effects were observed for both 100 and 250 meters buffers. Invertebrate richness was negatively predicted by deforested areas while positively predicted by natural areas. Richness was also positively predicted by the combination of all microhabitat traits, and dissimilarity of fauna was influenced by microhabitat diversity in mesoscale and microscale by all microhabitat elements. The results highlight the importance of the landscape surrounding the caves to conserve the subterranean habitats and their fauna. Due to the spatial and temporal changes in the global environmental scenario, we argue the urgency of further detailed studies in fragmented landscapes to define minimum areas of protection for cave environments.

Keywords: Cave ecology; Subterranean fauna; Land use; Multiscale analysis

Introduction

The biological diversity of cave communities is often related to a variety of environmental factors like the availability of food, climatic and microclimatic conditions, and availability and heterogeneity of habitats (Poulson & White, 1969; Mammola, 2019; Pacheco, Souza-Silva, Cano & Ferreira, 2020; Souza-Silva, Cerqueira, Pellegrini & Ferreira, 2021). Caves, when compared to epigean environments, are oligotrophic, present climate stability, and have

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lower species richness. Still, they contain a variety of trophic, physical, and climatical attributes that constitute microhabitats for vertebrates and invertebrates. Considered discrete environments similar to islands, these habitats represent patches of habitat within a matrix of unsuitable habitats (Culver, 1970; Balogh et al., 2020). They are sometimes connected by other smaller spaces (mesovoids) and cracks that allow cave fauna to transit between caves. The "insular" condition of a subterranean habitat will depend mainly on the scale under analysis and the species dispersal capability (Juberthie, Lopez & Kovoor, 1981; Mammola et al., 2020a; Souza-Silva, Iniesta & Ferreira, 2020). Such a set of physical components promotes habitat heterogeneity and biodiversity by reducing niche overlap, enhancing speciation rates, and decreasing dispersal that limits the movements across environments, consequently isolating the populations (Moldovan, Kováč & Halse, 2018; Balogh et al., 2020).

Microhabitats inside caves are often composed of different textures and porosity. They can be covered by clasts that vary in size and density and can encompass water pools, streams, rivers, and organic debris of varying compositions (guano, carcasses, roots, vegetal debris), among others (White, Culver & Pipan, 2019; Pacheco, Souza-Silva, Cano & Ferreira, 2020; Souza-Silva, Cerqueira, Pellegrini & Ferreira, 2021). These habitats can shelter communities of invertebrates in temperate and tropical regions, frequently including restricted and highly specialized troglobiotic species (Moldovan, Kováč & Halse, 2018; Kozel et al., 2019; Pacheco, Souza-Silva, Cano & Ferreira, 2020). However, colonization of fauna is filtered by selective pressures such as the absence of light and low food availability, imprinting a high dependence on external food resources as trophic supply (Schneider, Christman & Fagan, 2011; Culver & Pipan 2019).

External vegetation can be a direct food source for trogloxene species (those sheltering in caves but depending on the epigean environments for their life cycles such as bats, spiders, and harvestmen). It also provides organic debris that are carried to the cave environment (Machado, Ferreira & Martins, 2003; Schneider, Christman & Fagan 2011; Souza-Silva, Martins & Ferreira, 2011). The surroundings of a cave present potential colonizers of the subterranean environment and can determine entrance microclimate conditions, retain water, and prevent erosive processes (Prous, Ferreira & Jacobi, 2015; Gao, Du, Zuo & Jiang, 2020; Rabelo, Souza-Silva & Ferreira, 2021; Canedoli et al., 2022). Caves with preserved surrounding vegetation are more likely to be colonized by several bat species, which provide an important source of energy for many communities: the bat guano (Ferreira, 2019). Few studies evaluated how land use and land cover affect cave communities in the tropics (Souza-Silva, Martins & Ferreira, 2015; Pellegrini, Sales, Aguiar & Ferreira, 2016; Jaffé et al., 2018; Cardoso, Ferreira & Souza-Silva, 2021), even though this is a fundamental question in subterranean biology (Mammola et al., 2020b).

Recent studies have shown that historical climatic variability, microclimate zones, and speleogenesis, have also a significant effect on cave biodiversity (Zagmajster, Malard, Eme & Culver, 2018; Pacheco, Souza-Silva, Cano & Ferreira, 2020; Nicolosi et al., 2021). Habitat selection in caves probably results from a variety of biotic factors (such as behavioral, physiological, and morphological adaptations) and abiotic factors (such as habitat structure, the presence of organic matter, and the moisture content) (Mammola, Piano & Isaia, 2016; Bregović & Zagmajster, 2016; Souza-Silva, Cerqueira, Pellegrini & Ferreira, 2021).

The fragility and vulnerability of cave fauna to stochastic events and anthropogenic impacts have been increasingly studied (Mammola et al., 2019). Such studies are crucial for improving the conservation of such environments (Sanchez et al., 2021). Therefore, we aimed at understanding the effects and interactions of landscape elements on hypogean microhabitat diversity, as well as the composition and richness of subterranean invertebrates. We tested how microhabitat composition influences the richness and composition of the subterranean fauna. We hypothesized that changes in land cover promote alterations in both faunal richness and composition and microhabitat diversity: the more intensive the external land use is, the higher the effects on subterranean invertebrates communities and microhabitat diversity in caves. Finally, we expected that microhabitat features determined the richness and composition of the subterranean invertebrates.

