ORIGINAL RESEARCH



Spatiotemporal distribution of invertebrate fauna in a mesovoid shallow substratum in iron formations

Lígia Maria Saback Moreira Dornellas^{1,2} · Pedro Giovâni da Silva^{1,2} · Maria Elina Bichuette³ · Augusto S. Auler² · David C. Culver⁴ · Tanja Pipan⁵ · Lorena Oliveira Pires⁶ · Frederico de Siqueira Neves¹

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Abstract

Iron Formations (IF) are among the most threatened environments due to the extensive mining activities. Mesovoid Shallow Substratum (MSS) in IF represents a poorly known subterranean environment and evaluating its fauna has the potential for expanding knowledge about the distribution of troglobiotic populations. We evaluated the spatiotemporal distribution of the subterranean fauna in the MSS of IF in Brazil. We sampled the MSS invertebrate fauna and described the community patterns of troglobiotic and non-troglobiotic species. A total of 22,821 individuals and 276 morphospecies belonging to two phyla were found: Annelida and Arthropoda. Acariformes, Diptera, Hymenoptera, Blattodea, and Collembola represented 92.2% of the individuals sampled. Nine troglobiotic morphospecies belonging to four groups were sampled: Araneae (1), Entomobryomorpha (6), Poduromorpha (1), and Pseudoscorpiones (1). We found a high compositional dissimilarity of troglobiotic and non-troglobiotic species in terms of spatial β -diversity (among MSS sites) and temporal β -diversity (among months). The observed spatial β -diversity of troglobiotic species sampled in the MSS is greater than that of non-troglobiotic species. The temporal variation is similar for both groups. The richness difference component contributed more to spatial and temporal β -diversity for troglobiotic species, while higher replacement values for non-troglobiotic species were observed. Average values of temporal β-diversity and the replacement component were greater for non-troglobiotic than for troglobiotic species, while the richness difference component had an opposite pattern. The spatiotemporal β -diversity patterns suggest a medium-to-low connectivity of invertebrate populations that colonize the MSS, favoring the adoption of strategies for conserving broader areas in the context of IF.

Keywords Iron formations \cdot MSS \cdot Southern Espinhaço region \cdot Troglobiotic \cdot Beta diversity \cdot Connectivity

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Extended author information available on the last page of the article

Introduction

Although caves are the most well-known and studied subterranean habitats, they are just a small part of the subterranean environment, which extends through crevices and spaces that are too small for humans but are inhabited by smaller organisms (Vandel 1964; 1965). The superficial subterranean habitats, consisting of features like small voids (pores), fissures and cracks between the surface and the cave ceilings (epikarst), seeps, and small cavities within rocks and soil on mountain slopes, have three common characteristics: (1) the absence of light, (2) a close association with the surface, and (3) the presence of species that have undergone significant adaptations to subterranean life (Culver and Pipan 2019). Generally occurring at a depth of a few meters, the subterranean environment encompasses the *milieu souterrain superficiel* (Juberthie et al. 1980) or mesovoid shallow substratum (MSS) (Culver and Pipan 2008). The MSS is a shallow (superficial) subterranean habitat with intermediate-sized spaces and connections with the surface (Culver and Pipan 2014). The term MSS originally refers to areas with erosion characteristics, such as scree covered by soil or moss (Culver 2016). This habitat is generally found in mountains in temperate zones but less common in the tropics, where spaces are usually filled with sediment such as clay (Culver and Pipan 2019).

Iron Formations (IF), an umbrella term that includes all iron-rich rocks derived from the original Banded Iron Formation (BIF) rocks, can also be considered as superficial subterranean habitat. BIF rocks have undergone considerable alteration through geological time, displaying varying degrees of cohesion and porosity. An iron-rich duricrust, termed "canga", usually caps and protects from erosion the friable iron ore underneath. Canga is a highly porous rock, with porosity values reaching as much as 24% (Dias and Bacellar 2021), comprising fragments of BIF (or other rocks) cemented by a goethite-rich matrix. It can be up to 30 m thick (being normally just a few meters) and is present throughout the IF regions in Brazil. Canga also hosts thousands of caves, mostly oriented along the contact between the canga and the altered iron ore (Auler et al. 2022). These caves are interpreted as being the macro-dimensional equivalent of the pores within the canga (Auler et al. 2022) and also host a diverse cave-adapted fauna (Auler et al. 2019). The pore spaces within canga are generally small in size but can hold rainwater, which slowly percolates into deeper parts of the rock. These habitats often remain wet or very humid, due to the permeability contrast between canga and the less permeable iron ore underneath (Bertachini et al. 2018), allowing the establishment of aquatic invertebrate populations and amphibians. Canga pores can connect to edaphic epigean environments, such as soil, lapidicolous compartments, and leaf litter (Ferreira et al. 2018), which are expected to serve as crucial connectivity elements for invertebrate fauna between the caves and other habitats (Culver and Pipan 2008).

