Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 07 de agosto de 2025. Aceito: 12 de dezembro de 2025. Publicado: 23 de dezembro de 2025.

# Cave Community Instability in the Tropics: A Case Study on Environmental Filtering and β-Diversity Partitioning of Terrestrial Invertebrates

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**RESUMO:** Ambientes subterrâneos são caracterizados por condições atmosféricas relativamente estáveis e ausência de luz; no entanto, sua complexidade morfológica pode influenciar a conectividade com a superfície, tornando-os suscetíveis a flutuações ambientais que afetam as comunidades de invertebrados. Neste estudo, examinamos a relação entre temperatura, umidade e distância da entrada da caverna de Salitre, no município de Cordisburgo, Minas Gerais, Brasil, ao longo de duas estações (seca e chuvosa), e seus efeitos sobre a riqueza de espécies, composição e diversidade beta (β-diversidade) de invertebrados terrestres. A riqueza de espécies foi maior durante a estação chuvosa e em áreas mais próximas da entrada. A temperatura influenciou positivamente a riqueza de espécies, enquanto a umidade afetou principalmente a composição da comunidade. A β-diversidade temporal apresentou variação sazonal e foi impulsionada principalmente pela substituição de espécies (turnover). A distância da entrada afetou negativamente a β-diversidade espacial em ambas as estações, enquanto a temperatura teve um efeito positivo significativo apenas durante a estação seca. O particionamento da β-diversidade revelou a substituição de espécies como o principal processo por trás da diferenciação espacial das comunidades cavernícolas. Nossos resultados sugerem que tanto a heterogeneidade ambiental temporal quanto espacial molda a dinâmica das comunidades nesta caverna. Temperaturas elevadas sustentam maior riqueza de espécies, ressaltando seu papel na manutenção da biodiversidade. Além disso, a distância da entrada influencia a distribuição das espécies, refletindo gradientes de composição e riqueza ao longo do ecótono subterrâneo. De modo geral, a substituição de espécies (e não o aninhamento/nestedness) emerge como o principal mecanismo estruturador das comunidades cavernícolas, destacando a sensibilidade ecológica e a instabilidade inerente dos habitats subterrâneos frente às mudanças ambientais.

**Palavras-chave**: Gradientes ambientais, Substituição de espécies, Filtragem ambiental, Invertebrados neotropicais.

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**ABSTRACT:** Subterranean environments are characterized by relatively stable atmospheric conditions and the absence of light; however, their morphological complexity can influence connectivity with the surface, making them susceptible to environmental fluctuations that affect invertebrate communities. In this study, we examined the relationship between temperature, humidity, and distance from the entrance of Salitre cave, located in Cordisburgo, Minas Gerais, Brazil, across two seasons (dry and rainy), and their effects on species richness, community composition, and beta diversity (β-diversity) of terrestrial invertebrates. Species richness was higher during the wet season and in areas closer to the entrance. Temperature positively influenced species richness, whereas humidity primarily affected community composition. Temporal β-diversity showed seasonal variation and was mainly driven by species turnover. Distance from the entrance negatively affected spatial β-diversity in both seasons, while temperature had a significant positive effect only during the dry season. Partitioning of β-diversity revealed species turnover as the dominant process underlying spatial differentiation of cave communities. Our findings suggest that both temporal and spatial environmental heterogeneity shape community dynamics in this cave. Elevated temperatures support greater species richness, underscoring their role in sustaining biodiversity. Furthermore, distance from the entrance influences species distribution, reflecting compositional and richness gradients along the subterranean ecotone. Overall, species replacement (rather than nestedness) emerges as the primary mechanism structuring cave communities, highlighting the ecological sensitivity and inherent instability of subterranean habitats to environmental change.

**Keywords:** Environmental gradients, Species turnover, Habitat filtering, Neotropical invertebrates.

## 1. INTRODUCTION

Subterranean environments exhibit unique characteristics that distinguish them from surface ecosystems, including the permanent absence of light (except near entrances) and a tendency toward relatively stable atmospheric conditions, particularly in terms of light intensity, temperature and humidity (Mammola et al. 2019; Pipan et al. 2019; Mejía-Ortíz et al. 2020). However, the extent of this environmental stability may vary depending on the morphological complexity of cave conduits (Bento et al. 2016; Mejía-Ortíz et al. 2020; Cardoso et al. 2024). As a result, subterranean ecosystems exhibit varying degrees of connectivity with the surface, which can increase or decrease their susceptibility to external environmental fluctuations, which can directly impact cave-dwelling invertebrate communities (Rendoš et al. 2012; Ferreira et al. 2015; Souza-Silva et al. 2021).