Materials and methods

Study area

We conducted the study in limestone caves of a karst landscape located in the municipalities of Iuiú and Malhada in the south-central state of Bahia, Brazil (Fig. 1). The limestone formation belongs to carbonate rocks of the Bambuí Group, which form an extensive mosaic of carbonate massifs of approximately 300 km^2. The caves are distributed in four non-contiguous massifs called Serra de Iuiú, Serrinha, Vai Quem Quer, and Sepultamento, with altitudes ranging from 469 to 863 m asl. The karst landscape of Iuiú is located in the Caatinga domain according to the Brazilian Institute of Geography and Statistics (IBGE). The vegetation is composed of different habitat types, particularly seasonally dry tropical forests, that occur in limestone outcrops, with a history of intense land use, mainly deforestation and agribusiness (Apgaua et al., 2014). According to the Köppen-Geiger classification, the climate of the region is semi-arid tropical (Bsh), with an annual rainfall of 788 mm and an average annual temperature of 24 °C. The rainy season is between November and February and the dry season is between March and October (Hijmans et al., 2005).

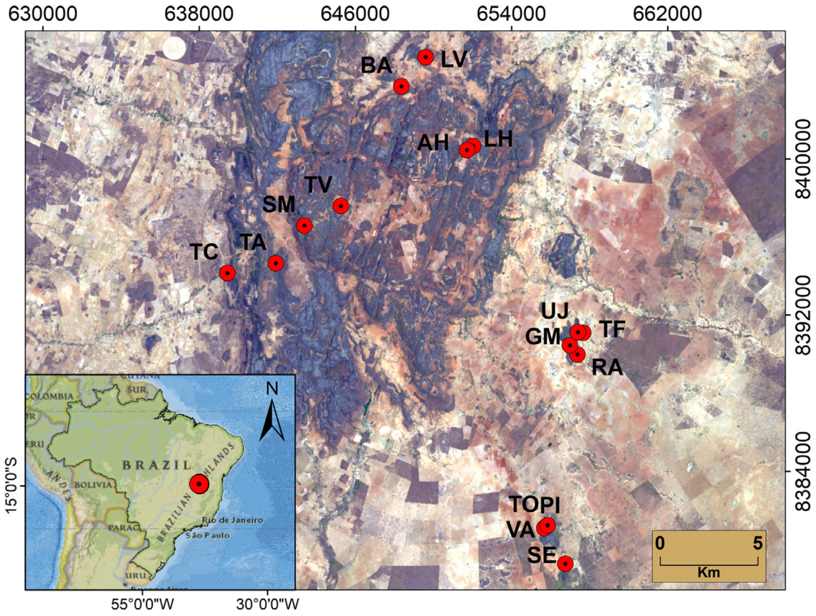

Fig. 1. Iuiú location in Brazil (red circle on the inset map) and the distribution of caves (red circles) in the karst region of Iuiú. (Coordinates Datum: SIRGAS 2000). Caves name: TF = Toca Fria; AH = Abrigo do Honorato; BA = Baixão; GM = Garganta do Macaco; LV = Lajedo da Veredinha; LH = Lapa do Honorato; PI = Picoteamento; RA = Raiz; SE = Sepultamento; SV = Sumidouro das Vacas; TA = Tapera D'água; TO = Toca da Onça; TV = Toca Valada; TC = Tocão; VA = Vai Quem Quer; UJ = Urubu Jatobá.

Sampling design

We defined two spatial scales in 16 caves to sample cave invertebrates (Table 1) and determine the structure of microhabitats on the cave floor, with a total of 125 quadrats (1 m^2) for the microscale, and 25 transects (100 × 3 m) for the mesoscale. We considered the fauna on a macroscale from data sampled in each cave (Fig. 2), which accounted for the sum of both specimens obtained from quadrats and transects. At caves smaller than 100 meters, the transect comprised their entire length. In larger caves, we added a transect every 500 meters of linear development. We sampled five quadrats of 1 m^2 equidistantly along each transect and obtained the physical and biological variables in each. To quantify epigean landscape cover, we extracted land cover classes in radii of 100 and 250 meters from the main entrance of each cave (macroscale units) from *Landsat 8* images. Due to the proximity of some caves and to avoid

Table 1. Cave extensions (CE), numbers of transects (NT), number of quadrats (NQ) and geographical coordinates (LAT= latitude; LONG= longitude; ALT= altitude). (Datum: SIRGAS 2000).

Cave name	CE (m)	NT 100m	NQ 1 × 1m	LAT (S)	LONG (W)	ALT (m)
Abrigo do Honorato I	100	1	5	14° 27′ 45"	43° 35′ 21"	517
Gruta da Raiz	100	1	5	14° 33′ 31"	43° 32′ 21"	505
Lajedo da Veredinha	60	1	5	14° 25′ 1"	43° 36′ 44"	618
Picoteamento	30	1	5	14° 38′ 17"	43° 33′ 12"	491
Sepultamento	510	2	10	14° 39′ 19"	43° 32′ 39"	469
Garganta do Macaco	400	1	5	14° 33′ 15"	43° 32′ 34"	502
Sumidouro das Vacas	150	1	5	14° 29′ 57"	43° 40′ 8"	808
Toca Fria	2500	4	20	14° 32′ 52"	43° 32′ 10"	504
Toca Valada	450	1	5	14° 29′ 26"	43° 39′ 7"	850
Toca do Urubu-Jatobá	3000	6	30	14° 32′ 53"	43° 32′ 20"	507
Vai Quem Quer	45	1	5	14° 38′ 20"	43° 33′ 16"	500
Lapa do Honorato	200	1	5	14° 27′ 51"	43° 35′ 32"	863
Toca da Onça	150	1	5	14° 38′ 15"	43° 33′ 1"	489
Baixão	150	1	5	14° 26′ 6"	43° 37′ 25"	630
Tocão	80	1	5	14° 31′ 19"	43° 42′ 20"	561
Tapera d'Água	150	1	5	14° 31′ 2"	43° 40′ 58"	627