Among the ecosystems found in Brazil, ferruginous outcrops are among the least studied and most endangered ecosystems (Gomes et al. 2019). This status is due to their restricted distribution, associated with the main iron ore deposits in the country, which increases the risk of destruction and loss through mining (Jacobi and Carmo 2008). It has been estimated that 50% of the IF in the Iron Quadrangle (Salles et al. 2019) and 20% in Carajás (Souza-Filho et al. 2019), the two largest iron deposits in Brazil, have already been destroyed by mining. The mining activities in these areas not only result in the loss of cavities but also lead to indirect impacts on the subterranean environment by altering or destroying the surface habitat. Hence, to ensure cave preservation, it is crucial to comprehend the biotic and abiotic components that constitute the entire subterranean ecosystem. Because mining operations require environmental studies, which include the sampling of the subterranean fauna, there is now a much-improved understanding of the fauna associated with IF caves (Jaffé et al. 2016; Auler et al. 2019). Using troglobiotic species as "biological tracers" is recommended to gain insight into the connectivity of the subterranean system and the other cavities that the cave is connected to (ICMBio/CECAV 2022). However, to obtain a more conclusive result, validation of connectivity can be achieved when the distribution of the analyzed species is limited to cavities within the same landscape compartment. It is noteworthy that few studies exist on the diversity patterns of invertebrate communities in MSS in Brazil (see Ferreira et al. 2018; Mendonça et al. 2023). The confirmation of spatiotemporal patterns enables the corroboration or not of gene flow maintenance among populations inhabiting such environments, thus promoting the conservation of larger areas in the context of IF.

Faunistic surveys in IF caves in Brazil have indicated a diverse fauna, including troglobiotic and troglomorphic species (e.g., Souza-Silva et al. 2011; Caetano et al. 2013; Bichuette et al. 2015b; Jaffé et al. 2016; Ferreira et al. 2018; Trevelin et al. 2019). Some troglomorphic species can be observed in multiple, distant cavities, indicating that their distribution is not limited to a single cavity (Jaffé et al. 2016). This observation implies the existence of a possible connectivity among the cavities, where a given species occurs, facilitated by interstitial spaces, and pores that connect continuous areas in the rock. Research aimed at identifying fauna in small spaces within the bedrock is crucial for a better understanding of population distribution along these formations. In Brazil, some surveys have investigated the presence of subterranean fauna inside IF environments, exploring spaces accessible to humans and yielding satisfactory results (Ferreira et al. 2018; Gomes et al. 2019; Zeppelini et al. 2022; Iniesta et al. 2023), although the number of collected troglobiotic animals is generally low. These findings corroborate the occurrence of fauna in small spaces within iron rocks and suggest probable connectivity between caves (Zeppelini et al. 2022). Surveys of subterranean fauna are crucial in making decisions about land use and can provide valuable insights into species distribution, connectivity, and the extent of the subterranean environment (e.g., Harvey et al. 2008; Smith et al. 2012). Furthermore, assessing patterns of diversity in subterranean fauna communities can determine whether there is subterranean connectivity between cavities, which is essential for understanding species range and providing protection for subterranean organisms, in accordance with the Brazilian legislation (Brasil 2008, 2022).

Large-scale ecological gradients are typically characterized by species replacement as the main component of spatial β -diversity (spatial or temporal variation in species composition) (Ricklefs 2004; Barton et al. 2013; Soininen et al. 2018). However, the contribution of local-scale ecological factors, such as those found in the MSS, to spatiotemporal patterns of biological diversity is an equally important but often overlooked facet of β -diversity analysis (Huston 1999). For instance, the distribution of epikarst fauna sampled from water drips in caves was better explained by species replacement, while nestedness in the form of hotspot drips was also important (Pipan et al. 2018). In cave and MSS habitats, seasonal samplings have also shown that there is significant variation in species composition (either replacement or species gain/loss) between different seasons (Nitzu et al. 2014; Mammola et al. 2017), highlighting the importance of sampling periods on β -diversity patterns. However, there is still a lack of information about the spatiotemporal patterns found for the entire community that inhabits the subterranean environment, those dependent on the subterranean system (non-troglobiotic), and those that use the subterranean and surface environment (troglobiotic) (Nitzu et al. 2014). Low values of β -diversity among MSS, which indicates more similar species composition between communities (Anderson et al. 2011), may suggest high subterranean connectivity between sites, allowing for the preservation of gene flow among subterranean species.

In this study, we aimed to enhance the understanding of the spatial and temporal distribution of subterranean fauna in canga MSS by comparing the composition of troglobiotic and non-troglobiotic fauna. The sampling of invertebrate fauna in the superficial subterranean habitats of IF was carried out, and the patterns of richness, abundance, and composition of invertebrate species (troglobiotic and non-troglobiotic) were evaluated. Species composition was described based on spatiotemporal components of β-diversity, and subterranean connectivity among invertebrate communities was discussed in the light of spatiotemporal patterns of β -diversity. In the MSS environments, a difference in the spatiotemporal distribution pattern of troglobiotic invertebrates is expected compared to non-troglobiotic invertebrates. Because many invertebrates may not be dependent on MSS, we expect that non-troglobiotic invertebrates would exhibit higher values of β -diversity and species replacement than troglobiotic invertebrates. The latter is restricted to the subterranean habitats, suggesting greater temporal stability responsible for housing species restricted to the subterranean environment. Additionally, to verify the spatial subterranean connectivity between MSS communities, β -diversity values were expected to be low accompanied by a high contribution from the richness difference component to spatiotemporal dynamics, particularly for the group of troglobiotic invertebrates.