In tropical regions, the wet season often brings an increased influx of organic matter, which influences both the abundance and reproductive activity of subterranean fauna (Souza-Silva et al. 2011; Bento et al. 2016). The food supply available to cave communities is predominantly allochthonous (originating from outside the cave) and supports distinct subterranean food webs (Schneider et al. 2011; Souza-Silva et al. 2011). Due to the environmental heterogeneity within caves, subterranean biodiversity is influenced by multiple factors, including variations in light exposure, the availability of organic resources, air flow, temperature, and humidity (Tobin et al. 2013; Prous et al. 2004, 2015; Mammola, 2019). Caves often exhibit well-defined environmental

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gradients, which provide valuable opportunities to investigate how linear transitions in abiotic conditions shape faunal composition (Mammola, 2019; Reis-Venâncio et al. 2024). Understanding the drivers of these community shifts is crucial for unraveling the biological complexity of distinct ecosystems (Bascompte & Solé, 1995; Körner, 2007; McDonnell & Hahs, 2008; Chen et al. 2011).

It is well established that species inhabiting the twilight zones of caves are typically trogloxenes and troglophiles, while the deeper, more humid, and aphotic zones are predominantly occupied by troglobites (Reis-Venâncio et al. 2024; Souza-Silva et al. 2021). This zonation pattern is commonly attributed to factors such as microclimate (Tobin et al. 2013; Souza-Silva et al. 2021), light intensity (Reis-Venâncio et al. 2024; Silveira et al. 2024), availability of food resources (Souza-Silva et al. 2012; Rendoš et al. 2012), and competitive exclusion dynamics (Silveira et al. 2024; Vaz et al. 2025; Junta et al. 2025).

Caves are among the few natural systems characterized by relatively homogeneous microclimatic conditions, as most subterranean environments maintain nearly constant temperatures throughout the year and exhibit high relative humidity, often approaching saturation in their deeper regions (Badino, 2010). Consequently, variables such as temperature, humidity, and distance from the cave entrance are widely studied in cave invertebrate ecology, with distance from the entrance recognized as a key factor influencing community structure (da Rocha Melo et al., 2025). Cave entrances typically exhibit high environmental heterogeneity, which gradually decreases with increasing depth (Souza-Silva et al. 2021; Reis-Venâncio et al. 2024).

With increasing depth, environmental heterogeneity progressively declines, giving rise to more homogeneous and stable conditions within aphotic zones (Souza-Silva et al., 2021). These permanently dark regions are characterized by relatively constant temperature and humidity levels, coupled with a limited influx of organic matter, factors that exert a strong influence on the composition, structure, and dynamics of subterranean invertebrate communities (Tobin et al. 2013; Mammola et al. 2015).

For non-troglobitic species, cave entrances may serve either as preferred habitats or as transitional zones connecting to surface environments. In contrast, for troglobites and some non-troglobitic species, this ecotonal region can act as a strong environmental filter and represent a source of disturbance (Mammola, 2019; Souza-Silva et al. 2021). Nevertheless, multiple independent colonization events of subterranean habitats have been documented in cave-adapted taxa (Porter, 2007), as well as in surface-dwelling species likely dispersing through superficial subterranean habitats (Růžička, 1999; Culver & Pipan, 2019). These patterns suggest a complex network of ecological connectivity between surface and subterranean systems, enabling various pathways for species to colonize, persist in or retreat from hypogean environments.

This study aimed to assess whether the richness and composition of non-troglobitic terrestrial invertebrates vary in response to climatic and spatial factors within a Neotropical limestone cave. To address this objective, we tested the following hypotheses: (i) species composition varies along the entrance-to-depth gradient in relation to temperature and humidity, as well as between the dry and wet seasons; (ii) species richness increases with temperature and decreases with both humidity and distance from the cave entrance, with higher richness expected during the wet season; and (iii) invertebrate β-diversity is greater during the wet season and responds to variation in temperature, humidity, and distance from the entrance, with species turnover representing the dominant component of β-diversity in both seasons.

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## 2. MATERIALS AND METHODS

### *Study area*

This study was conducted in Salitre Cave (-19.121918°, -44.351499°), located within the Peter Lund State Natural Monument (MNEPL), a protected area established in 2005 by the government of the state of Minas Gerais (Decree No. 44.120, 2005), in the municipality of Cordisburgo, Minas Gerais, Brazil (Figure 1). Regional geomorphology is characterized by an elongated relief with prominent rocky outcrops, caves, sinkholes, temporary lagoons, and grassland formations (Travassos & Kohler, 2009), and is situated within the Cerrado ecoregion (Olson et al., 2001). According to Köppen's climate classification, the area presents a mesothermal climate (Cwa), defined by hot, humid summers and dry winters. The regional climate is distinctly seasonal, with a wet season from October to March and a dry season from April to September. The annual mean temperature is approximately 22 °C, and annual precipitation ranges between 1,300 and 1,600 mm (Alvares et al., 2013).