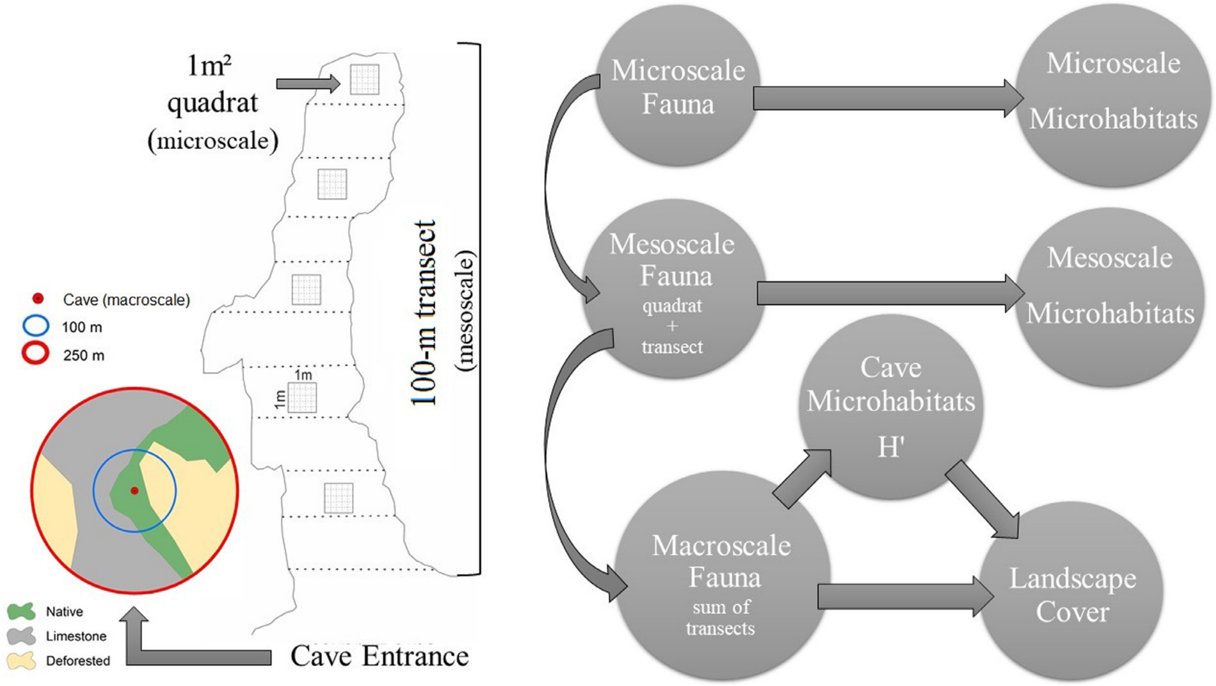

Fig. 2. Infographic showing a cave map and the sample design composed of a 100 transect (mesoscale), five quadrats of one square meter (microscale), and buffers of 100 and 250 m represented in a classified *Landsat 8* image with the three land cover classes (left). Walkthrough with the analytical procedures used to build statistical models. Linear arrows indicate the hypothesis test from the response to explanatory variables.

too many overlaps of a buffer, which can cause spatial autocorrelation between them, we analyzed locations with of a maximum of 250 meters.

Invertebrate sampling and identification

We sampled invertebrates on the cave floor following Wynne, Howarth, Sommer, and Dickson (2019). A team of four biologists sampled the transects, while two biologists sampled the quadrats. All collectors had experience in caving and manual sampling of invertebrates. The time spent sampling in the quadrats and transects varied due to differences in species richness and substrate composition. We sampled each cave only once (September 2016). To calculate species richness, we grouped sampled invertebrates into morphospecies (Oliver & Beattie, 1996). To characterize the potentially troglobiotic invertebrate species, we used troglomorphic traits such as depigmentation, anophthalmia, and elongation of appendages (Christiansen, 1962, Sket, 2008).

Assessing land cover

To access the land cover, we used *Landsat 8* satellite images from the year 2016 pan-sharpened to 15 meters resolution. We classified them inside buffers of 100 and 250 meters in the surroundings of caves, using the largest cave entrance as a reference (Pellegrini, Sales, Aguiar & Ferreira, 2016). We obtained three land cover and land use classes (limestone outcrops, deforested area, and native forest cover) and their respective proportions (Fig. 2 and Table 2) (image courtesy of the U.S. Geological Survey - https://www.usgs.gov).

Assessing microhabitat structure

We quantified components of the substrate in microscale inside the quadrats with 100 subsamples (grids of 10 × 10cm) to obtain the proportion of each one inside the quadrat (Fig. 2). To quantify the components of the substrate inside the transects, we adapted the method proposed by Peck et al. (2006) for aquatic environments and modified it to cave habitats by Pellegrini, Sales, Aguiar, and Ferreira (2016). For this, we arranged ten sections per transect to count the substrate components of the cave floor (Fig. 2). The substrates quantified on the cave floor comprised water bodies, cobbles, gravels, organic debris, cattle droppings, bat guano, coarse gravel, roots, rocky outcrops, dry sediment, wet sediment, and termite mud tubes (Table 2).