Methods

Study area

The study was conducted in canga areas of Serra do Sapo, part of the Southern Espinhaço Range located in the municipality of Conceição do Mato Dentro, in the state of Minas Gerais, southeastern Brazil (19°00'17"S, 43°23'43"W, 848–991 m a.s.l.; Fig. 1). Geology comprises Fe-rich deposits belonging to the Serra do Sapo Formation, Serra da Serpentina Group (Rolim et al. 2016), which occur at the flanks of ridges oriented N-S. The study area is located in an ecotone of two biomes Atlantic Forest and Cerrado (Brazilian savannah), and where relic communities of mountain vegetation also occur. In the region on the eastern edge of the Espinhaço, the montane semideciduous seasonal forest predominates, with forested and woody grassland savannahs occurring as well, along with upper-mountain and montane refuges. The climate is highly seasonal, with an average annual temperature of 20.6 °C in the sampled location, with the highest monthly averages in February (summer; 23.2 °C) and the lowest in July (winter; 16.6 °C). The annual accumulated precipitation is 1424.4 mm, while the average annual relative humidity is 76.1%. The rainiest months extend from October to March. The months from April to September are marked by the dry season (INMET 2022).



Fig. 1 Sampling points with installation of traps in the mesovoid subterranean substratum (MSS) of canga. Oblique aerial view with 3× vertical exaggeration. The 20 sampling points were named MSS-01 to MSS-21, excluding MSS-10. Image from Google Earth

Sampling of invertebrates in the MSS

Aiming to understand the distribution of subterranean fauna in IF and the local environment connectivity, 20 sampling points were established in a 17.8-hectare area of canga, with an average distance of 354.02 ± 207.7 m (mean \pm standard deviation) between them. The elevation of the sampling points varied between 848 and 991 m a.s.l. (925.2±43.4 m a.s.l.). A total of 20 traps were placed in suitable locations in portions of the canga in the study area (Fig. 1), where a larger portion of rock and less soil and vegetation was observed. A mesovoid shallow substratum trap (López and Oromí 2010) was used to sample the fauna in the superficial subterranean environment of the study area, in pores and smaller spaces in the rock. This trap consisted of a PVC tube with holes along its surface, with an attractive bait container (an Eppendorf containing cooked ham) and a fixative liquid container (propylene glycol) inside (Fig. 2). Portable drilling equipment was used to drill shallow holes of approximately 1 m to install the trap in the rock. The traps remained in the field throughout the study period, and the preservative liquid container was periodically removed, and the bait replaced in a monthly basis. The traps were inspected monthly, and thus, one sample was obtained for each trap over 11 months, resulting in 220 samples. The monitoring of fauna in the MSS was conducted from September 2015 to July 2016, covering both the dry and wet seasons. The 20 sampling points were named MSS-01 to MSS-21. Sampling point MSS-10 was discarded due to being clogged with mud.



Fig. 2 Study site (a) showing the drilling of a hole in the rock (canga) (b), core material taken from the rock (canga) with small pores (c), and trap being installed (d)

The collected samples were transported to the laboratory, where they were sorted using a stereoscopic microscope and kept in 70% alcohol for preservation. The organisms were then grouped by morphospecies and identified at the lowest possible taxonomic level using dichotomous keys (Righi 1984; Brinkurst and Marchese 1989; Smithers 1990; Constantino 1999; Mahnert and Adis 2002; Krantz and Walter 2009; Carvalho et al. 2012; Duarte et al. 2012; Grandcolas and Pellens 2012; Grazia et al. 2012; Haas 2012; Melo et al. 2012; Monteiro and Mound 2012; Sperber et al. 2012; Terra and Agudelo 2012; Triplehorn and Johnson 2013; Baccaro et al. 2015). These organisms were then compared with reference collections of organisms found in caves in the same area. Once identified, the invertebrates were classified by specialists (see Acknowledgments) as either troglobiotic or non-troglobiotic species according to their morphological characteristics. Troglobiotic species represent populations restricted to the subterranean environment, identifiable by unique traits specific to exclusively subterranean species that are directly influenced by the subterranean selective conditions (Bichuette et al. 2015a; Trajano and Carvalho 2017). Thus, troglomorphy was used as the definition of troglobiotic organisms. Due to the lack of information on their life and evolutionary history, all other species with no such traits were grouped as non-troglobiotic organisms, even though some are likely subterranean-limited species (Culver and Pipan 2015). We also acknowledge that our database has limitations regarding to the identification of biological material, which often remained at the morphospecies level. Invertebrates are a very diverse group with a high potential for discovering new species, which makes the correct identification of many groups difficult (Eisenhauer and Hines 2021). This scenario is very common in studies in the MSS (Mammola et al. 2017), where new species are constantly discovered (Zeppelini et al. 2022).