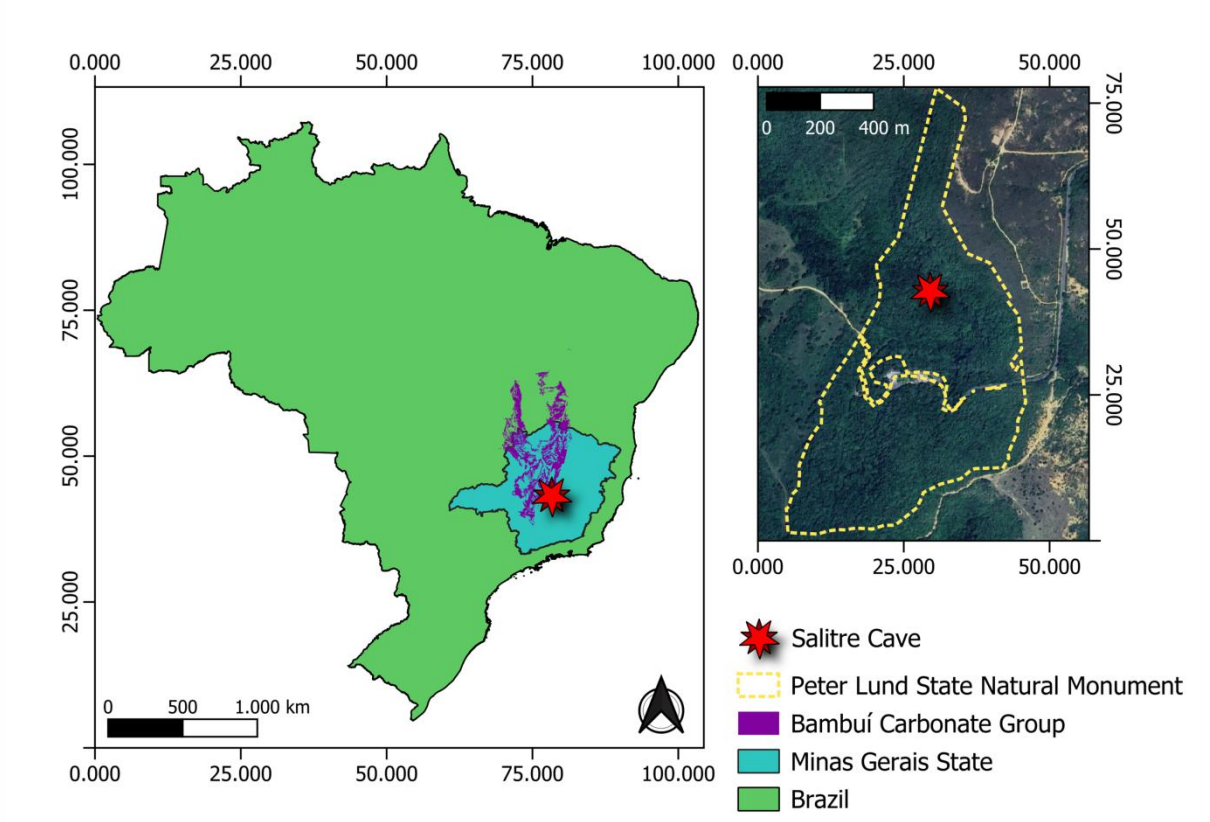


*Figure 1. Location of Salitre Cave (red star) in the state of Minas Gerais, Brazil. The cave is situated within the Bambuí Carbonate Group and lies within the boundaries of the Peter Lund State Natural Monument, as outlined by the dashed yellow line.*

The karst landscape in the region belongs to the Bambuí Geological Group, which dates to the Upper Proterozoic. Salitre Cave has developed within stratified, folded, and fractured carbonate rocks of the Lagoa do Jacaré Formation. It exhibits a predominantly horizontal profile, extending over 1,908 meters (Silva & Simões, 2002). Seasonal water flow occurs throughout most of the cave galleries, resulting in the accumulation of sediment deposits such as gravel, sand, and silt. The cave entrance is situated on a steep rock face, approximately halfway up the doline wall, with a sinkhole

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at its base where the surface stream disappears. Internally, the cave is traversed by a stream whose flow intensity varies with external precipitation. During the wet season, some low-ceiling passages may become completely flooded (Silva & Simões, 2002). A detailed cave map is provided in Silva & Simões (2002).

**S*ampling design***

Sampling was conducted in January (wet season) and July (dry season) along a 750-meter transect extending from the cave entrance to its deeper zones. The transect was divided into 25-meter-long sectors, resulting in a total of 30 sampling points. The methodology followed Ferreira (2004), in which each observed species is assigned a unique identifier, and its occurrences are spatially mapped within the cave. This approach allows for detailed analyses of species distribution and abundance patterns.

