CECAV
CENTRO NACIONAL DE PESQUISA E CONSERVAÇÃO DE CAVERNAS
ICMBio-MMA

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

Who´s inside, and who´s outside? Habitat structure determines the richness and composition of invertebrates in quartzite caves and surrounding habitats

Felipe Carvajal Jordão
Programa de Pós-graduação em Ecologia Aplicada,
Universidade Federal de Lavras, Minas Gerais, Brasil
E-mail: carvajal.fj1@gmail.com

Gabrielle Soares Muniz Pacheco
Vale S.A., Espeleologia e Tecnologia de Ferrosos, Pará, Brasil
E-mail: gabrielle.pacheco@hotmail.com

Rodrigo Lopes Ferreira
Centro de Estudos em Biologia Subterrânea (CEBS), Departamento de Ecologia e Conservação,
Universidade Federal de Lavras, Minas Gerais, Brasil
E-mail: drops@ufla.br

Marconi Souza Silva
Centro de Estudos em Biologia Subterrânea (CEBS), Departamento de Ecologia e Conservação,
Universidade Federal de Lavras, Minas Gerais, Brasil
E-mail: marconisilva@dbi.ufla.br

RESUMO: Nos últimos anos, estudos têm buscado compreender como as estruturas físicas e ambientais dentro das cavernas influenciam as comunidades de invertebrados. No entanto, ainda há uma escassez de pesquisas que explorem como a composição do substrato e a heterogeneidade do habitat influenciam as comunidades faunísticas em cavernas de quartzito e em áreas epígeas adjacentes, apesar da importância de entender essas relações ecológicas para embasar estratégias eficazes de conservação. Este estudo avaliou a similaridade das comunidades de invertebrados entre cavernas de quartzito e habitats de superfície circundantes, bem como as variáveis ambientais que influenciam a composição e a riqueza faunística. O estudo foi conduzido em três sistemas cavernícolas de quartzito, com amostragens realizadas no interior das cavernas e em zonas epígeas adjacentes. Os resultados revelaram dissimilaridade na composição faunística entre os ambientes subterrâneo e de superfície, enquanto as comunidades dentro das cavernas apresentaram maior similaridade entre si. A substituição de espécies foi identificada como o principal componente da diversidade βsør total entre os dois ambientes. As composições faunísticas distintas observadas são impulsionadas por filtros ambientais, sendo que as condições restritivas das cavernas limitam a colonização e favorecem invertebrados especializados. Além disso, variáveis distintas de substrato emergiram como fator-chave na estruturação das comunidades, com detritos vegetais influenciando a fauna epígea, e guano e substratos inorgânicos estruturando a fauna cavernícola. Esses achados avançam a compreensão da dinâmica dos ecossistemas subterrâneos, destacando a importância das características do habitat na formulação de estratégias de conservação da biodiversidade.
Palavras-chave: invertebrados cavernícolas; similaridade; heterogeneidade de habitat; Neotrópicos

ABSTRACT: In recent years, studies have aimed to understand how physical and environmental structures within caves influence invertebrate communities. However, there is still a lack of research exploring how substrate composition and habitat heterogeneity influence faunal communities in

CECAV CENTRO NACIONAL DE PESQUISA E CONSERVAÇÃO DE CAVERNAS ICMBio-MMA
Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

quartzite caves and adjacent epigean areas, despite the importance of understanding these ecological relationships to inform effective conservation strategies. This study evaluated the similarity of invertebrate communities between quartzite caves and surrounding surface habitats, as well as the environmental variables influencing faunal composition and richness. The study was conducted across three quartzite cave systems, with sampling carried out within the caves and in adjacent epigean zones. Results revealed dissimilarity in faunal composition between subterranean and surface environments, while communities within caves exhibited higher similarity. Species turnover was identified as the primary component of total βsør-diversity between the two environments. The distinct faunal compositions observed are driven by environmental filters, with restrictive cave conditions limiting colonization and favoring specialized invertebrates. Additionally, distinct substrate variables emerged as a key driver of community structure, with plant debris influencing epigean fauna, and guano and inorganic substrates structuring cave fauna. These findings advance understanding of subterranean ecosystem dynamics, highlighting the importance of habitat features in informing biodiversity conservation strategies.
Keywords: cave invertebrates; similarity; habitat heterogeneity; Neotropics.

1. INTRODUCTION

Variations in habitat heterogeneity have been widely used to explain species diversity in both natural and human-modified environments (MacArthur & MacArthur, 1961; Tews et al., 2004; Previati et al., 2007; Souza et al., 2014). Heterogeneity, driven by variations in environmental conditions and resources, directly influences species diversity by expanding ecological niche availability (MacArthur & MacArthur, 1961; Pianka, 1966; Magurran, 2013). Additionally, heterogeneity has been instrumental in clarifying community structuring across different taxonomic groups, as its effects can vary based on species-specific habits and traits (MacArthur & MacArthur, 1961; Atauri & Lucio, 2001; Travassos-de-Britto & da Rocha, 2013; Stein et al., 2014). Thus, substrate diversity and habitat heterogeneity play critical roles in facilitating the coexistence of multiple organism groups within a given area (MacArthur & Levins, 1967; May, 1986).

In recent years, numerous studies have explored how substrate diversity and habitat heterogeneity influence fauna composition in cave environments (Prous et al., 2015; Pellegrini et al., 2016; Pacheco et al., 2020a; Souza-Silva et al., 2021; Reis-Venâncio et al., 2022). However, relatively few have examined the contrasting roles of hypogean (subterranean) and adjacent epigean (surface) environments in shaping invertebrate community structures (Mendes-Rabelo et al., 2021; Cardoso et al., 2022; Pacheco et al., 2025).

Different types of substrates and the availability of trophic resources are crucial factors enabling invertebrate colonization in cave environments (Mammola et al., 2016; Zagmajster et al., 2018). Caves are generally more stable than surface environments and are characterized by constant temperature, high humidity, and the absence of light (Barr, 1968; Poulson & White, 1969; Culver, 1982; Badino, 2010; Mammola et al., 2019a). Allochthonous organic resources, primarily plant or animal matter, provide the primary energy source for caves, transported through physical processes like water flow, wind, and gravity or introduced by animals in the form of feces, guano, and carcasses. These resources are vital nutrient sources for cave fauna and play a fundamental role in the trophic dynamics of these ecosystems (Poulson & White, 1969; Simon et al., 2007; Culver & Pipan, 2019; Souza-Silva et al., 2011; Souza-Silva et al., 2013).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

Research on the influence of substrate types and habitat heterogeneity in cave fauna has predominantly focused on limestone caves (Prous et al., 2015; Pellegrini et al., 2016; Pacheco et al., 2020a; Furtado et al., 2022). However, for quartzite caves, there remains a significant research gap regarding the role of these variables in shaping community structures. Studies on quartzite caves to date have addressed trophic ecology, physical characteristics, and the impact of lithology on cave fauna organization (Souza-Silva et al., 2013, 2020a, 2020b). Nonetheless, few studies have investigated how substrate types and habitat heterogeneity influence invertebrate communities within both caves and nearby epigean habitats or examined the similarity between the fauna in these environments (Prous et al., 2004; 2015; Mammola et al., 2016; Oliveira & Ferreira, 2024; Pacheco et al., 2025).

This study aimed to investigate the similarity of fauna between caves and the surrounding epigean habitats. Additionally, we sought to assess the environmental parameters that influence fauna composition and richness in a system comprising three interconnected quartzite caves linked by intermittent drainage and their adjacent epigean habitats.

We hypothesize that the epigean fauna adjacent to the caves will show greater species richness and a distinct composition compared to the cave-dwelling fauna due to the colonization constraints imposed by the trophic and microclimatic conditions within the caves. We expect that the cave fauna represents a subset of the epigean fauna. Furthermore, the distance from the entrance of the first cave to the remaining caves (in the upstream to downstream direction) is anticipated to be a key factor in determining species composition and richness throughout the cave system. Finally, we expect that due to differences in habitat structure, the environmental variables influencing the composition and richness of the epigean fauna near the caves will differ from those affecting the cave fauna.