Data analysis

Our sample design was discontinuous, comprising two distinct sets of sampling points due to access limitations (see Fig. 1). Three sampling points were separated from the others by a patch of vegetation. Besides, there is a variation in elevation among sampling points. Therefore, we first determined if location (two sets of sampling points) and elevation might have affected species composition among sampling points via Analysis of Similarities (ANOSIM). ANOSIM is a robust non-parametric statistical test widely used for testing for differences in compositional dissimilarities among groups of samples (Clarke 1993). Then, we assessed differences in species richness between these two sets of points and looked for effects of elevation on species richness. We used the *t*-test and Pearson's correlation for these purposes.

To calculate species richness and abundance, the number of morphospecies or individuals of invertebrates collected at each sampling point in each campaign was used. To avoid overestimating species richness, a juvenile taxon was only counted if there was no adult with a more precise identification at the same point and in the same campaign. Initially, the cumulative species richness was determined for each sampling month and for each of the 20 sampling points, as well as the species richness for each of the 11 sampling events at each point, resulting in a total of 220 samples. Then, we performed species accumulation curves for troglobiotic and non-troglobiotic species based on species abundance per site, season (dry and rainy) and for the entire period of sampling aiming to evaluate the sample completeness and compare profiles of species diversity. We estimated the same sample coverage (or completeness) by calculating the final slope of the species accumulation curves relating the increase in the number of species with the addition of individuals. The sample coverage based on the final curve slope is a measure of the inventory completeness and is carried out using Hill numbers ("true diversity" approach) (Chao et al. 2014; Hsieh et al. 2016). The sample size-based rarefaction and extrapolation curves (formerly species accumulation curves) were calculated for Hill numbers of q=0 (species richness) by doubling the reference sample (Chao et al. 2014; Hsieh et al. 2016). For extrapolated portions of the curves, the number of individuals was twice the actual reference size, as suggested by Chao et al. (2014). We estimated the sample coverage with 100 bootstrap replications and implemented these methods using the package "iNEXT" (Hsieh et al. 2016) of the R software (R Core Team 2023).

We used the Sorensen dissimilarity measure to determine the spatial and temporal variation in species composition between points in the MSS and between sampling months, separately for troglobiotic and non-troglobiotic species. The Sorensen coefficient was chosen because it emphasizes the importance of shared species between samples (Legendre 2014). Spatial β -diversity was used to measure the dissimilarity of species composition among the 20 MSS points, while temporal β -diversity was used to measure the variation in species composition at each sampling point over 11 months. We partitioned the spatial and temporal β -diversity values (using Sorensen dissimilarity) into species replacement and richness difference to determine which of these processes (species replacement or gain/loss) was the main driver of species composition of troglobiotic and non-troglobiotic species over space and time. The replacement component refers to the fact that species or individuals can be replaced by other species across ecological gradients (Legendre 2014). The richness difference component describes the pattern where one community may include a larger number of species than another (Legendre 2014). Since the Baselga approach (turnover and nestedness components) may not be suitable for calculating the species loss/gain component of β -diversity when there is not at least one species shared among all sites or samples, we used the Podani approach (replacement and richness difference components) (Legendre 2014; Schmera et al. 2020). The "beta.multi" function of the "BAT" package was used to calculate both β -diversity components for multiple locations or sampling periods and account for total dissimilarity (Cardoso et al. 2020).

Finally, we conducted a mixed generalized linear model (GLMM) analysis to compare the temporal variation of species composition between troglobiotic and non-troglobiotic invertebrates. The analysis used temporal β -diversity (Sorensen dissimilarity) as a response variable, as well as replacement and richness difference values per sampling point. The identity of the sampling points was treated as a random variable, since they were counted multiple times in the analysis of both troglobiotic and non-troglobiotic species (Bolker et al. 2009). We employed the Gaussian distribution of errors and assessed the residuals for normality and heteroscedasticity (Crawley 2013). After removing non-significant variables (*p*-value>0.05), we defined the minimal model. All statistical analyses were performed using the R software (R Core Team 2023).

Results

We sampled 22,821 individuals and 276 morphospecies belonging to two phyla: Annelida (S=1, N=23) and Arthropoda (S=275, N=22,798) (Table S1). Twenty-three main groups were recognized (from the most abundant to the least): Acariformes, Diptera, Hymenoptera, Blattodea, Collembola, Parasitiformes, Coleoptera, Araneae, Orthoptera, Pseudoscorpiones, Diplura, Psocodea, Palpigradi, Oligochaeta, Hemiptera, Dermaptera, Zygentoma, Diplopoda, Chilopoda, Lepidoptera, Thysanoptera, Mantodea, and Scorpiones (Table 1).