Although studies based on a single cave inherently present limitations, particularly in terms of spatial representativeness and the number of sampling events, repeated seasonal sampling, as employed in the present study, is recommended to improve the understanding of temporal dynamics and the structure of subterranean communities (da Rocha Melo et al., 2025).

***Sampling of Terrestrial Invertebrates***

Terrestrial invertebrates were collected through intensive visual surveys and manual sampling using soft forceps and brushes, following established protocols (Ferreira, 2004; Wynne et al. 2019). All accessible microhabitats were thoroughly examined, including plant debris, guano deposits, spaces beneath rocks, and moist substrates. The sampling team consisted of five experienced researchers, all proficient in manual invertebrate collection and the identification of cave-dwelling fauna.

Collected specimens were preserved in 70% ethanol and identified to the lowest possible taxonomic level, then grouped into morphospecies for subsequent analyses (Souza-Silva et al., 2021) using a stereomicroscope. Troglobitic species (Figure 2) were identified based on the presence of troglomorphic traits, including reduced pigmentation, elongated appendages, and ocular reduction (Culver & Pipan, 2009; Deharveng et al. 2024). Taxonomic specialists (acknowledged in the Acknowledgments section) were consulted to confirm the troglobitic status of morphologically specialized taxa. All voucher specimens were deposited in the Subterranean Invertebrate Collection of Lavras (ISLA), housed at the Center for Studies in Subterranean Biology, Department of Ecology and Conservation, Federal University of Lavras (CEBS-UFLA) (biologiasubterranea.com.br).

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*Figure 2. Troglomorphic species found in the Salitre Cave: A) Oxarthrius sp. (B,C) Isopoda, D) Pseudochthonius sp., E) Acari: Parasitengona, F) Spaeleoleptes spaeleus, (G,H) Rhamdiopsis sp.*

### *Sampling of Environmental Variables*

Temperature and relative humidity were measured in each sector using a thermo-hygrometer positioned at the center of the sampling area. The instrument had an accuracy of ±1 °C for temperature and ±5% for relative humidity. Readings were recorded after allowing the device to stabilize for approximately 15 minutes. To minimize potential interference with the measurements, the presence of researchers near the instrument was avoided during this period (Furtado-Oliveira et al., 2022).

### *Data analysis*

Seasonal variation in abiotic conditions (temperature and humidity) was assessed using Analysis of Similarities (ANOSIM) based on a Euclidean distance matrix (Clarke et al., 2008). Faunal dissimilarity between seasons was also evaluated using ANOSIM, this time based on a Bray–

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Curtis similarity matrix. Both sets of results were visualized through Metric Multidimensional Scaling (MDS) ordinations. In order to identify the taxa contributing most to seasonal differences in faunal composition, a Similarity Percentage Analysis (SIMPER) was performed (Clarke, 1993).

The influence of environmental variables (temperature, relative humidity, and distance from the cave entrance) on species composition was investigated using a Distance-Based Linear Model (DistLM) with a Bray–Curtis similarity matrix, square root–transformed to reduce the influence of highly abundant species (McArdle & Anderson, 2001). Variable selection followed the forward selection procedure based on the corrected Akaike Information Criterion (AICc) (Anderson, 2008). To assess model fit and quantify the variation in community composition explained by environmental factors, a Distance-Based Redundancy Analysis (dbRDA) was applied (Anderson, 2008). All multivariate analyses were performed using PRIMER 7 software (Plymouth Routines in Multivariate Ecological Research; https://www.primer-e.com/software).

To evaluate the effects of distance from the cave entrance, temperature, and humidity on species richness, a Generalized Linear Mixed Model (GLMM) was applied. Species richness of terrestrial invertebrates was used as the response variable, with distance from the entrance, temperature, and humidity as fixed effects, and season included as a random effect. Prior to model fitting, Spearman's correlation analysis was conducted to assess multicollinearity among predictors. Due to a correlation coefficient exceeding 0.80, humidity was excluded from the model.

The initial model was fitted using a Poisson distribution; however, overdispersion was detected, necessitating the use of a negative binomial distribution. Model adequacy was verified through residual diagnostics, which revealed no significant overdispersion ($p = 0.224$). Multicollinearity was further evaluated using the Variance Inflation Factor (VIF), with all values below 2, indicating an absence of problematic collinearity among predictors.

To test whether species richness differed between seasons, a Generalized Linear Model (GLM) was constructed with season as the explanatory variable. As with the GLMM, the Poisson model exhibited overdispersion and was subsequently replaced with a negative binomial distribution. Residual diagnostics confirmed no significant overdispersion ($p = 0.208$).

Seasonal differences in β-diversity were examined using the Temporal Beta-diversity Index (TBI), based on a presence–absence matrix and the Sørensen dissimilarity index. Statistical significance was assessed through a permutation-based t-test ($n = 999$).