2. METHODOLOGY

Study area

This study was conducted in Andrelândia, situated in the southern region of Minas Gerais, southeastern Brazil. It focuses on a system of three interconnected quartzite caves (Gruta Cabeça de Vaca, Gruta Barra, and Gruta João Japonês) linked by intermittent drainage (Fig. 1). These caves are located within the Andrelândia Quartzite Speleological Province, part of the Andrelândia Group, which is characterized by rocks belonging to the Andrelândia Megasequence (Corrêa-Neto, 1997). The study area is situated in the Atlantic Forest biome, which has significantly degraded agricultural and pastoral activities. As a result, only a few fragments of forest remain near the three caves, with most of the surrounding land being used for grazing. Gruta Cabeça de Vaca (UTM 23 L: 565534.22 – 7592086.46) has four entrances and a linear extent of 53 meters. Gruta Barra (UTM 23 L: 565557.27 – 7592026.41) has two entrances and a linear extent of 45 meters. Gruta João Japonês (UTM 23 L: 565609.90 – 7591985.42) also features two entrances, with a linear extent of 52 meters (Figure 1).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

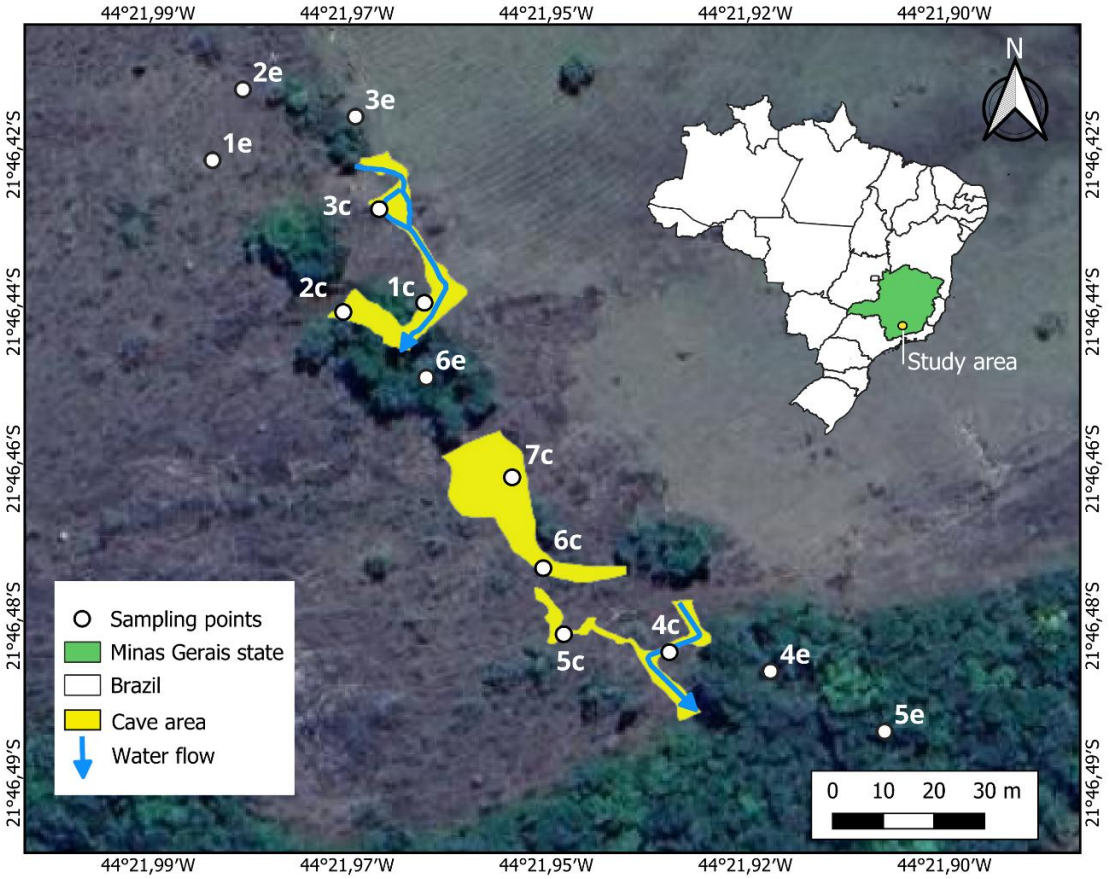

Figure 1. The study area and cave are in the municipality of Andrelândia, Minas Gerais, Brazil. The letters 'e' indicates epigean sampling points, and 'c' indicates cave sampling points.

Sampling

Biotic and abiotic data were collected during a single sampling event on June 16 and 17, 2022. The sampling units were arranged in transects, each measuring ten meters long and comprising three quadrants, each 1 m^2 in size, positioned at least five meters apart. Six transects were sampled in the epigean area adjacent to the caves, encompassing 18 quadrants. In comparison, seven transects were sampled within the caves, resulting in 21 quadrants. Sampling was conducted exclusively within these quadrants.

A modified sampling methodology was adapted from Souza-Silva et al. (2021), Pacheco et al. (2025). Invertebrates were actively collected by hand for 10 minutes per quadrant using forceps and brushes. The collected samples were placed in containers filled with 70% ethanol and are currently deposited in the subterranean invertebrate collection (ISLA) at the Federal University of Lavras (https://www.biologiasubterranea.com.br/pt/).

Invertebrates were sorted, identified to the most accessible taxonomic level, and grouped into morphotypes with the aid of stereomicroscopes, following the methodologies outlined by Oliver & Beattie (1996), Derraik et al. (2002), Derraik et al. (2010), and Pellegrini et al. (2016).

To document the habitat's structural characteristics, we took photographs at chest height, positioning the camera at a 90-degree angle to each quadrant. Subsequently, these photographs were analyzed using ImageJ software (Rasband, 1997) to characterize the substrate types and quantify their coverage area in each quadrant (Pacheco et al., 2020b; Furtado et al., 2022).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

The substrate types analyzed included guano, green plants, plant debris, rocks (250–500 mm), blocks (64–250 mm), fine gravel (2–16 mm), coarse gravel (17–63 mm), sand, silt (0.2–0.05 mm), bedrock, and hardpan.

Data analysis

Abiotic data

To evaluate the differences in substrate types between the epigean area and the caves, we compared the percentage coverage of each substrate within the quadrants using a one-way ANOVA non-parametric test (Kruskal-Wallis). A similarity analysis (ANOSIM) was performed to determine whether there were differences in substrate composition between the epigean and cave environments, utilizing a Bray-Curtis similarity matrix (Clarke, 1993). The Kruskal-Wallis and ANOSIM analyses were conducted using R software (R Core Team, 2025).

Based on habitat characteristics and resources, the substrates were categorized into five variables: Guano, Green Plants, Plant Debris, Shelter (rocks 250-500 mm, blocks 64-250 mm, fine gravel 2-16 mm, coarse gravel 17-63 mm), and Inorganic Substrate (hardpan, sand, silt 0.2-0.05 mm and bedrock). A shade plot was generated to visualize the distribution of these environmental substrate variables in both the epigean area and the caves.

Biotic data

Species richness was assessed by adding the morphotypes identified in each area. We evaluated the normality of the data using the Shapiro-Wilk test ($p = 0.001$) and examined the variance among groups with Levene's test for homogeneity of variances ($p = 0.011$). Since the data did not conform to a normal distribution and the variances between the sampled groups were unequal, we employed the non-parametric Mann-Whitney U test to explore differences in richness between the epigean and cave environments (Levene, 1960; Shapiro and Wilk, 1965; Sprent & Smeeton, 2000). The Mann-Whitney U statistical analysis was performed using Jamovi software (2023), with a significance level set at $p < 0.05$.

To investigate differences in faunal group composition between the epigean and cave environments, we conducted a similarity analysis (ANOSIM) employing the Bray-Curtis similarity index, with the locations (epigean and caves) serving as the grouping factor (Clarke, 1993). Additionally, to compare the composition of faunal groups among the caves, we carried out another similarity analysis (ANOSIM), using the caves as the grouping factor and also utilizing the Bray-Curtis similarity index (Clarke, 1993).

To illustrate variations in faunal similarity between the epigean and cave environments and among the caves we employed non-metric multidimensional scaling (MDS) in conjunction with a Bray-Curtis similarity matrix.

Spatial β-diversity was calculated for each quadrant based on differences among sampling points within each environment using the βsør index. This index was partitioned into its two additive components, turnover (βsim) and nestedness (βsne), ranging from 0 (0%) to 1 (100%), thereby representing their contributions to the total βsør turnover. The turnover component captures species replacement between sites, while nestedness reflects patterns where the species composition of one site constitutes a subset of another.

To evaluate whether turnover constitutes the dominant component of total βsør-diversity, beta regression models were employed, using βsim and βsne as explanatory variables. Statistical significance was determined through Type III Analysis of Variance (ANOVA), and the relative

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

effects of each component were visualized using boxplots comparing chi-square (χ^2) statistics associated with turnover and nestedness.

All β-diversity analyses were conducted in RStudio version 4.3.3 (R Core Team, 2025). Type III ANOVAs were performed using the *car* package (Fox et al., 2012), and visualizations were generated with *tidyverse*. The βsør index and its components were calculated using the *betapart* package (Baselga, 2010), while beta regression models were fitted with the *betareg* package (Cribari-Neto & Zeileis, 2010).