To minimize estimation errors, the same person surveyed and quantified the substrate components of the habitats in the ten cross-sections, resulting in the percentage of each class contained in the transect (Pacheco, Souza-Silva, Cano & Ferreira, 2020). To obtain the microhabitat diversity value

Table 2. Components of the substrate and landscape features accessed in a scaled gradient of a tropical limestone outcrop.

Cave Quadrats (microscale)	Cave Transects (mesoscale)	Landscape (mesoscale)
Water Bodies	Water Bodies	Limestone Outcrops
Gravel (2-16mm)	Cobble (64-250mm)	Deforested Area
Organic Debris	Organic Debris	Native Forest Cover
Mud Crack	Cattle Droppings	
Guano	Guano	
Coarse Gravel (17-64mm)	Coarse Gravel (17-64mm)	
Roots	Roots	
Rocky Outcrops	Rocky Outcrops	
Dry Sediment	Dry Sediment	
Wet Sediment	Wet Sediment	
	Termite Mud Tube	

of each cave, we used the Shannon index (H') (Pacheco, Souza-Silva, Cano & Ferreira, 2020).

Data analysis

We conducted a Principal Coordinates Analysis (PCoA), with Bray-Curtis dissimilarity distances and faunal abundance matrix data to obtain species composition, considering the first two axis scores (MDS axis 1 and MDS axis 2) as species composition and using them as the response variable in regression analysis (Jaffé et al., 2018). We ran this analysis in the *vegan R* package (Oksanen et al., 2013).

We constructed Linear Models (LM) and Generalized Linear Models (GLM) for the macroscale, according to the normality of the residuals of the response variable. For micro and mesoscales, we constructed Linear Mixed Models and Generalized Linear Mixed Models (GLMM) using caves as the random effect (Bolker et al., 2009). For the response variables, we used morphospecies number (species richness) and composition (MDS axis 1 and MDS axis 2) to test the effect of the components of the substrate (organic and inorganic) in micro and mesoscales. As the predictor variable in the macroscale, we used land cover (deforested, native and limestone outcrop cover) to test its effects on cave invertebrate richness, composition (MDS axis 1 and MDS axis 2), and microhabitat diversity (H') (Fig. 2). We performed the GLMs and GLMMs using Poisson error distributions with a log link function for count data and Quasipoisson when the data showed significant overdispersion (Crawley, 2007, Bates, Mächler, Bolker & Walker, 2014). To account for spatial autocorrelation, we ran *Moran's I* test on the residuals of all constructed models.

To avoid multicollinearity between explanatory variables, we considered only those with Spearman correlations equal to or lower than 0.6 in each model (Booth, Niccolucci & Schuster, 1994; Zuur et al., 2009). In analyses with more than one model built, we selected the best model using the second-order Akaike information criterion (AICc), which is more robust for small samples (Burnham, Anderson, & Huyvaert, 2011). We ran all analyses in *R* software (*R* Development Core Team, 2010).

Results

Land cover components

Altogether, the average land cover within 100 buffers comprised 53% (± 21%) of deforested areas and 47% (± 21%) of natural areas. Within the natural areas, native forest cover represented 27% (± 17%) and limestone outcrops represented 18% (± 14%). In 250 buffers, deforested areas represented 38% (± 21%), while natural areas represented 61% (± 21%). From these natural areas, native forest cover represented 34% (± 22%) and limestone outcrops represented 27% (± 19%).

Urubu-Jatobá, Toca Fria, and Garganta do Macaco caves had the highest proportion of deforested area (>70%) among 100 buffers. Meanwhile, Tapera D'água cave had the lowest (18%). Among 250 buffers sites, Sepultamento cave had the highest proportion of deforested area (71%) while Urubu Jatobá cave had the lowest (8%)(see Appendix A: Table 2).

Components of the substrate on the floor of the cave

In the quadrats, average dry sediment and coarse gravel were the most common substrates, representing 36% (± 24%) and 14% (± 16%) of the total, respectively. Water bodies and roots were less common (<1%). Regarding transects, dry sediment (50% ± 28), cobbles (13% ± 10), and matrix rock (15% ± 14) was the most common substrates, while termite mud tubes (<1%) were the least common structure. Cave microhabitat diversity (H') ranged from 0.21 (Raiz cave) to 1.77 (Tocão cave), with an average of 1.21 per cave (see Appendix A: Table 2).

Invertebrate composition and richness

In all 16 sampled caves, we found 258 morphospecies, 117 being found in the quadrats and 206 along the transects. A total of 66 morphospecies occurred in both quadrats and transects.

The richest groups were Hexapoda (185 spp.), Arachnida (84 spp.), Myriapoda (30 spp.), and the orders Araneae (38 spp.), Coleoptera (37 spp.), and Hymenoptera (30 spp.). A total of 13 morphospecies presented troglomorphic traits (Fig. 3) occurring in all four caves. Of these, 11 were observed in transects only, and one was in quadrats only. The groups richest in troglomorphic morphospecies were Arachnida (5 spp.), Myriapoda (3 spp.), and Mollusca (2 spp.). Regarding troglobiotic species, we recorded *Loxosceles troglobia* Souza & Ferreira (2018 The reference 'Souza & Ferreira (2018′ is cited in the text but is not listed in the references list. Please either delete the in-text citation or provide full reference details following journal style.), *Spelaeobochica iuiu* Ratton, Mahnert & Ferreira (2012), and *Iuiuia caeca* Hoch & Ferreira (2016).