Spatial β-diversity was calculated for each sector by assessing dissimilarities among sampling points within each season separately, using the Sørensen dissimilarity index (βsør). This index was further partitioned into its turnover (βsim) and nestedness (βsne) components, both ranging from 0 (0%) to 1 (100%), indicating their relative contributions to overall βsør. Turnover represents species replacement among sites, while nestedness reflects differences due to species loss, where communities with lower richness are subsets of richer ones.

To assess the influence of environmental variables on βsør, two GLMs were fitted (one for each season) with βsør as the response variable and temperature and distance from the cave entrance as predictors. Given the bounded nature of the response variable (0–1), a beta distribution was applied to the models. To determine whether turnover (βsim) is the dominant component of total βsør, beta regression models were constructed using βsim and βsne as explanatory variables. Significance was evaluated using Type III ANOVA, and chi-square ($\chi^2$) statistics were used to compare the relative influence of turnover and nestedness. Boxplots were generated to visually illustrate the contributions of these components.

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All species richness and β-diversity analyses were conducted in RStudio version 4.3.3 (R Core Team 2025). The GLMM was fitted using the lme4 package (Bates et al., 2015), and negative binomial models were implemented using MASS (Ripley, 2013). Spearman's correlation was calculated with PerformanceAnalytics (Peterson et al., 2018), and residual diagnostics were performed with DHARMa (Hartig, 2022). VIF and Type III ANOVA were computed using car (Fox et al., 2012). Effect graphs were produced using tidyverse (Wickham et al., 2019). The TBI was calculated using adespatial (Dray et al., 2018), while βsør and its components were obtained using betapart (Baselga, 2010). Beta regression models were implemented with betareg (Cribari-Neto & Zeileis, 2010), and GLMs with beta distributions were fitted using glmmTMB (Brooks et al., 2017).

Due to the limited number of troglomorphic species and their confinement to the deeper, aphotic regions of the cave, the influence of environmental filters on their richness and distribution was not evaluated in the present study.

## 3. RESULTS

### *Faunal Composition and richness*

A total of 3,938 individuals were recorded along the sampled transect of the cave, comprising 142 species assigned to 18 taxonomic orders. Hexapoda was the most dominant group, both in terms of species richness (89 species; 62.7% of the total) and abundance (3,290 individuals; 88.7% of the total).

The most species-rich groups across both seasons were Coleoptera (33 species; 23.2%), Diptera (24 species; 16.9%), Araneae (20 species; 14.0%), Collembola (14 species; 9.8%), Lepidoptera (13 species; 9.15%), and Psocodea (7 species; 4.9%). Other groups included Acari (5 species; 3.5%), Pseudoscorpiones and Hemiptera (4 species each; 2.8%), Hymenoptera, Spirostreptida, and Polydesmida (3 species each; 2.11%), as well as Opiliones, Blattodea, and Trichoptera (2 species each; 1.40%). Ensifera, Archaeognatha, and Pauropoda were represented by a single species each (0.70% of the total). Species richness was higher during the wet season, with 101 species recorded, compared to 68 species in the dry season.

Seven species exhibited troglomorphic characteristics, including two isopods (Styloniscidae), one millipede (Polydesmida), one beetle (*Oxarthrius* sp.), one pseudoscorpion (*Pseudochthonius* sp.), and two harvestmen (*Spaeleoleptes spaeleus* H. Soares, 1966 and *Spinopilar* sp.).

### *Environmental conditions and faunal similarity between seasons*

Temperature and humidity significantly differed between seasons (Global R = 0.106; $p$ = 0.01; Figure 3A), with lower humidity values recorded near the entrance sectors during the dry season. Seasonal variation was also observed in species composition (Global R = 0.244; $p$ = 0.01; Figure 3B). The SIMPER analysis identified *Endecous* sp. 1, *Keroplatidae* sp. 2, *Carabidae* sp. 3, *Hypena* sp. 2, *Lutzomyia* sp. 1, *Entomobryomorpha* sp. 66, and *Plato* sp. 1 as the taxa contributing most to compositional dissimilarity between seasons.