To assess how habitat components influence faunal composition in epigean and cave environment, we utilized distance-based linear models (DistLM) (Anderson et al., 2008). The substrate variables considered included Guano (GUA), Green Plants (GP), Plant Debris (PD), Shelter (SH), and Inorganic Substrate (IS). Additionally, we incorporated substrate diversity (SD) for each quadrant, which was calculated using the Shannon Index (H') (Magurran & McGill, 2010). The SD value was derived from all components present in the substrate of the quadrants, allowing for an assessment of substrate diversity in the areas where collections occurred (modified from Pacheco et al., 2020a; Cardoso et al., 2022). Statistical models in DistLM were constructed using the Bray-Curtis species similarity matrix and a forward selection procedure, employing adjusted R^2 as the criterion for model selection, and we performed 999 permutations (Anderson et al., 2008).

The adjustments and explanatory power of the models for the variation in composition data were assessed using distance-based redundancy analysis (dbRDA) (Clarke & Gorley, 2006; Anderson et al., 2008). ANOSIM and DistLM analyses for the faunal data were performed using the statistical software Plymouth Routine in Multivariate Ecological Research - Primer 7 + Permanova Software (Anderson et al., 2008), available at https://www.primer-e.com/. A significance level of $p < 0.05$ was adopted for the analyses.

We employed Generalized Linear Models (GLMs) to evaluate the influence of habitat components on the variation in invertebrate fauna richness in epigean and cave environments. The predictor variables included GUA, GP, PD, SH, IS, and SD. To assess collinearity among predictors, we calculated Spearman's correlation coefficients using the *chart.Correlation* function from the *PerformanceAnalytics* package (Peterson & Carl, 2020). Additionally, we applied Variance Inflation Factors (VIF) to exclude variables with VIF values greater than 3 (Zuur et al., 2013). For the epigean environment model, the variables SD and GP were excluded to avoid multicollinearity, as their pairwise correlation coefficient exceeded 0.70 (Schober et al., 2018). Furthermore, the variable GUA was removed from the analysis due to its absence in the epigean environment, rendering it uninformative for the model.

To ensure independence among variables, we further assessed multicollinearity diagnostics. The model was initially fitted using the Poisson distribution, and we employed the *simulateResiduals* function from the *DHARMa* package to test for overdispersion and the test Zero Inflation function to assess zero inflation in the model (Hartig, 2022). As the Poisson model exhibited overdispersion, we corrected the error structure by fitting a model using the negative binomial distribution.

The adjusted R^2 value was obtained using the *rsq* function from the *rsq* package. A significance level of $P \leq 0.05$ was adopted for all statistical tests. All GLM analyses were performed in R software (R Core Team, 2025).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

3. RESULTS

Substrate characteristics in the caves and epigean habitats

Eleven substrate categories were identified, including plant debris, green plants, block, bedrock, and silt, which were present in both the caves and the surrounding epigean areas. In contrast, guano, rock, fine gravel, coarse gravel, sand, and hardpan were found exclusively within the caves. In the epigean environment, the predominant substrate was "green plants," primarily comprising grasses (70.91%). The most frequently recorded component within the caves was "plant debris," found in 66% of the quadrants. However, the most abundant substrate was "hardpan," accounting for 22.90% of the total substrate collected across all quadrants in the caves (Figure 2A).

The Kruskal-Wallis test indicated a significant difference in substrate occupancy between the epigean and cave areas (KW = 4.64; p = 0.03) (Figure 3A). ANOSIM further revealed significant differences in substrate composition between the two environments, indicating a high degree of separation between the groups (GlobalR = 0.758; p = 0.001).

Among the environmental variables analyzed, the "green plants" category was the most abundant in the epigean environment, comprising 70.91% of the total sampled area, followed by "plant debris," which accounted for 24.07%. In contrast, within the cave environment, the "inorganic substrate" was the most prevalent, representing 50.42% of the total, followed by "shelter," which occupied 30.39% of the cave area (Figure 2B).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

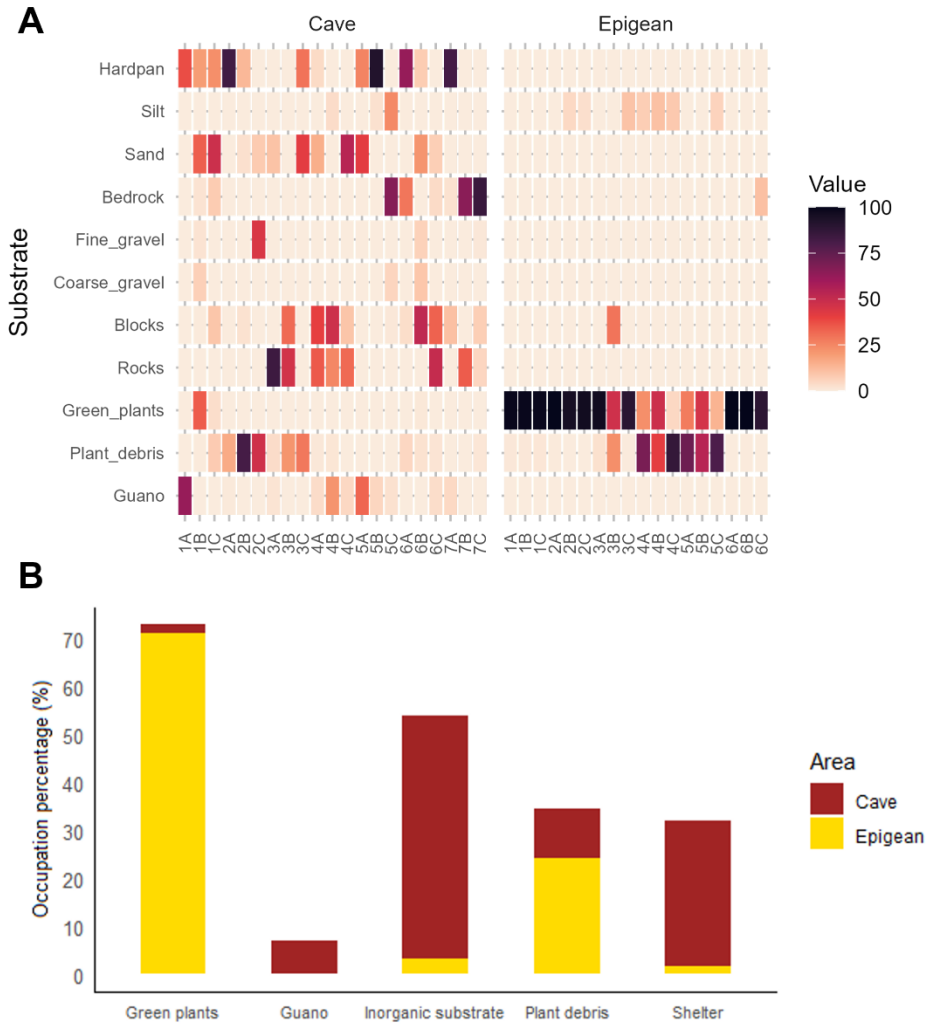

Figure 2. Shade plot showing the distribution and percentage of occupancy of different substrate types at each sampling area. Numbers 1 to 7 denote the collection stations, and letters A, B, and C indicate the quadrants (A). Percentage of substrate variables occupancy in epigean and cave environments, with the x-axis representing the variables and the y-axis representing the occupancy percentage of these variables in the respective regions (B).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

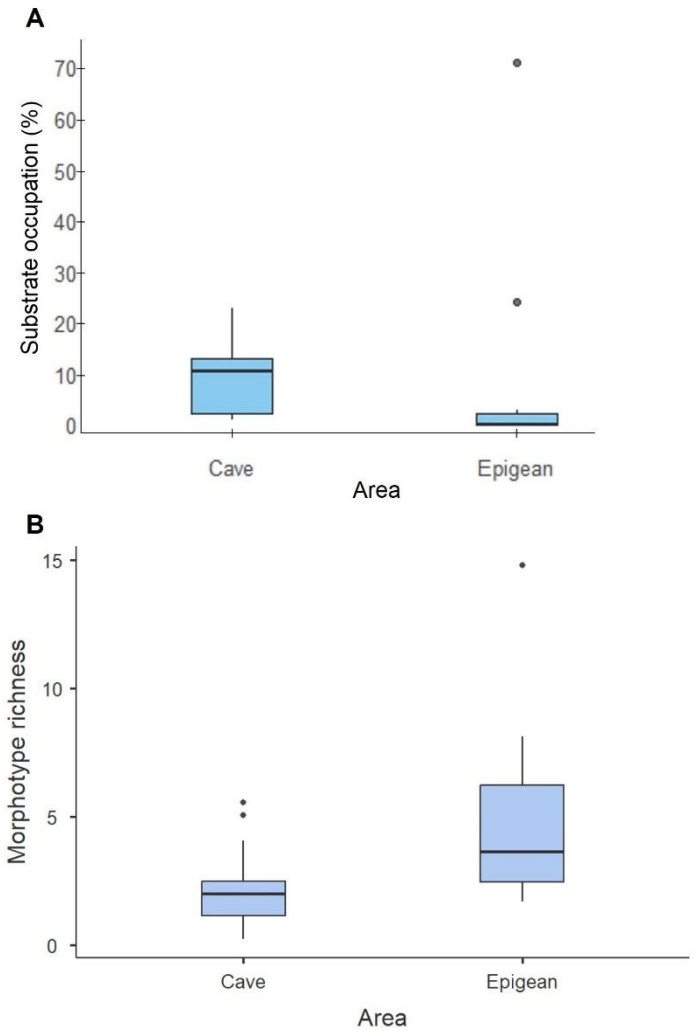

Figure 3. Average substrate occupancy percentage in cave and epigean areas (A). Average morphotype richness in the cave and epigean regions (B).