Cave communities, microhabitat structures, and land cover

We found no correlation between explanatory variables of the microhabitat components in the quadrats in the analysis of multicollinearity ($|r| \geq 0.6$). The model with substrate composition inside quadrats showed that morphospecies richness and composition could be predicted by the combination of dry and wet sediment, water bodies, gravel, mud cracks, coarse gravel, organic debris, rock outcrop, roots, and guano. The models explained about 28% of the total variance of morphospecies richness and about 11% of the variance of species composition (MDS axis 1). GLMMs coefficients and variable effects are shown in Appendix A (see Table 1, Fig. 4).

Our final models of land cover within 100 buffers surrounding cave entrances showed that native forest cover (GLM; t=2.63, p= 0.02) and limestone outcrops (GLM; t=2.16, p= 0.04) positively affected cave morphospecies richness (Moran's I= 0.02; p= 0.57) (Fig. 4A). Deforested areas, however, had negative effects (GLM; t=-3.36, p= 0.004) (Moran's I= 0.04; p= 0.5) (Fig. 4B). Within the 250 buffers, richness was not predicted by any landscape metric.

Morphospecies dissimilarities within transects (Mesoscale - MDS axis 1) were best predicted by microhabitat diversity (H') (t= 2.820, p= 0.01) (Moran's I= -0.1; p= 0.66), explaining about 21% of the total variance. The similarity was greater at intermediate values (close to 1.0), while at higher or lower values of substrate diversity, communities tended to be more dissimilar (Fig. 4C).

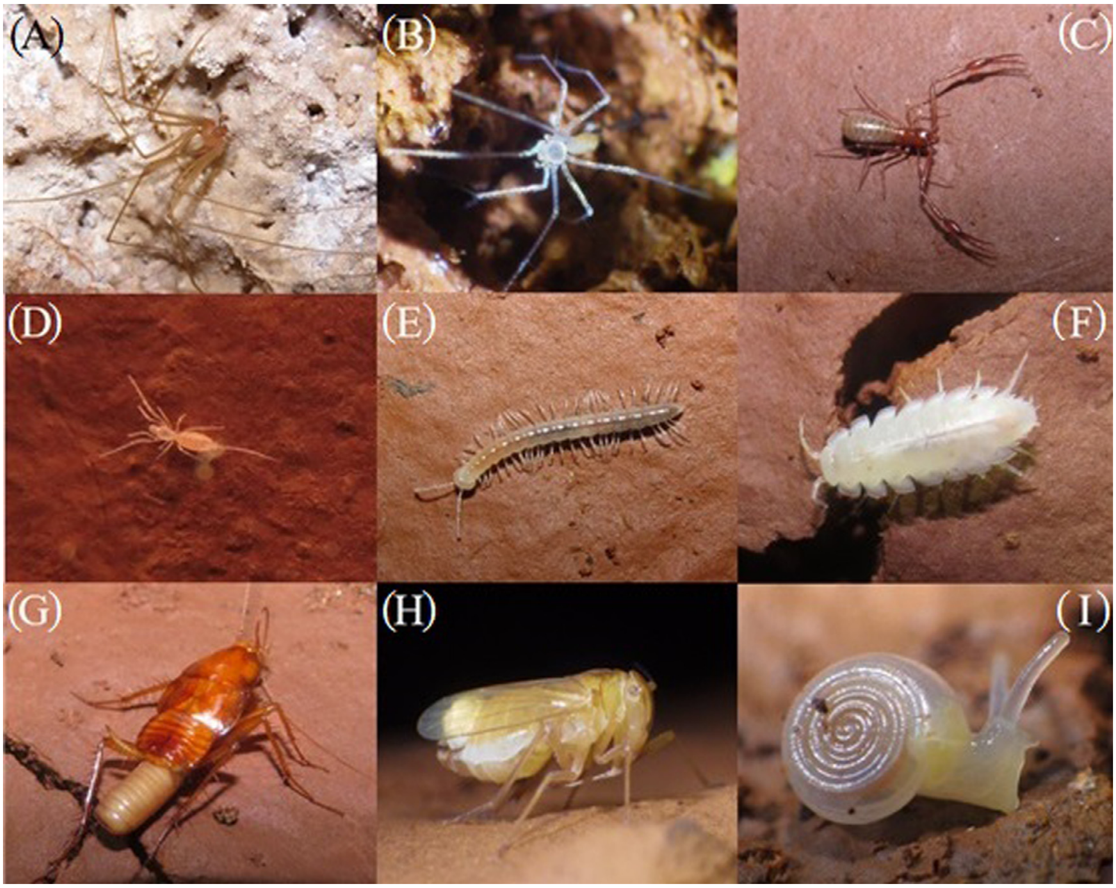

Fig. 3. Some troglobiotic species recorded for the caves in the karstic region of Iuiú, Bahia, Brazil: (A) *Loxosceles troglobia* (Araneae Sicariidae); (B) Ochiroceratidae (Araneae); (C) *Spelaeobochica iuiu* (Pseudoscorpiones: Bochicidae); (D) *Eukoenenia* sp. (Palpigradi: Eukoeneniidae); (E) Polydesmida (Diplopoda); (F) Styloniscidae (Isopoda); (G) Blattodea; (H) *Iuiuia caeca* (Auchenorrhyncha: Kinnaridae); (I) Gastropoda (Mollusca).