Acariformes (43.5%), Diptera (18%), Hymenoptera (15.3%), Blattodea (8.9%), and Collembola (6.5%) together represented 92.2% of the total individuals sampled. Nine troglobiotic morphospecies belonging to four groups were sampled: Araneae (Caponiidae; S=1) and Pseudoscorpiones (Chthoniidae; S=1) from Arachnida; Entomobryomorpha (2 Entomobryidae, 2 Paronellidae, 1 Isotomidae, 1 Oncopoduridae; S=6) and Poduromorpha (Tullbergiidae; S=1) from Collembola (Fig. 3). The troglobiotic morphospecies were sampled from 1 to 8 sites each (occurring in 14 of the 21 sites sampled). Similar number of species and individuals of troglobiotic species were found between the dry and rainy seasons, while we found 1.8 and 1.2 times more individuals and species of non-troglobiotic species during the rainy season (Table 2; Fig. 4). The sample coverage was higher than 94.1% for all periods (each season and the entire sampling period) for both groups. Per MSS, the sampling coverage varied between 33.3 and 100% for troglobiotic species, and between 95.7 and 99.2% for non-troglobiotic species (Table 1).

Our first assessment showed that troglobiotic species (ANOSIM statistic R=0.073, p-value=0.379, permutations=999) and non-troglobiotic species (ANOSIM statistic R=0.231, p-value=0.120, permutations=999) had no differences in species composition

Higher taxonomic levels	Group	Group Number of morphospecies (%)	
Annelida Clitellata	Oligochaeta	1 (0.004)	23 (0.0010)
Arthropoda Arachnida	Acariformes	31 (0.112)	9,915 (0.4345)
Arthropoda Arachnida	Araneae	25 (0.091)	105 (0.0046)
Arthropoda Arachnida	Parasitiformes	8 (0.029)	680 (0.0298)
Arthropoda Arachnida	Pseudoscorpiones	4 (0.014)	57 (0.0025)
Arthropoda Arachnida	Palpigradi	2 (0.007)	32 (0.0014)
Arthropoda Arachnida	Scorpiones	1 (0.004)	1 (0.00001)
Arthropoda Chilopoda	Scolopendromorpha	2 (0.007)	4 (0.0002)
Arthropoda Collembola	Collembola	30 (0.109)	1,488 (0.0652)
Arthropoda Diplopoda	Diplopoda	3 (0.011)	6 (0.0003)
Arthropoda Diplura	Diplura	3 (0.011)	52 (0.0023)
Arthropoda Insecta	Hymenoptera	50 (0.118)	3,487 (0.1528)
Arthropoda Insecta	Diptera	47 (0.170)	4,108 (0.1800)
Arthropoda Insecta	Coleoptera	32 (0.116)	676 (0.0296)
Arthropoda Insecta	Blattodea	9 (0.033)	2,024 (0.0887)
Arthropoda Insecta	Hemiptera	8 (0.029)	12 (0.0005)
Arthropoda Insecta	Dermaptera	5 (0.018)	12 (0.0005)
Arthropoda Insecta	Orthoptera	5 (0.018)	83 (0.0036)
Arthropoda Insecta	Psocodea	5 (0.018)	40 (0.0018)
Arthropoda Insecta	Lepidoptera	2 (0.007)	3 (0.0001)
Arthropoda Insecta	Mantodea	1 (0.004)	1 (0.00001)
Arthropoda Insecta	Thysanoptera	1 (0.004)	2 (0.0001)
Arthropoda Insecta	Zygentoma	1 (0.004)	10 (0.0004)
Total		276	22,821

 Table 1
 Number of morphospecies and individuals of invertebrates sampled in the canga MSS. Percentages

 (%) in relation to the observed values are in parentheses

between two sets of sampling points. T-tests also showed no differences in mean species richness between the two sets of sampling points for troglobiotic species (t=0.652, df=2.575, p-value=0.568) and non-troglobiotic species (t=-0.059, df=2.414, p-value=0.957). Also, we found no correlation between MSS elevation and species richness for both groups (troglobiotic species: Pearson statistic R = -0.0395, t = -0.1369, df=12, p-value=0.893; non-troglobiotic species: Pearson statistic R = -0.195, t = -0.845, df=18, p-value=0.409). Such results ensure that the dataset can be evaluated as a robust and representative sample of the canga MSS.

We found a high dissimilarity in the composition of troglobiotic and non-troglobiotic species, both between sampling points (spatial β -diversity) and between sampling months (temporal β -diversity) (Fig. 5). However, we found that the spatial variation in the composition of the troglobiotic species sampled in the MSS is greater than the spatial variation of non-troglobiotic species, and the temporal variation considering both groups (Fig. 5). The component of richness difference contributes more to spatial and temporal β -diversity for troglobiotic species, while we observed higher replacement values for non-troglobiotic species (Fig. 5).