Invertebrate richness and composition among areas

A total of 310 individuals were recorded, representing 121 species. The most diverse taxa included Hymenoptera (23 species), Araneae (22 species), and Coleoptera (17 species) (Supplementary material).

The epigean environment exhibited greater species richness, with 85 species and 186 individuals, compared to the cave environment, which contained 46 species and 124 individuals. The most diverse groups in the epigean environment were Hymenoptera (23 species), Araneae (16 species), and Coleoptera (12 species). In contrast, the cave environment was dominated by Araneae (8 species), Coleoptera (6 species), and Diptera, Hymenoptera, and Hemiptera, each represented by four morphotypes (Figure 4). A total of 10 morphotypes were found in both environments, including members of the Araneae, Coleoptera, Collembola, Hymenoptera, and Isopoda groups. Additionally, 14 morphotypes were identified in more than one quadrant within the cave, while 24 were recorded across multiple epigean quadrants.

The Mann-Whitney test revealed significant differences in mean richness between the cave and epigean environments ($W = 74.0$; $p = 0.001$). The mean richness in the epigean environment

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

was 4.72 (sd = 3.28), whereas the cave environment had a mean richness of 2.19 (sd = 1.42) (Figure 3B).

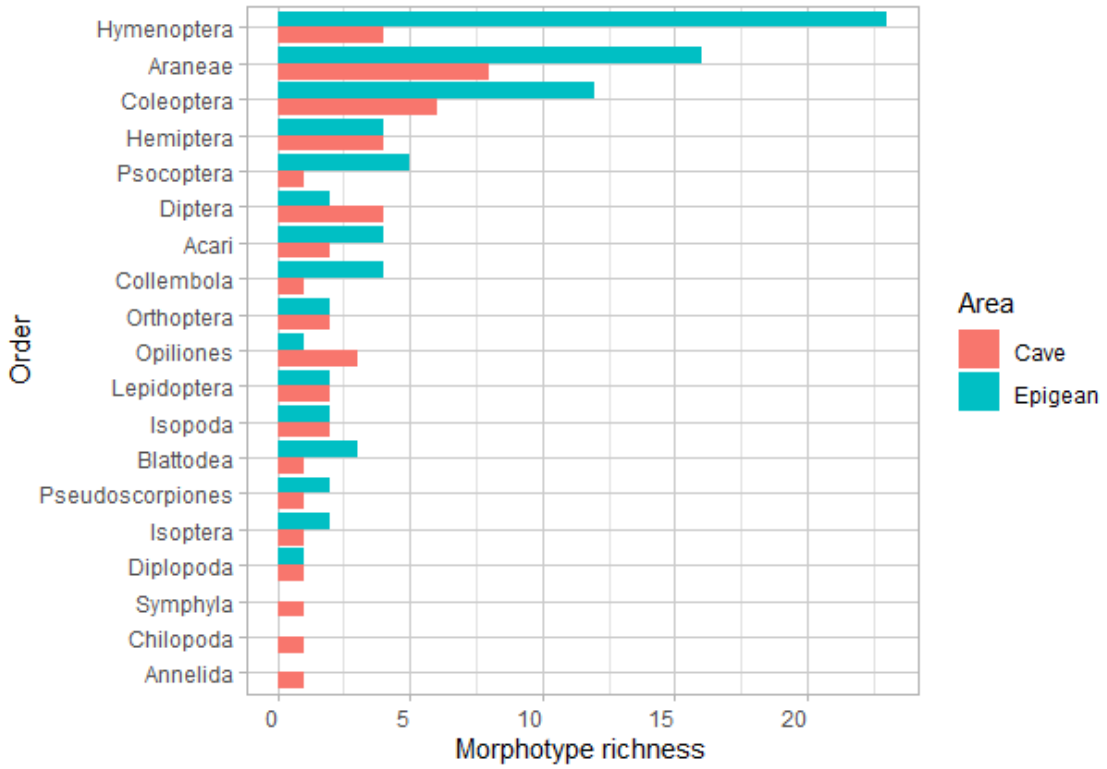

Figure 4. Species richness of terrestrial invertebrates recorded in quartzite caves and adjacent epigean areas.

The ANOSIM analysis revealed significant differences in faunal composition between the cave and epigean areas (p = 0.001; GlobalR = 0.127), highlighting a clustering of cave fauna distinct from that of the epigean environment in the MDS (Figure 5A). In contrast, the similarity analysis of faunal composition among the caves showed no significant differences.

Spatial βsør-diversity across epigean and cave indicate that the turnover was the predominant component ($p < 0.001$; pseudo $R^2 = 0.693$), accounting for approximately 69% of the observed variation. The nestedness component was also statistically significant ($p < 0.001$; pseudo $R^2 = 0.351$), explaining 35% of the variation in total βsør-diversity (Figure 6).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

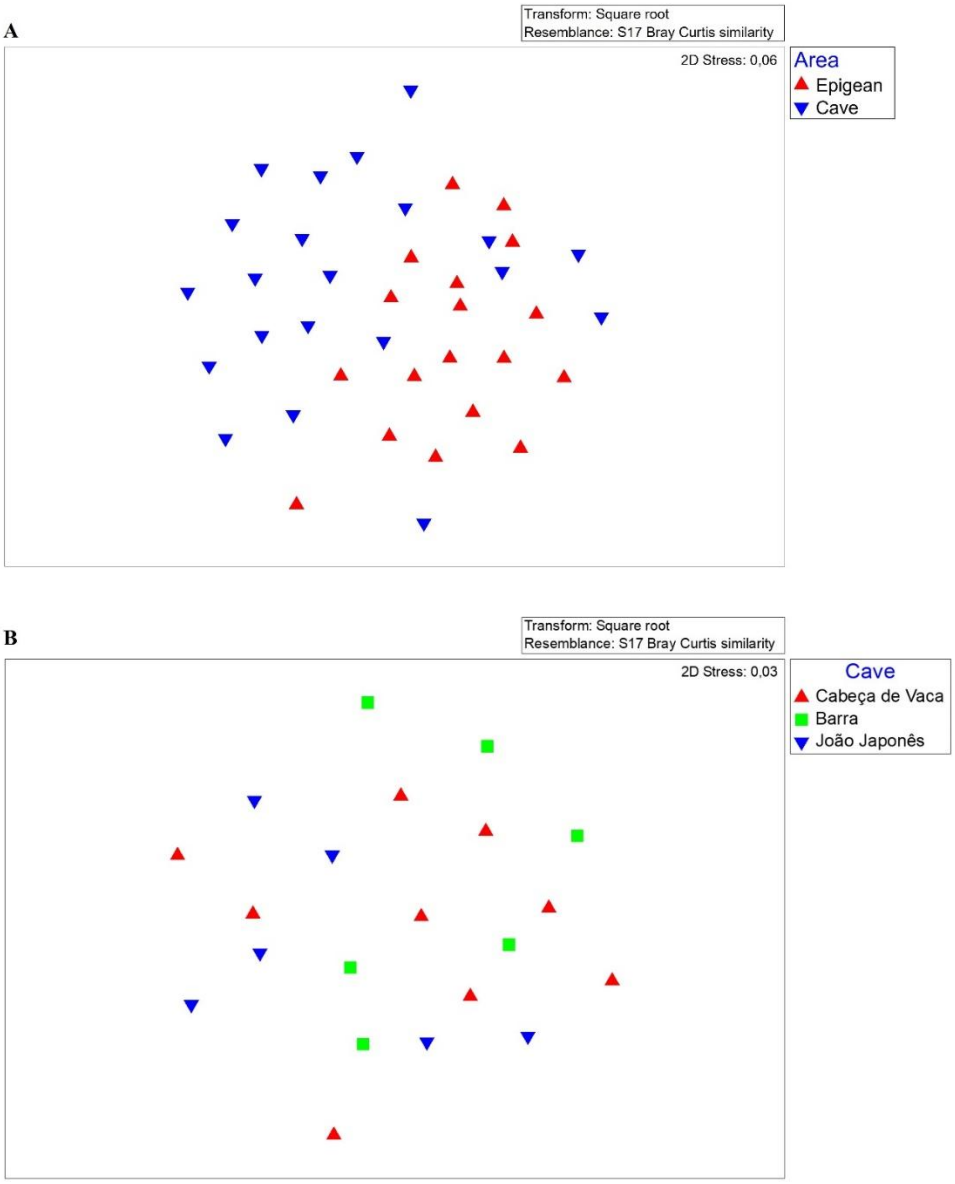

Figure 5. Multidimensional Scaling (MDS) showing the similarity in fauna composition between epigean and cave environments (A); and the among fauna composition at Cabeça de Vaca, Barra, and João Japonês caves (B).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