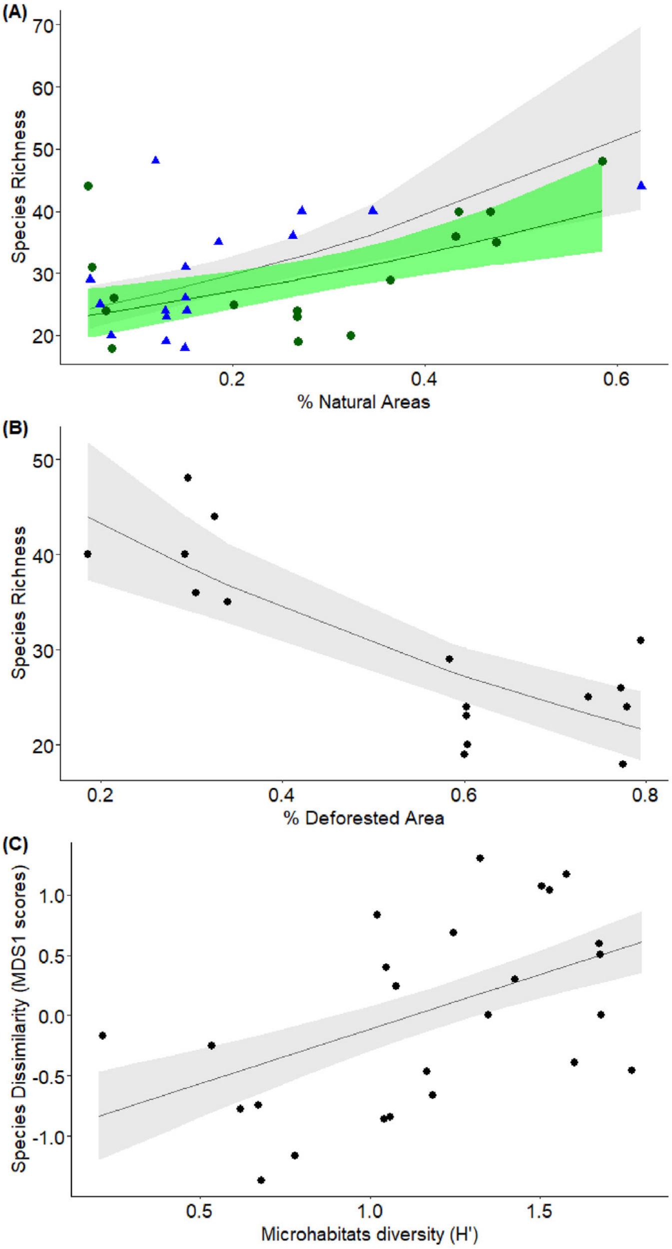

Fig. 4. Predicted values plotted from the Generalized Linear Models showing the relationships between Cave Invertebrate Species Richness and Natural Areas (Limestone Outcrops and Native Forest Cover) (A) and Percent Deforested Area (B) within 100 buffers). Green dots and shaded Confidences Intervals (CI) represent Native Forest Cover, and blue triangles and gray CIs represent Deforested Area in panel (A). In panel (C) the predicted values of the Linear Mixed Model showing effects of microhabitat diversity (H') on species dissimilarity represented by MDS1 scores at the mesoscale (C).

The caves' microhabitat diversity (H') was positively predicted by natural areas (native forest cover plus limestone outcrops) ($F_{(2,\ 13)}$= 5.248, p= 0.02, R^2 =0.44) (Moran's I= -0.06; p= 0.98) (Fig. 5A) and negatively predicted by deforested area ($F_{(1,\ 14)}$= 11.3, p= 0.004, R^2=0.44) (Moran's I= -0.06; p= 0.99) within 100 buffers (Fig. 5B). In the models performed with buffers of 250 m, native forest cover positively predicted H' ($F_{(1,\ 14)}$= 6.17, p= 0.026, R^2=0.3) (Moran's I= 0.06; p= 0.42) (Fig. 5C) and deforested area affected H' negatively ($F_{(1,\ 14)}$= 8.02, p= 0.013, R^2=0.36) (Moran's I= 0.11; p= 0.26) (Fig. 5D).

Discussion

Our results show that land cover and land use surrounding the cave entrances influenced subterranean environments, regarding both microhabitat features and terrestrial invertebrate communities. As expected, subterranean microhabitats had effects on the richness and composition of terrestrial invertebrates. Considering the external landscape, we have evidence that deforested areas had negative effects, while natural areas have positive effects on subterranean invertebrate richness. The same effects were observed for both 100 and 250 buffers. Deforested areas seem to change the composition of the fauna and decrease subterranean microhabitat diversity, while conserved areas increase the diversity of microhabitats on the cave floors. Subterranean invertebrate richness was positively determined by the combination of all microhabitat features. Faunal dissimilarity was also significantly affected by all the same components, both on transects and quadrats.