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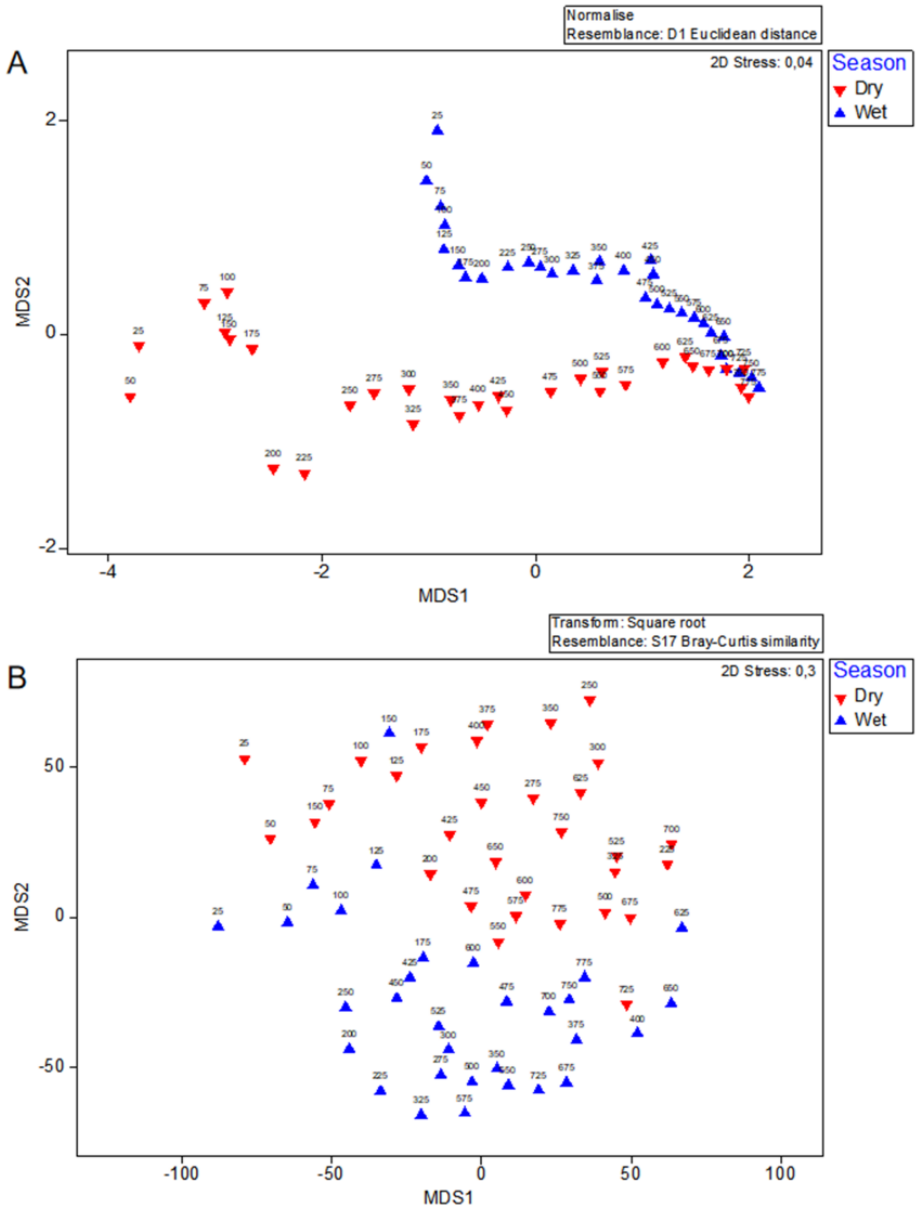


*Figure 3. Non-metric multidimensional scaling (nMDS) ordinations showing the variation between dry (red, downward triangles) and wet (blue, upward triangles) seasons. (A) nMDS based on environmental variables using Euclidean distance (normalized data), stress = 0.04; (B) nMDS based on species composition using Bray–Curtis similarity (square root–transformed data), stress = 0.3. Numbers indicate the distance from the cave entrance (in meters).*

### *Environmental influences on faunal similarity and species richness*

The DistLM analysis revealed a significant relationship between species composition and both relative humidity and distance from the cave entrance ($R^2 = 0.26$; AICc = 237.74; $p = 0.001$). The dbRDA further indicated that the abiotic variables collectively explained 26.2% of the spatial variation in faunal composition (Figure 4).