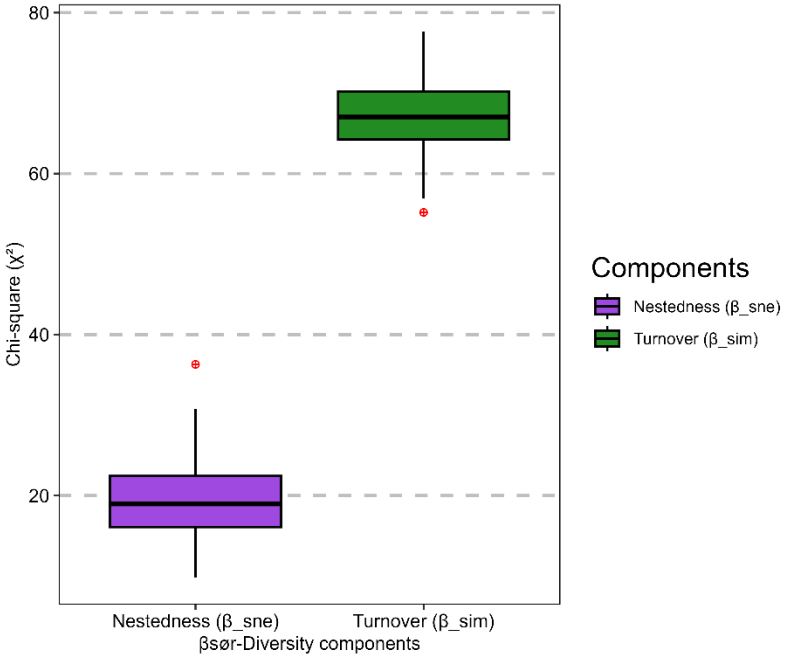

Figure 6. Contribution of β-diversity components to overall β-diversity. Boxplots represent the distribution of chi-square (χ²) values derived from model comparisons, illustrating the contributions of turnover and nestedness components to total β-diversity.

Factors determining the faunal composition and richness

The DistLM analysis indicated that the faunal composition in the epigean environment adjacent to the caves was solely influenced by Plant Debris (p = 0.002; adjusted R^2 = 0.047). Conversely, within the caves, the composition was determined by Guano (p = 0.001; adjusted R^2 = 0.039) and Inorganic Substrates (p = 0.001; adjusted R^2 = 0.080).

The dbRDA analysis demonstrated that the measured variables accounted for16.4% of the variation in faunal composition in the epigean area, while in the cave environment, the model accounted for 17.4% (Figure 7A-B).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

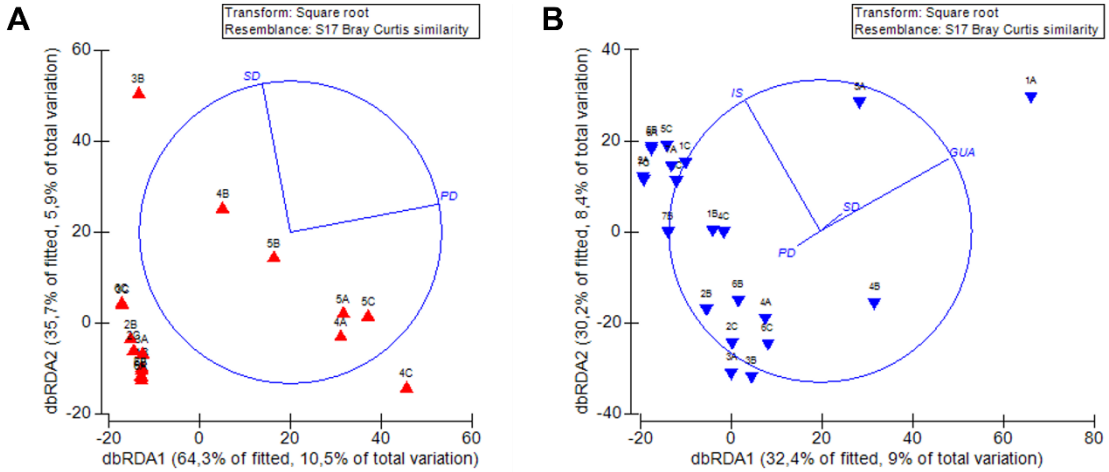

Figure 7. Distance-based redundancy analysis (dbRDA) showing the influence of variables on fauna composition in the epigean (A) and cave (B) environments. Numbers 1-7, labeled with A, B or C, denote the sampled area and quadrant. Variables: Plant debris (PD), Guano (GUA), Inorganic substrate (IS), and Substrate diversity (SD).

In the epigean environment, the variable Plant Debris exhibited a positive and significant relationship with species richness (Table 1 and Figure 8). In contrast, none of the evaluated variables accounted for the variation in species richness in the cave environment.

*Table 1. Model selection for variables. The table shows each predictor's estimated coefficients, standard errors, z-values, and p-values in the final Negative Binomial Generalized Linear Model (GLM.nb). The predictor variables used in the model were: SH (Shelter), IS (Inorganic substrate), PD (Plant Debris). A significance levels of the variables are denoted as (*** $p < 0.001$, ** $p < 0.01$).*

Variable	Estimate (β)	Std. Error	z value	p-value	Significance
Intercept	1.8783	0.1048	17.919	< 0.001	***
SH	0.1086	0.0908	1.196	0.23156	
IS	-0.1182	0.1182	-1.0	0.31737	
PD	0.3026	0.1057	2.862	0.00421	**

B) AIC (97.131); adjusted R^2 (0,2833); Zero-inflation Test (ratioObsSim = 0, p = 1).

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

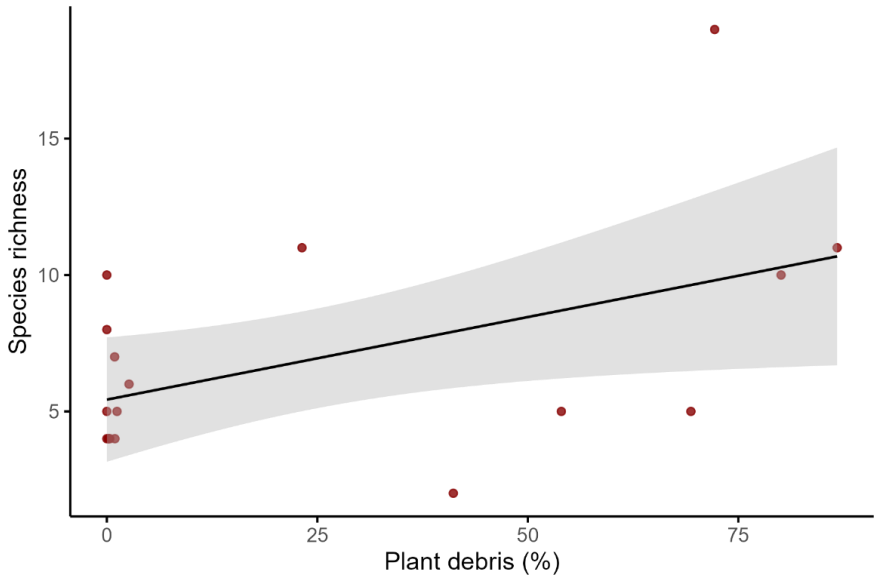

Figure 8. Distribution of fauna richness concerning the percentage of positively significant variable Plant Debris.

4. DISCUSSION

Differences in species richness and composition between areas

Faunal surveys revealed significantly higher species richness in the epigean environment compared to the cave, as evidenced by greater mean richness values. In addition to differences in richness, faunal composition varied markedly between the two environments. Spatial β-diversity was primarily driven by species turnover, with a secondary contribution from nestedness, indicating that both taxonomic replacement and differential species loss occurred across habitats.