Effects of land cover on subterranean environments

The cave surroundings presented deforested areas, which also occur in many karst regions worldwide and represent one of the major threats to caves, affecting both biotic and abiotic factors of the subterranean environments (Gams & Gabrovec 1999; Brinkmann & Parise, 2012; Souza-Silva et al., 2015; Jaffé et al., 2018; Canedoli et al., 2022). Subterranean environments associated with karst areas are intricately linked to surface processes, due to the high permeability of such landscapes. Deforested areas surrounding cave entrances can lead to soil exposure and subsequent erosion; carried sediments can silt up watercourses in hypogean habitats (Bárány-Kevei, 1999). Depending on the intensity, silting can cover the cave floor with layers of different thicknesses, burying structures that comprise microhabitats for the fauna such as gravels, organic debris, or roots. This was highlighted in our results, which showed that caves with more homogeneous microhabitats presented a higher rate of deforestation in their surroundings, indicating possible processes of silting of the subterranean environments.

The silting, in addition to causing microhabitats loss, negatively affects the input of allochthonous organic resources to the subterranean environment, which impacts the fauna that depends on it to establish and maintain their populations in these environments where primary production is absent. (Schneider, Christman & Fagan, 2011; Souza-Silva, Martins & Ferreira, 2011; Muylaert, Stevens & Ribeiro, 2016; Ferreira, 2019).

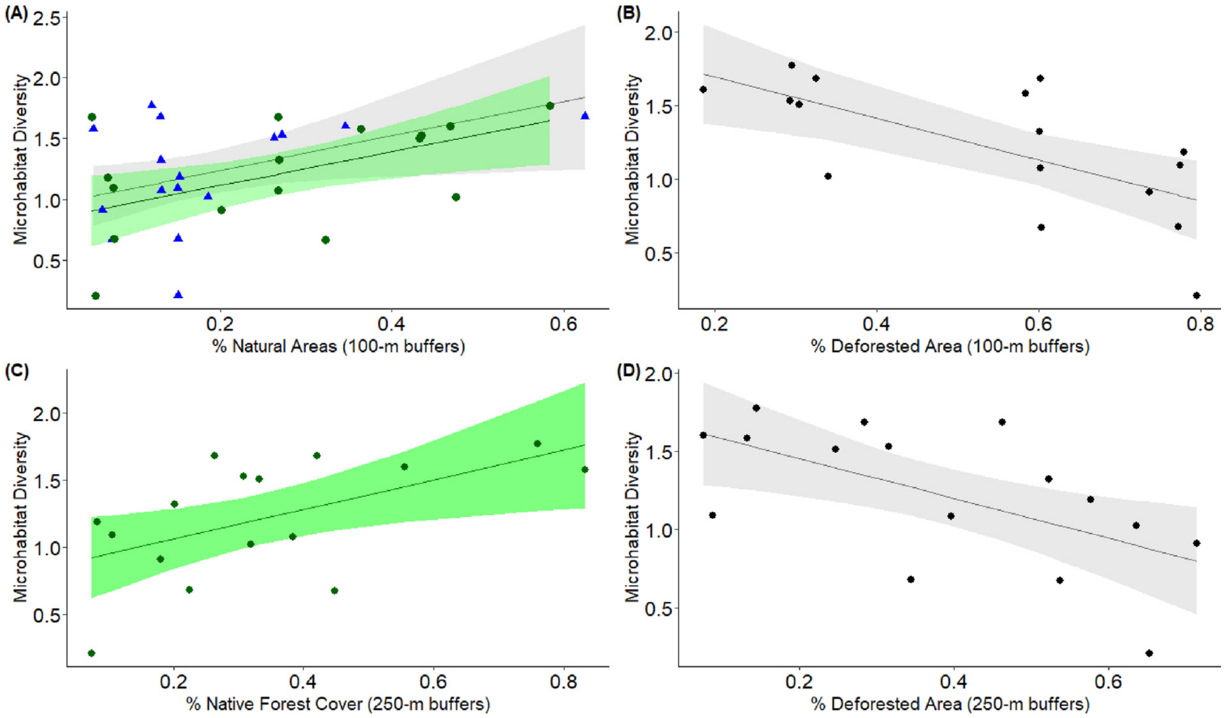

Fig. 5. Predicted values plotted from the Linear models showing the positive effects of natural landscape cover (Limestone Outcrops and Native Forest Cover) (A) and the negative effect of the proportion of Deforested Area (B) within 100 m buffers surrounding cave entrances on the microhabitat diversity inside caves (H'). The positive effect of Native Forest Cover (C) and the negative effect of the proportion of Deforested Area (D) within 250 buffers surrounding cave entrances on microhabitats diversity (H'). Green dots and confidence intervals (CI) represent Native Forest Cover, while blue triangles and gray CI represent Percent Deforested Area in panel (A).

In this sense, and considering our results, the conservation of landscapes surrounding cave entrances seems to be an important factor in determining the richness of terrestrial subterranean invertebrates, since the proportion of natural areas within an immediate radius of 100 m from the entrances, was positively related with a greater number of species. Habitat loss causes ecosystem fragility and functional degradation, also influencing both ecosystem services and maintenance of the local pool of epigean species in karst landscapes (Wang et al., 2019; Gao, Du, Zuo & Jiang, 2020; Rabelo, Souza-Silva & Ferreira, 2021; Canedoli et al., 2022).