We also found that average values of temporal β -diversity (Sorensen dissimilarity) and the replacement component were greater for non-troglobiotic species than for troglobiotic



Fig. 3 Troglobiotic morphospecies sampled in the canga MSS: (a) Araneae: juvenile Caponiidae; (b) Pseudoscorpiones: *Pseudochthonius* sp. 1; Collembola: (c) *Folsomina* sp. 2; (d) *Oncopodura* sp. 1; (e) *Pseudosinella* sp. 1; (f) *Trogolaphysa* sp. 2; (g) *Trogolaphysa* sp. 6; (h) *Pseudosinella* sp. 5; (i) *Tullbergia* sp. 1

Table 2 Summary of number of morphospecies, number of individuals, and sample coverage for troglobiotic
and non-troglobiotic species per site, season, and the entire sapling period. Sample coverage (or complete-
ness) was calculated as the final slope of the species accumulation curves relating the increase in the number
of species with the addition of individuals

species individuals coverage Troglobiotic species MSS-01 3 4 0.625 MSS-02 5 22 0.959 MSS-03 1 2 1.000 MSS-06 1 1 1.000 MSS-06 1 1 1.000 MSS-11 4 5 0.486 MSS-12 2 2 0.667 MSS-15 2 8 1.000 MSS-15 2 8 1.000 MSS-15 2 8 1.000 MSS-15 2 8 1.000 MSS-15 2 3 0.833 MSS-15 10 0.836 Dry season 8 50 0.941 Rainy season 7 51 1.000 MSS-02 77 1.396 0.982 MSS-03 42 5.16 0.957 MSS-04 54 1.542 0.983 MSS-0	Group	Site/Period	Number of	Number of	Sample
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Rainy season 7 51 1.000 All year 9 101 0.980 Non-troglobiotic species MSS-01 54 1.357 0.983 MSS-02 77 1.396 0.982 MSS-03 42 5,16 0.957 MSS-04 54 1.542 0.983 MSS-05 54 1,102 0.983 MSS-06 34 1,409 0.991 MSS-07 43 674 0.975 MSS-08 59 2,240 0.991 MSS-09 32 1,051 0.987 MSS-11 52 629 0.971 MSS-12 42 1,713 0.992 MSS-13 48 1,108 0.991 MSS-14 45 947 0.987 MSS-15 51 1,232 0.984 MSS-17 34 504 0.970 MSS-19 52 1,261 0.987 MSS-20 37<		Dry season	8	50	0.941
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MSS-15511,2320.984MSS-16521,7760.988MSS-17345040.970MSS-18621,0470.984MSS-19521,2610.987MSS-20375870.978MSS-21546290.965Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-14	45	947	0.987
MSS-16521,7760.988MSS-17345040.970MSS-18621,0470.984MSS-19521,2610.987MSS-20375870.978MSS-21546290.965Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-15	51	1,232	0.984
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MSS-18621,0470.984MSS-19521,2610.987MSS-20375870.978MSS-21546290.965Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-17	34	504	0.970
MSS-19521,2610.987MSS-20375870.978MSS-21546290.965Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-18	62	1,047	0.984
MSS-20375870.978MSS-21546290.965Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-19	52	1,261	0.987
MSS-21546290.965Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-20	37	587	0.978
Dry season1598,0090.994Rainy season18814,7110.996All year26722,7200.997		MSS-21	54	629	0.965
Rainy season18814,7110.996All year26722,7200.997		Dry season	159	8,009	0.994
All year 267 22,720 0.997		Rainy season	188	14,711	0.996
		All year	267	22,720	0.997



Fig. 4 Sample-size based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves with 95% confidence intervals (shaded areas) for troglobiotic (upper panels) and non-troglobiotic (lower panels) invertebrate fauna. Left panels show curves for the total set of samplings and for each season. Central and right panels show curves for each MSS divided into sets of 10 sites or less for best viewing





species (Sorensen: $\chi^2 = 47.115$, p < 0.001; Replacement: $\chi^2 = 464.6$, p < 0.001; Fig. 6a,b). However, the richness difference component was greater for troglobiotic than for non-troglobiotic species ($\chi^2 = 4.823$, p = 0.0281, Fig. 6c).

Discussion

The communities associated with IF have as a striking feature the dominance of species with interstitial habits, which prefer to shelter in crevices, spaces under rocks or other interstitial spaces (Souza-Silva et al. 2011; Ferreira et al. 2018). When microhabitats such as the MSS are investigated, a great deal of species richness is revealed (Ledesma et al. 2020; Eusébio et al. 2021), as we observed in this study. The evaluation of biodiversity patterns in the MSS is challenging (Ledesma et al. 2020) and the sampling work is difficult, with a predominance of low-prevalence species (Jiménez-Valverde et al. 2015; Ledesma et al. 2019). This is demonstrated by a high spatiotemporal heterogeneity and moderate-to-low connectivity between species sets in the MSS (Růžička and Klimeš 2005; Giachino and Vailati 2010; Jiménez-Valverde et al. 2015), which may explain the high values of β -diversity, even for subterranean specialist species.