These patterns in species richness and composition are likely shaped by the environmental constraints inherent to cave ecosystems. The absence of light, limited trophic resources, and reduced structural complexity act as strong ecological filters, limiting the colonization and persistence of many species (Poulson & White, 1969; Humphreys, 1991). Consequently, cave communities are structured by distinct selective pressures, leading to unique biological assemblages, even when ecological connectivity with adjacent epigean habitats exists (Prous et al., 2015; Mendes-Rabelo et al., 2021).

The composition of cave fauna is closely linked to the regional species pool found in adjacent epigean environments, which serves as a source of potential colonizers of subterranean ecosystems (Mendes-Rabelo et al., 2021). Many of these species are capable of moving between surface and cave habitats, particularly within cave entrance zones, where they often play key ecological roles in the dynamics and structuring of subterranean communities (Prous et al., 2004; 2015). However, their successful entry and persistence within cave systems are governed by environmental filters that selectively permit only certain organisms to establish and survive under the prevailing extreme conditions (Prous et al., 2015; Mendes-Rabelo et al., 2021; Reis-Venâncio et al., 2022).

In contrast, epigean areas typically offer a wider range of habitats and organic resources, supporting a more varied and abundant set of species (Ferreira & Marques, 1998; Loyola et al., 2006; Prous et al., 2015; Mammola et al., 2019b; Cardoso et al., 2022). The observed differences can be understood through various factors, including environmental conditions, climatic

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

influences, and trophic interactions. These elements often limit the successful establishment and persistence of different invertebrate groups within specific ecosystems (Loyola et al., 2006). Inside caves such ecological factors may encompass habitat type, availability of resources, and physical conditions such as soil porosity and microhabitat availability (Pacheco et al., 2020a; Souza-Silva et al., 2021). Microclimate conditions could include temperature variations, moisture patterns, and seasonal changes that affect invertebrate cycles in number and composition (Bento et al., 2016; Lunghi et al., 2017; Cardoso et al., 2024).

The environmental conditions within caves play a pivotal role in shaping the composition and diversity of cave-dwelling fauna. These habitats, defined by the absence of light, relatively stable temperatures, and high humidity, give rise to distinct ecological niches that foster the development of specialized biological communities. Consequently, the faunal assemblages found in caves often differ markedly from those in adjacent epigean ecosystems (Souza-Silva et al., 2021; Oliveira & Ferreira, 2024). This pattern was also evident in the present study, which revealed pronounced dissimilarities between invertebrate communities inhabiting cave and surface environments.

Additionally, the oligotrophic nature of cave habitats significantly restricts the variety of species that can thrive within these environments. The low-nutrient condition leads to a reduction in primary production, thereby limiting the availability of food resources. As a result, the food webs within cave ecosystems tend to be less complex and are often characterized by fewer trophic levels (Ferrreira & Martins, 1999; Gibert, 2001). The simplicity of these food webs may increase the ecosystem's vulnerability to changes, as each species contributes significantly in the overall balance of this specialized habitat. (Huxel & McCann, 1998; Schneider et al., 2011).

Therefore, allochthonous resources play an important role in shaping the biodiversity of cave ecosystems (Schneider et al., 2011). These resources, which originate from outside the cave, serve as the main source of nutrients for the various species inhabiting these subterranean spaces. They can include organic matter such as guano, leaves, plant detritus, and other materials that enter the cave from the surface (Ferreira & Martins 1999, Souza-Silva et al., 2011; 2013). Introducing these external nutrients not only supports the growth and survival of cave-dwelling organisms but also influences the overall structure and dynamics of the cave food web (Venarsky et al., 2014; Venarsky & Huntsman, 2018). This interaction highlights the importance of outside environments in sustaining the complex life forms found within caves (Schneider et al., 2011; Venarsky & Huntsman, 2018; Culver & Pipan, 2019).

Sket (1999) proposed three factors that may explain this disparity between caves and external environments: limited habitat access due to the small number and size of cave entrances, habitat homogeneity, and low energy availability. However, it is important to note that the caves sampled in this study have multiple entrances and lack extensive linear development, reducing these limitations compared to other caves. Cave entrances can offer shelter to epigean invertebrates by providing resources and protection and acting as a filter that promotes the colonization of certain species (Prous et al., 2004; 2015). Regarding habitat homogeneity, the epigean environment was more homogeneous than the subterranean environment, with sampling conducted primarily in pasture areas. The third factor Sket (1999) mentioned, related to low energy availability, is corroborated by our findings, which revealed greater availability of trophic resources in the epigean region. This factor might explain the observed results, with significant differences in faunal composition between the two environments.

Our results indicate that cave fauna does not follow a dissimilarity gradient based on distance from the cave entrances, where the watercourse is situated. Despite an intermittent stream

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

shared among the caves, which might facilitate species dispersal, no similarity was observed across the quadrants along this drainage down to the cave's furthest downstream point, contrary to initial expectations. This dissimilarity pattern may be attributed to the multiple entrances within the cave system, which enable considerable exchange of fauna and resources between subterranean and epigean environments. This finding further suggests that colonization and dispersal within the subterranean habitats of this system do not depend mainly on the watercourse.

Habitat traits determining patterns of richness and composition

As expected, the findings support the hypothesis that substrate variables influencing faunal composition differ markedly between cave and epigean environments. In epigean environments, fauna mirrored trends observed in previous studies, with "plant debris" emerging as a key resource for community structuring. For cave areas, guano was an important nutritional source for sustaining oligotrophic cave environments (Ferreira & Martins, 1999; Ferreira, 2019). Additionally, the other substrate significant for faunal structuring, the inorganic substrate primarily composed of compacted floor material, is the most common substrate in the study caves.

In epigean environments, the composition and richness of invertebrate communities can be influenced by "key landscape elements," defined as spatial structures that offer resources, shelter, or specific conditions for species (Tews et al., 2004). Thus, the variables affecting fauna in these environments are tied to physical substrate structures, trophic resources, and shelter, emphasizing the importance of such structural factors. Both autochthonous and allochthonous food resources are essential for animal communities across various environments (Marczak et al., 2007; Schneider et al., 2011). In oligotrophic habitats like caves, invertebrate communities depend heavily on allochthonous resources, which positively impact species richness and shape community composition (Ferreira et al., 2009; Schneider et al., 2011; Souza-Silva et al., 2011).

5. CONCLUSIONS

The findings of this study deepen our understanding of how microhabitat variables shape cave invertebrate communities and their adjacent epigean environments. Moreover, the differences in faunal composition between the subterranean and epigean habitats emphasize the critical need for conservation efforts to protect these communities. While distinct, these environments form interconnected and interdependent ecosystems, underscoring the necessity for integrated strategies to conserve and manage these areas.

ACKNOWLEDGMENTS

The authors thank Fapemig and Vale S/A for the scholarship granted to Gabrielle Soares Muniz Pacheco. The data used in this article were part of her thesis in Applied Ecology at the Federal University of Lavras. We like to thank the team at the Center for Studies in Subterranean Biology (CEBS/UFLA) for their support during field trips. Additionally, acknowledgment is extended to CNPq (National Council for Scientific and Technological Development) for the productivity scholarship awarded to RLF (CNPq n. 302925/2022-8) and to MSS (CNPq n. 303434/2025).

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

Author Contributions

Rodrigo Lopes Ferreira was responsible for the conceptualization, methodology, translation, and English corrections. Gabrielle Soares Muniz Pacheco participated in field activities. Felipe Carvajal was for the statistical analysis and original draft preparation. Gabrielle Soares Muniz Pacheco, Rodrigo Lopes Ferreira, and Marconi Souza Silva were responsible for the artwork, reviewing, and editing. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement

The data supporting this study's findings are available on request from the corresponding author. The Editor-in-Chief has waived the required archiving due to privacy or ethical restrictions.

Conflicts of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated

REFERENCES

ANDERSON, M. J.; GORLEY, R. N.; CLARKE, K. R. ***PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.*** Massey University, Albany Campus, Auckland: New Zealand, 2008.