Human impact near cave entrances can lead to alterations of an important ecotonal region, affecting the input of organic resources from the external environments and potential colonizers to access caves (Prous, Ferreira & Martins, 2004, Culver, 2005, Prous, Ferreira & Jacobi, 2015). Furthermore, the deforestation of karst landscapes can impose barriers to the movements of trogloxen species between caves, since the dispersal of such organisms is facilitated by corridors of conserved vegetation. Hence, deforestation can act by restricting genetic exchanges and interspecific interactions and, as a result, may lead to the extinction of cave-dwelling metapopulations (Campbell Grant, 2011).

External vegetation roots can penetrate rock fractures reaching subterranean habitats, and providing food resources for cave organisms (Stone, Howarth, Hoch & Asche, 2004). However, deforestation can limit the roots growing in subterranean habitats. Some cave species from Iuiu karst are phytophagous, thus, directly depending on the presence of roots, including some cave-restricted taxa, such as the planthopper *Iuiuia caeca*.

Cave species can be highly sensitive to small changes in microclimate conditions (Culver, 2005). Hence, preserved cave surroundings can maintain the stability of subterranean microclimatic conditions by changing external airflow and temperatures, and by retaining water (Prous, Ferreira & Jacobi, 2015). Cave invertebrates are usually ombrophilous species with a low ability to avoid water loss due to their thin cuticle, leading to low tolerance against desiccation (Friedrich, 2019; Pallarés et al., 2019; 2020). In a study performed in small limestone caves in Brazil, Pellegrini, Sales, Aguiar, and Ferreira (2016) measured land cover in radii of 50 m, 100 m, and 250 m around each cave entrance and observed a positive effect of conserved surroundings on the cave arthropod community. Jaffé et al. (2018) found negative effects of agropastoral activities near caves on terrestrial troglobiotic communities from ferruginous caves in Brazil. This demonstrates how closely the external landscape can be related to the physical and biological processes of the subterranean environment.

In this sense, identifying factors associated with habitat loss and degradation is essential to conserve these environments and subsidize stakeholders to follow sustainable management practices and the creation of protected areas to maintain the cave habitats and their specific and sensitive fauna (Mammola et al., 2019, 2020; Canedoli et al., 2022).

Effects of cave microhabitats on subterranean fauna

In both sampling scales analyzed, microhabitat structure was important in the structuring of subterranean communities. While microhabitat features influenced richness and community composition at the microscale, microhabitat diversity affected species composition at the mesoscale. These results show that alterations in the structure of subterranean habitats, either by changes in the landscape or by direct alterations in the subterranean environment by humans, may significantly impact cave communities at different scales.

The effects of all microhabitat components surveyed on increasing invertebrate richness indicate that communities inhabiting more complex habitats may be richer than communities occurring in more simplified ones. The "habitat heterogeneity hypothesis", proposed by MacArthur and Wilson (1967) assumes that habitat diversification directly increases species richness, thus reducing niche overlap. More complex habitats allow species to explore the conditions and resources in distinct ways. More heterogeneous habitats can provide shelter and refuge to the fauna, maintaining communities for a longer period in that environment (Fjeldsa, Bowie & Rahbek, 2012; Zagmajster, Malard, Eme & Culver, 2018; Pacheco, Souza-Silva, Cano & Ferreira, 2020).

At the mesoscale (transects), invertebrate communities were more similar at intermediate values of microhabitat diversity, while habitats with higher or lower values showed more dissimilar communities (Fig. 4C). Transects with higher values of microhabitat diversity are more dissimilar to each other, probably because the more types of microhabitats, the greater the chances of more species to co-exist. Considering that most species found in caves tend to be rare (Wynne, Howarth, Sommer & Dickson, 2019), there should be hardly any redundancy when comparing transects from distinct caves. Nonetheless, transects with lower habitat diversity values do not necessarily present the same types of microhabitats. For instance, two transects can have only two types of microhabitats (thus presenting a lower value of microhabitats diversity), one containing only rock and clay while the other contains guano and boulders. As they have distinct microhabitats, the chance of attracting different species is high. This may have been the reason why the low diversity of the habitat led to a high dissimilarity of fauna among the transects.

Management implications

Economic activities in karst areas that lead to deforestation, such as agriculture, pastures, or crops in large areas, can cause serious damage to subterranean environments and associated fauna (Souza-Silva, Martins & Ferreira, 2015; Auler, 2016; Mammola et al., 2019). As we could see in this study, deforestation can affect both the fauna and its habitat. In Brazil, environmental decrees use to require a protected area of 250 m surrounding the cave extent projected on the surface. This value was not defined based on scientific experiments and a variety of epigean environmental factors should be considered for such a definition. Some factors that should be included are hydrographic micro-basins, phytogeographic domains, topography, geomorphology, and the presence of corridors (Canedoli et al., 2022). Our results indicate that the landscape surrounding cave entrances affects the subterranean environments in different ways, reinforcing the fact that conserving and/or restoring its natural elements can protect cave invertebrate communities.

Brazilian environmental legislation has undergone several changes in the last decade to regulate the use and economic exploitation of caves, leading to conflicts of interest between the industrial and infrastructure sectors and conservation efforts, including a recent government decree capable of bringing irreversible damage even to the most relevant and unique Brazilian caves (Ferreira et al., 2022). Therefore, we need to accelerate scientific research to consolidate knowledge for decision-makers who determine the protection and conservation of subterranean habitats. Our results addressed the importance of the landscape surrounding the caves to conserve the subterranean habitats and their fauna. However, additional studies are required for understanding the consequences of habitat fragmentation and alteration, which causes loss of diversity in these sensitive environments.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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