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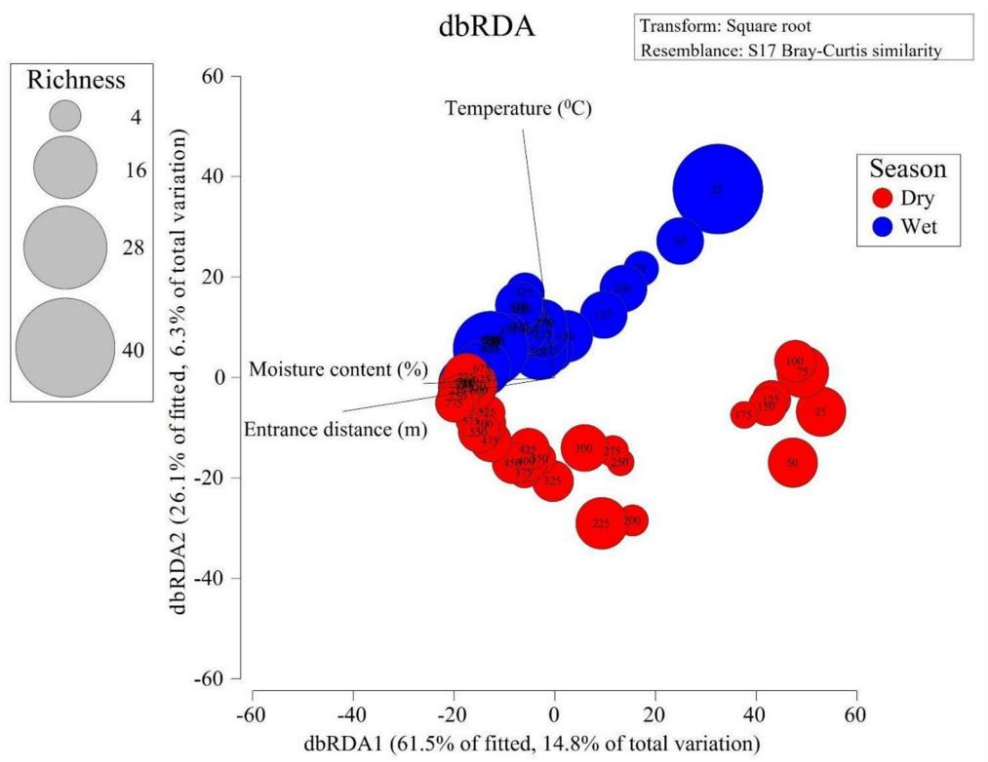


*Figure 4. Distance-based redundancy analysis (dbRDA) showing the relationship between species composition and environmental variables across seasons. The analysis is based on Bray–Curtis similarity using square root–transformed species abundance data. Each point represents a sampling unit, with colors indicating the season (red = dry; blue = wet) and point size proportional to species richness. Vectors represent the direction and strength of environmental gradients: distance from the cave entrance (m), moisture content (%), and temperature (°C). The first and second dbRDA axes explain 14.8% and 6.3% of the total variation, respectively.*

Species richness increased significantly with temperature ($\chi^2 = 13.730$; $p < 0.001$; Figure 5A) and declined with increasing distance from the entrance, indicating lower richness in the deeper cave sectors ($\chi^2 = 11.969$; $p < 0.001$; Figure 5B). Furthermore, richness varied significantly between seasons, with lower values recorded during the dry season ($\chi^2 = 11.056$; $p < 0.001$; Figure 5C).

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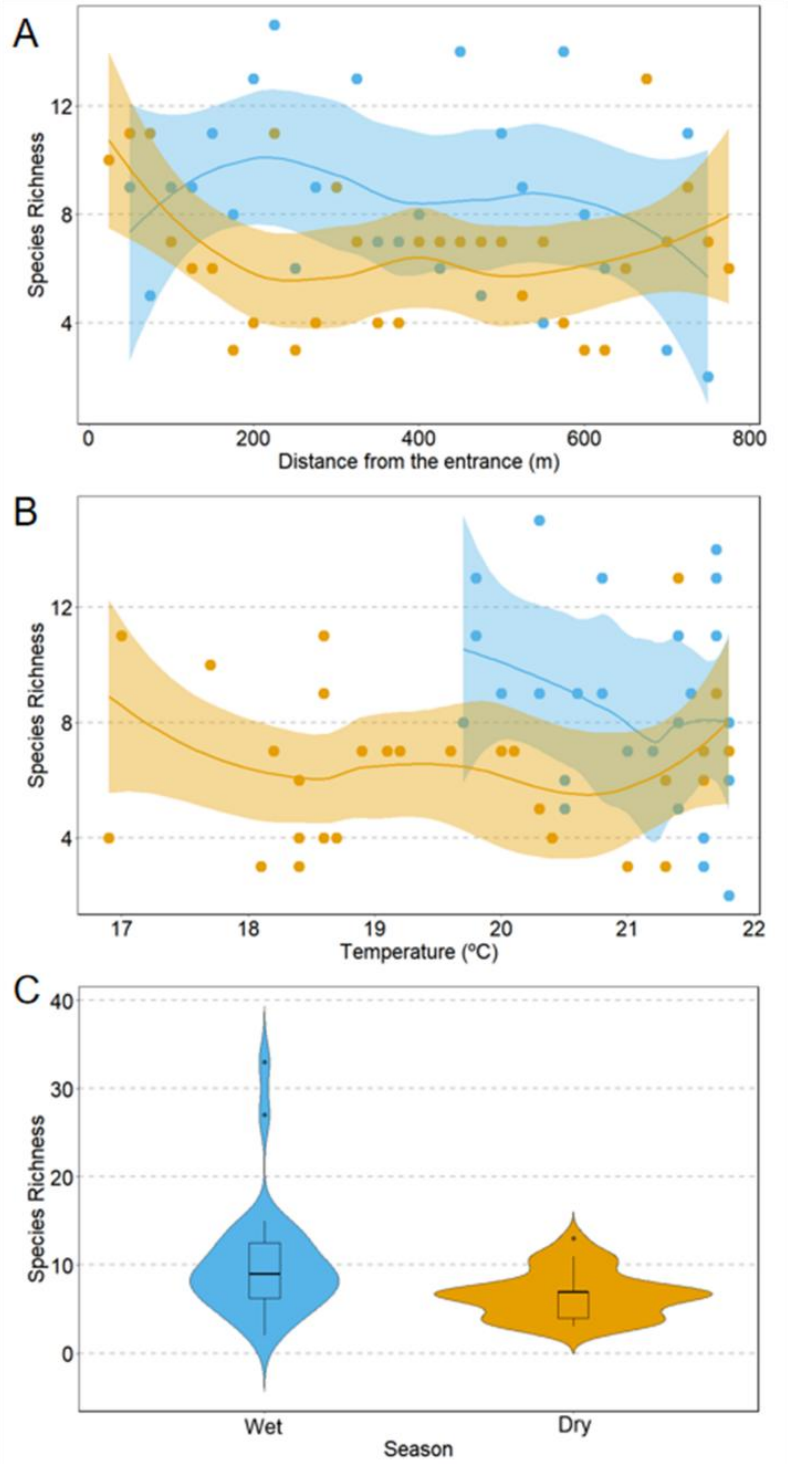