ATAURI, J. A.; DE LUCIO, J. V. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. **Landscape ecology**, v. 16, p. 147-159, 2001. https://doi.org/10.1023/A:1011115921050

BADINO, G. Underground meteorology – "What's the weather underground?". **Acta Carsologica**, v. 39, n. 3, 2010. https://doi.org/10.3986/ac.v39i3.74

BARR JR, T. C. Cave ecology and the evolution of troglobites. In: DOBZHANSKY, T.; HECHT, M. K.; STEERE, W. C. **Evolutionary biology**. Boston, MA: Springer US, 1968. v. 2, p. 35-102. https://doi.org/10.1007/978-1-4684-8094-8_2

BASELGA, A. Partitioning the turnover and nestedness components of beta diversity. **Global ecology and biogeography**, v. 19, n. 1, p. 134-143, 2010. https://doi.org/10.1111/j.1466-8238.2009.00490.x

BENTO, D. D. M. et al. Seasonal variations in cave invertebrate communities in the semiarid Caatinga, Brazil. **Journal of Cave and Karst Studies**, v. 78, n. 2, p. 61-71, 2016. https://doi.org/10.4311/2015LSC0111

CARDOSO, R. C.; FERREIRA, R. L.; SOUZA-SILVA, M. Multi-spatial analysis on cave ecosystems to predict the diversity of subterranean invertebrates. **Basic and Applied Ecology**, v. 65, p. 111-122, 2022. https://doi.org/10.1016/j.baae.2022.11.007

CARDOSO, R. C.; FERREIRA, R. L.; SOUZA-SILVA, M. Caves' environmental stability shaping subterranean biodiversity in the neotropics. **Acta Oecologica**, v. 125, 104036, 2024. https://doi.org/10.1016/j.actao.2024.104036

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

CLARKE, K. R. Non-parametric multivariate analyses of changes in community structure. **Australian journal of ecology**, v. 18, n. 1, p. 117-143, 1993. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

CLARKE, K. R.; GORLEY, R. N. **PRIMER v6: User Manual/Tutorial**. Plymouth: PRIMER-E, 2006. 192 p.

CORRÊA-NETO, A.V.; DUTRA, G. A Província Espeleológica Quartzítica Andrelândia, sudeste de Minas Gerais. In: RASTEIRO, M.A.; PEREIRA-FILHO, M. (orgs.) CONGRESSO BRASILEIRO DE ESPELEOLOGIA, 24, 1997. Ouro Preto. **Anais**... Campinas: SBE, 2017. p.37-43. http://www.cavernas.org.br/anais24cbe/24cbe_037-043.pdf

CRIBARI-NETO, F.; ZEILEIS, A. Beta regression in R. **Journal of statistical software**, v. 34, p. 1-24, 2010. https://doi.org/10.18637/jss.v034.i02

CULVER, D. C. **Cave life: evolution and ecology**. Cambridge: Harvard University Press, 1982. https://doi.org/10.4159/harvard.9780674330214.c6

CULVER, D. C.; PIPAN, T. **The biology of caves and other subterranean habitats**. 2. ed. Oxford: Oxford University Press, 2019.

DERRAIK, J. G. et al. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. **Conservation Biology**, v. 16, n. 4, p. 1015-1023, 2002. https://doi.org/10.1046/j.1523-1739.2002.00358.x

DERRAIK, J. G. et al. Morphospecies and taxonomic species comparison for Hymenoptera. **Journal of Insect Science**, v. 10, n. 1, p. 108, 2010. https://doi.org/10.1673/031.010.10801

FERREIRA, R. L. Guano communities. In: WHITE, W. B.; CULVER, D. C. (ed.). **Encyclopedia of caves. Cambridge**: Academic Press, 2019. p. 474-484. https://doi.org/10.1016/B978-0-12-814124-3.00057-1

FERREIRA, R. L.; MARQUES, M. M. A fauna de artrópodes de serrapilheira de áreas de monocultura com Eucalyptus sp. e mata secundária heterogênea. **Anais da Sociedade Entomológica do Brasil**, v. 27, p. 395-403, 1998. https://doi.org/10.1590/S0301-80591998000300007

FERREIRA, R. L.; MARTINS, R. P. Mapping subterranean resources: The cave invertebrates distribution as indicator of food availability. **Revista Brasileira de Zoociências**, v. 11, n. 2, 2009.

FERREIRA, R. L.; MARTINS, R. P. Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. **Tropical zoology**, v. 12, n. 2, p. 231-252, 1999. https://doi.org/10.1080/03946975.1999.10539391

FOX, J. et al. Package 'car'. Vienna: R Foundation for Statistical Computing, 2012. 16 p.

FURTADO-OLIVEIRA, L. F. et al. Recreational caving impacts of visitors in a high-altitude cave in Bolivian Andes: main effects on microhabitat structure and faunal distribution. **International Journal of Speleology**, v. 51, n. 2, p. 2, 2022. https://doi.org/10.5038/1827-806X.51.2.2418

GIBERT, J. Basic attributes of groundwater ecosystems. In: GIBERT, J. et al. (ed.). **Groundwater Ecology**. San Diego: Academic Press, 2001. p. 39-52.

HARTIG, F. DHARMa: **residual diagnostics for hierarchical (Multi-Level/Mixed) regression models (version 0.4.6)**. R package, 2022.

HUMPHREYS, W. F. Experimental re-establishment of pulse-driven populations in a terrestrial troglobite community. **The Journal of Animal Ecology**, p. 609-623, 1991. https://doi.org/10.2307/5301

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

HUXEL, G. R.; MCCANN, K. Food web stability: the influence of trophic flows across habitats. **The American Naturalist**, v. 152, n. 3, p. 460-469, 1998. https://doi.org/10.1086/286182

LEVENE, H. Robust tests for equality of variances. In: OLKIN, I. (ed.). **Contributions to probability and statistics**. Stanford: Stanford University Press, 1960. p. 278-292.

LOYOLA, R. D.; BRITO, S. L.; FERREIRA, R. L. Ecosystem disturbances and diversity increase: implications for invertebrate conservation. In: MORENO, C. E.; PÁEZ, R. (ed.). **Arthropod diversity and conservation**. New York: Springer, 2006. p. 25-42. https://doi.org/10.1007/978-1-4020-5204-0_3

LUNGHI, E.; MANENTI, R.; FICETOLA, G. F. Cave features, seasonality and subterranean distribution of non-obligate cave dwellers. **PeerJ**, v. 5, e3169, 2017. https://doi.org/10.7717/peerj.3169

MACARTHUR, R. H.; MACARTHUR, J. W. On bird species diversity. **Ecology**, v. 42, n. 3, p. 594-598, 1961. https://doi.org/10.2307/1932254

MACARTHUR, R.; LEVINS, R. The limiting similarity, convergence, and divergence of coexisting species. **The American Naturalist**, v. 101, n. 921, p. 377-385, 1967. https://doi.org/10.1086/282505

MAGURRAN, A. E. **Ecological diversity and its measurement**. New York: Springer Science & Business Media, 2013.

MAGURRAN, A. E.; MCGILL, B. J. (ed.). **Biological diversity: frontiers in measurement and assessment**. Oxford: OUP Oxford, 2010.

MAMMOLA, S. Finding answers in the dark: caves as models in ecology fifty years after Poulson and White. **Ecography**, v. 42, n. 7, p. 1331-1351, 2019a. **https://doi.org/10.1111/ecog.03905**

MAMMOLA, S.; CARDOSO, P.; ANGYAL, D.; BALÁZS, G.; BLICK, T.; BRUSTEL, H. et al. Continental data on cave-dwelling spider communities across Europe (Arachnida: Araneae). **Biodiversity Data Journal**, v. 7, e38492, 2019b. doi: 10.3897/BDJ.7.e38492

MAMMOLA, S.; PIANO, E.; ISAIA, M. Step back! Niche dynamics in cave-dwelling predators. **Acta Oecologica**, v. 75, p. 35-42, 2016. https://doi.org/10.1016/j.actao.2016.06.011

MAY, R. M. The search for patterns in the balance of nature: advances and retreats. **Ecology**, v. 67, n. 5, p. 1115-1126, 1986. https://doi.org/10.2307/1938668

MARCZAK, L. B.; THOMPSON, R. M.; RICHARDSON, J. S. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. **Ecology**, v. 88, n. 1, p. 140-148, 2007. https://doi.org/10.1890/0012-9658(2007)88[140:MTLHAP]2.0.CO;2

MENDES RABELO, L.; SOUZA-SILVA, M.; LOPES FERREIRA, R. Epigean and hypogean drivers of Neotropical subterranean communities. **Journal of Biogeography**, v. 48, n. 3, p. 662-675, 2021. https://doi.org/10.1111/jbi.14031

OLIVEIRA, M. P.; FERREIRA, R. L. Extending beyond individual caves: a graph theory approach broadening conservation priorities in Amazon iron ore caves. **PeerJ**, v. 12, e16877, 2024. https://doi.org/10.7717/peerj.16877

OLIVER, I.; BEATTIE, A. J. Invertebrate morphospecies as surrogates for species: a case study. **Conservation Biology**, v. 10, n. 1, p. 99-109, 1996. https://doi.org/10.1046/j.1523-1739.1996.10010099.x