When evaluating the components of β -diversity, as already described by Soininen et al. (2018) for several groups and ecosystems, we found that replacement was the main process for both spatial and temporal β -diversity of non-troglobiotic fauna. Such a result can be justified by the fact that a significant proportion of the arthropod species that are collected in the MSS may be exogenous elements (Nitzu et al. 2014; Jiménez-Valverde et al. 2015; Mammola et al. 2016; Ledesma et al. 2019), transient fauna that occasionally inhabit the MSS or that do not depend on the MSS as the main habitat or source of resources for the completion of their life cycle (Ledesma et al. 2020). Despite being richer and more abundant than troglobiotic species, this fauna shows a significantly higher species replacement across MSS sites and collection months. On the other hand, for troglobiotic animals, we found that changes in species richness was the predominant process for both spatial and temporal β -diversity, with high contribution found when we evaluated the MSS spatially. This suggests a moderate-to-low ecological connectivity between sets of MSS, with troglobiotic species being more or less richer in these sites, but not necessarily in a nested pattern (Legendre 2014) since none of the troglobiotic species was found in all MSS sites or in



Fig. 6 Temporal β -diversity (Sorensen dissimilarity; **a**) and its components of species replacement (**b**) and richness difference (**c**) between troglobiotic and non-troglobiotic species. Asterisk (*) indicates that the difference between troglobiotic and non-troglobiotic is significant (p < 0.05)

all months sampled. This is a surprising result since the troglobiotic fauna have specific adaptations to the subterranean environment, such as the canga MSS. Another factor that may justify such compositional pattern would be the inability to sample the entire MSS layer, since we limited the sampling to 1 m depth. In harsh environments such as the high mountain canga surface, arthropods must develop different strategies to avoid adverse environmental conditions found closer to the surface, and the selection of microhabitats through vertical movements, beyond the layer that was possible to sample, is a common adaptive behavior (Dowdy 1944; May 1979). These deeper habitats possess specific microclimatic features which differ from those of surface habitats (Romero 2009; Culver and Pipan 2014). Although we used a standardized method developed to sample the invertebrate fauna present in the MSS (López and Oromí 2010), like all passive collection methods, this type of sampling has limitations in terms of selecting individuals, favoring the sampling of more active organisms or those largely attracted to the bait, while repelling others due to the use of some preservative fluid (Schmidt et al. 2006; Jureková et al. 2021; Mendonca et al. 2023). Thus, even with robust results, further investigations are needed to elucidate the distribution patterns found for the troglobiotic fauna inhabiting the canga MSS.

Tropical subterranean environments experience great seasonal oscillation, which influences the dynamics of the subterranean environments (Trajano 2000). The canga MSS is located in a region with a marked seasonality in both temperature and precipitation regimes (INMET 2022). Some studies have demonstrated that the floristic composition of canga could vary between dry and wet seasons (Skirycz et al. 2014), which can influence the input of organic matter into the MSS. Both flora and fauna of canga are exposed to high ultraviolet exposure, high daily temperatures, rapid water loss, strong winds, and poorly developed soil cover (Jacobi et al. 2007). Therefore, the canga MSS may be subjected to strong environmental variability among seasons, which may explain the temporal patterns of β -diversity of both groups of invertebrates. There is a high compositional change over the months in the canga MSS, but that does not translate into changes in the total richness observed between the dry and rainy seasons. It is expected that over its depth and over time, microclimatic conditions change in the MSS, and species may become associated with different microhabitats throughout the year (Lunghi et al. 2017). Thus, the MSS emerges as a refuge for the arthropod fauna (Ledesma et al. 2020), allowing the survival of many species avoiding the unfavorable surface conditions. Furthermore, nutrient availability is another crucial limiting factor in the MSS (Gers 1998). The main form of energy input into the system is by the infiltration of water and organic matter or by the active vertical movement of animals from the most superficial layers (Juberthie et al. 1980; Gers 1998). Thus, the presence of surface vegetation can contribute a substantial amount of resources to the MSS, which can have a determining influence on biodiversity patterns in this environment (Rendoš et al. 2016). In the evaluated canga MSS, there is a difference between sampling points more or less close to shrubby vegetation, most of which are dominated by grassy vegetation. Evaluating the presence of, or distance to, shrubby vegetation at MSS points may provide insights into possible effects on the spatiotemporal patterns of the fauna inhabiting there.

As the MSS is understood as an extension of the cave environment, when discussing the preservation of caves and biodiversity, it must be understood that the MSS is also part of the subterranean environment and must be included in the conservation measures. The legal definition of cave in Brazil considers only subterranean spaces accessible to humans (Brasil 2022), although there are studies that consider other spaces in the hypogean environment,