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

PACHECO, G. S.; SOUZA SILVA, M.; CANO, E.; FERREIRA, R. L. The role of microhabitats in structuring cave invertebrate communities in Guatemala. **International Journal of Speleology**, v. 49, n. 2, p. 8, 2020a. https://doi.org/10.5038/1827-806X.49.2.2333

PACHECO, G. S. M.; DE OLIVEIRA, M. P. A.; CANO, E.; SOUZA SILVA, M.; FERREIRA, R. L. Tourism effects on the subterranean fauna in a Central American cave. **Insect Conservation and Diversity**, v. 14, n. 3, p. 294-306, 2020b. https://doi.org/10.1111/icad.12451

PACHECO, G. S. M.; SOUZA-SILVA, M.; FERREIRA, R. L. Environmental factors influencing invertebrate communities in caves and surrounding habitats in the Neotropics. **Journal of Tropical Ecology**, v. 41, e8, 2025. doi:10.1017/S0266467425000082

PELLEGRINI, T.; SALES, L. P.; AGUIAR, P.; FERREIRA, R. L. Linking spatial scale dependence of land-use descriptors and invertebrate cave community composition. **Subterranean Biology,** v. 18, p. 17-38, 2016. https://doi.org/10.3897/SUBTBIOL.18.8335

PETERSON, B. G.; CARL, P. **PerformanceAnalytics: econometric tools for performance and risk analysis.** R package, version 2.0.4.P, 2020.

PIANKA, E. R. Convexity, desert lizards, and spatial heterogeneity. **Ecology**, v. 47, n. 6, p. 1055-1059, 1966. https://doi.org/10.2307/1935656

POULSON, T. L.; WHITE, W. B. The cave environment: limestone caves provide unique natural laboratories for studying biological and geological processes. **Science**, v. 165, n. 3897, p. 971-981, 1969. DOI:10.1126/science.165.3897.971

PREVIATI, E.; FANO, E. A.; LEIS, M. Arthropods biodiversity in agricultural landscapes: effects of land use and anthropization. **Italian Journal of Agronomy**, v. 2, n. 2, p. 135-141, 2007. https://doi.org/10.4081/ija.2007.127.

PROUS, X.; FERREIRA, R. L.; JACOBI, C. M. The entrance as a complex ecotone in a Neotropical cave. **International Journal of Speleology**, v. 44, n. 2, p. 5, 2015. http://dx.doi.org/10.5038/1827-806X.44.2.7

PROUS, X.; FERREIRA, R. L.; MARTINS, R. P. Ecotone delimitation: epigean–hypogean transition in cave ecosystems. **Austral Ecology**, v. 29, n. 4, p. 374-382, 2004. https://doi.org/10.1111/j.1442-9993.2004.01373.x

R CORE TEAM. R: **a language and environment for statistical computing**. Vienna, Austria: R Foundation for Statistical Computing, 2025.

RASBAND, W. S. **ImageJ64**. Bethesda, MD: US National Institutes of Health, 1997.

REIS-VENÂNCIO, P. C.; RABELO, L. M.; PELLEGRINI, T. G.; FERREIRA, R. L. From light to darkness: the duality of influence of habitat heterogeneity on Neotropical terrestrial cave invertebrate communities. **Studies on Neotropical Fauna and Environment**, v. 59, n. 2, p. 255-264, 2022. https://doi.org/10.1080/01650521.2022.2095832

SCHNEIDER, K.; CHRISTMAN, M. C.; FAGAN, W. F. The influence of resource subsidies on cave invertebrates: results from an ecosystem-level manipulation experiment. **Ecology**, v. 92, n. 3, p. 765-776, 2011. https://doi.org/10.1890/10-0157.1

SCHOBER, P.; BOER, C.; SCHWARTE, L. A. Correlation coefficients: appropriate use and interpretation. **Anesthesia & Analgesia**, v. 126, n. 5, p. 1763-1768, 2018. DOI: 10.1213/ANE.0000000000002864

SHAPIRO, S. S.; WILK, M. B. An analysis of variance test for normality (complete samples). **Biometrika**, v. 52, n. 3-4, p. 591-611, 1965. https://doi.org/10.1093/biomet/52.3-4.591

ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

SIMON, K. S.; PIPAN, T.; CULVER, D. C. A conceptual model of the flow and distribution of organic carbon in caves. **Journal of Cave and Karst Studies**, v. 69, n. 2, p. 279-284, 2007.

SKET, B. The nature of biodiversity in hypogean waters and how it is endangered. **Biodiversity & Conservation**, v. 8, p. 1319-1338, 1999. https://doi.org/10.1023/A:1008916601121

SOUZA, F. L.; MARTINS, F. I.; RAIZER, J. Habitat heterogeneity and anuran community of an agroecosystem in the Pantanal of Brazil. Phyllomedusa: **Journal of Herpetology**, v. 13, n. 1, p. 41-50, 2014. https://doi.org/10.11606/issn.2316-9079.v13i1p41-50

SOUZA-SILVA, M.; CERQUEIRA, R. F. V.; PELLEGRINI, T. G.; FERREIRA, R. L. Habitat selection of cave-restricted fauna in a new hotspot of subterranean biodiversity in Neotropics. **Biodiversity and Conservation**, v. 30, p. 4223–4250, 2021. https://doi.org/10.1007/s10531-021-02302-8

SOUZA-SILVA, M.; INIESTA, L. F. M.; FERREIRA, R. L. Cave lithology effect on subterranean biodiversity: a case study in quartzite and granitoid caves. **Acta Oecologica**, v. 108, 103645, 2020b. https://doi.org/10.1016/j.actao.2020.103645

SOUZA-SILVA, M.; INIESTA, L. F. M.; FERREIRA, R. L. Invertebrates diversity in mountain Neotropical quartzite caves: which factors can influence the composition, richness, and distribution of the cave communities? **Subterranean Biology**, v. 33, p. 23-43, 2020a. https://doi.org/10.3897/subtbiol.33.46444

SOUZA-SILVA, M.; MARTINS, R. P.; FERREIRA, R. L. Trophic dynamics in a neotropical limestone cave. **Subterranean Biology**, v. 9, p. 127-138, 2011. https://doi.org/10.3897/subtbiol.9.2515

SOUZA-SILVA, M.; SALVIO, A.; FERREIRA, R. L. Food resource availability in a quartzite cave in the Brazilian Montane Atlantic Forest. **Journal of Cave and Karst Studies**, v. 75, p. 177–188, 2013. https://dx.doi.org/10.4311/2010JCKS0158

SPRENT, P.; SMEETON, N. C. **Applied nonparametric statistical methods**. Boca Raton: Chapman and Hall/CRC, 2000. 480 p.

STEIN, A.; GERSTNER, K.; KREFT, H. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. **Ecology Letters**, v. 17, n. 7, p. 866-880, 2014. https://doi.org/10.1111/ele.12277

TEWS, J.; BROSE, U.; GRIMM, V.; TIELBÖRGER, K.; WICHMANN, M. C.; SCHWAGER, M.; JELTSCH, F. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. **Journal of Biogeography,** v. 31, n. 1, p. 79-92, 2004. https://doi.org/10.1046/j.0305-0270.2003.00994.x

THE JAMOVI PROJECT. **Jamovi (version 2.4)** [Computer software], 2023.

TRAVASSOS-DE-BRITTO, B.; ROCHA, P. L. B. D. Habitat amount, habitat heterogeneity, and their effects on arthropod species diversity. **Ecoscience**, v. 20, n. 3, p. 207-214, 2013. https://doi.org/10.2980/20-3-3606

VENARSKY, M. P.; HUNTSMAN, B. M. Food webs in caves. In: **Cave ecology**, p. 309-328, 2018. https://doi.org/10.1007/978-3-319-98852-8_14

VENARSKY, M. P.; HUNTSMAN, B. M.; HURYN, A. D.; BENSTEAD, J. P.; KUHAJDA, B. R. Quantitative food web analysis supports the energy-limitation hypothesis in cave stream ecosystems. **Oecologia**, v. 176, p. 859-869, 2014. https://doi.org/10.1007/s00442-014-3042-3

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 05 de junho de 2025. Aceito: 11 de novembro de 2025. Publicado: 23 de dezembro de 2025.

ZAGMAJSTER, M.; MALARD, F.; EME, D.; CULVER, D. C. Subterranean biodiversity patterns from global to regional scales. In: **Cave ecology**, p. 195-227, 2018. https://doi.org/10.1007/978-3-319-98852-8_9

ZUUR, A. F.; HILBE, J. M.; IENO, E. N. **A beginner's guide to GLM and GLMM with R**. Newburgh, UK: Highland Statistics Ltd, 2013.