including meso- and micro-cavities, accessible to many small animals, especially invertebrates (e.g., Juberthie et al. 1980; Culver and Pipan 2009; Pipan and Culver 2012). The existence of such spaces is directly related to the lithology, because the more compact and less porous the rock formation, the smaller the capacity for animals to move between the caves. Caves in IF tend to present a greater porosity when compared to several other rock types. The Brazilian legislation establishes the delimitation of a buffer area necessary to ensure the physical integrity and maintenance of the ecological balance of caves and there are guidelines for delimiting such areas (ICMBio/CECAV 2022). Among the criteria, the use of troglobiotic species as "biological tracers" is suggested to understand the connectivity of the subterranean system and the extent of this connection, by mapping the dispersion of these species. In the event that there is no sharing of troglobiotic species, physical connections between the caves can act in this regard. Our study demonstrates a great heterogeneity in the distribution of troglobiotic animals in the MSS of IF, a system totally integrated to the caves. This finding may question the use of the criterion of "biological tracers" as evidence of the connectivity of the subterranean system based solely and exclusively on the presence of troglobiotic species in caves or MSS, even with the expected natural connectivity of the environment, considering the physical characteristics of the rock (Auler et al. 2022). However, even if a high spatial heterogeneity was demonstrated in the composition of this fauna, this, by itself, does not mean that there would or would not be evidence of gene flow between populations of the same species, since the data tested belong exclusively to the superficial layer of the MSS. Furthermore, although some studies have discussed that IF caves with more troglobiotic species have lower species replacement values, considering them more ecologically "stable" (Di Russo et al. 1997; Mammola et al. 2019), contrary to our expectations, the values of total β -diversity in the MSS were high for both troglobiotic and non-troglobiotic animals. This fact reinforces the idea of moderate-to-low ecological connectivity between the sampling sites in the MSS, even if the environment presents favorable conditions for the evolution and permanence of the fauna. As shown by the study of diversity over time and space, another important factor that can be discussed is the superficiality of this system, which is very close to the surface and is subject to the instabilities of the surface environment, such as changes in temperature and humidity (Culver and Pipan 2014; Niemiller et al. 2018). Such a characteristic may explain the high change in non-troglobiotic species composition, since the animals may be using the MSS only as a passage to enter more stable environments inside the rock.

We consider it important to mention that the species composition was evaluated aiming to demonstrate the ecological connectivity of the subterranean system, subsidizing the conservation of important areas for the maintenance of species, mainly those specific to such system, such as troglobiotic species. β -diversity studies are instructive in the context of biodiversity conservation and help in decision-making for the management of changing environments (Gossner et al. 2016). Furthermore, comparing patterns of β -diversity across different cave-associated groups, habitats, and geographic contexts has the potential to contribute greatly to understanding the factors underlying spatial variation in ecosystem functionality and shed light on how environmental changes can affect the ecology of subterranean communities (Graco-Roza et al. 2022). This is particularly important to iron-rich formations subjected to ongoing pervasive threats (Salles et al. 2019; Souza-Filho et al. 2019).

Conclusions

In summary, we found high values of variation in spatial and temporal composition of troglobiotic and non-troglobiotic invertebrate communities in canga MSS, and this pattern proved to be dynamic, much more than expected for troglobiotic species. Furthermore, we found greater temporal stability of troglobiotic species composition compared to non-troglobiotic fauna, although each group showed different dominant process driving the changes in invertebrate composition in the MSS. Despite the actual connection between the pores of the canga MSS, these results suggest a moderate-to-low ecological connectivity or a certain degree of isolation of the subterranean fauna based on the species composition sampled in the MSS, given the high β -diversity in space and time. Relying solely on the distribution criterion of troglobiotic species as evidence of subterranean connectivity of species can be understood as an inconsistent argument. Considering all the complexity of the subterranean environment, as well as the processes responsible for the evolutionary dynamics and ecological balance of the hypogean environment, it is worth pointing out the crucial importance of preserving the MSS for keeping the dynamics of the cave and surrounding ecosystems. However, there is a great dynamic between the MSS and the external environment, whose conservation is also necessary to maintain the balance of the cave environment and the surroundings as a whole.

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Author contributions LMSMD: Conceptualization (supporting); Data collection (lead); Data curation (lead); Visualization (supporting); Writing—original draft (lead); Methodology (lead). PGdS: Writing—original draft (lead); Data curation (supporting); Visualization(lead); Methodology (supporting); Formal analysis (lead). MEB: Conceptualization (supporting); Writing—original draft (supporting); Supervision (lead). ASA: Conceptualization (lead); Writing—original draft (lead); Visualization (supporting); Supervision (lead). ASA: Conceptualization (lead); Writing—original draft (lead); Visualization (supporting); Supervision (lead). DCC: Writing—original draft (supporting). TP: Writing—original draft (supporting). LOP: Writing—original draft (supporting). FSN: Conceptualization (supporting); Writing—original draft (supporting); Methodology (supporting); Formal analysis (supporting); Supervision (lead). All authors read and approved the final manuscript.

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Data availability The datasets analyzed during the current study are provided as supplementary materials.

Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Lígia Maria Saback Moreira Dornellas^{1,2} · Pedro Giovâni da Silva^{1,2} · Maria Elina Bichuette³ · Augusto S. Auler² · David C. Culver⁴ · Tanja Pipan⁵ · Lorena Oliveira Pires⁶ · Frederico de Siqueira Neves¹

Lígia Maria Saback Moreira Dornellas ligia.moreira@carste.com.br

- ¹ Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais 31270-901, Brazil
- ² Instituto do Carste/Carste Ciência Ambiental, Belo Horizonte, Minas Gerais 31275-090, Brazil
- ³ Laboratório de Estudos Subterrâneos, Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, São Carlos, São Paulo 13565-905, Brazil
- ⁴ Department of Environmental Science, American University, Washington, DC 20016, USA
- ⁵ Karst Research Institute at Research Centre of the Slovenian Academy of Sciences and Arts, Postojna 6230, Slovenia
- ⁶ Anglo American Minério de Ferro Brasil, Belo Horizonte, Minas Gerais 30360-740, Brazil