*Figure 5. Relationship between species richness and environmental variables. (A) Species richness as a function of distance from the cave entrance (meters); (B) species richness in response to temperature (°C); and (C) comparison of species richness between the dry (yellow) and wet (blue) seasons. (A,B) Lines represent model fits with 95% confidence intervals (shaded areas); the yellow line corresponds to the dry season and the blue line to the wet season.*

### *Variations in temporal and spatial β-diversity*

Temporal β-diversity analysis using the TBI revealed distinct patterns in the contributions of turnover and nestedness components to total dissimilarity among sampled sectors (Figure 6). On average, species turnover emerged as the dominant driver of temporal dissimilarity, accounting for 43% of total β-diversity, while nestedness contributed 28%. The relationship between

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components showed that, on average, species turnover accounted for 60.5% of the total dissimilarity, while nestedness contributed 39.5% (Table 1A). A paired *t*-test confirmed the statistical significance of this difference ($t = -2.736$; $p < 0.05$; Table 1B), reinforcing that species turnover plays a greater role in seasonal community shifts than nested species loss or gain (Table S1). Nonetheless, despite the predominance of turnover, some sectors exhibited higher nestedness values, particularly sectors 1C (75 m), 3A (225 m), 5A (425 m), 5C (475 m), 6B (550 m), 7D (700 m), and 8B (750 m) from the cave entrance.

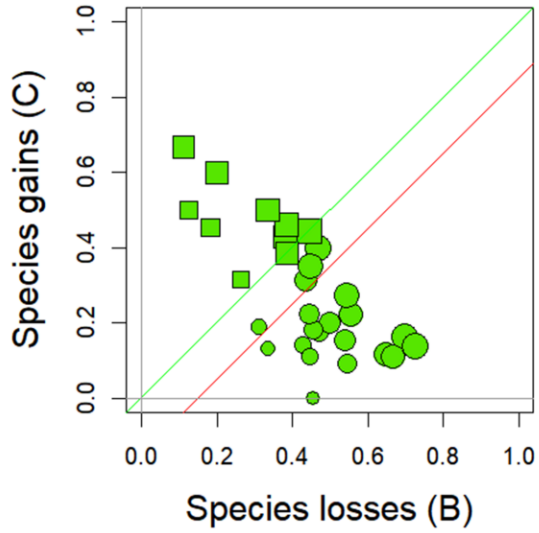


*Figure 6. Temporal beta-diversity partitioning between wet and dry seasons based on species presence/absence data. Each point represents a sampling unit comparison, where the x-axis indicates species losses during the transition from dry to wet season (component B), and the y-axis indicates species gains (component C). Circular symbols represent sampling points where species gains exceed losses (C > B), while squares represent points where losses are greater than gains (B > C). The red diagonal line marks the 1:1 ratio between gains and losses, and the green diagonal line highlights deviations where gains are greater than losses.*

*Table 1. Temporal beta diversity analysis between dry and wet seasons. A) Mean values of the partitioning of total beta diversity (D) into turnover (species replacement) and nestedness (species subset inclusion), with relative proportions calculated in relation to the total number of differing species between seasons. B) Results of the paired t-test comparing the nestedness and turnover components between seasons. The negative mean difference (C - B) indicates a predominance of turnover over nestedness. Significant differences (p ≤ 0.05) are indicated with a ✓ symbol*

A) **Summary of Turnover and Nestedness Analysis (TBI)**

| Average Turnover (B/den) | Average Nestedness (C/den) | Average Beta Total (D) | Turnover Proportion (B/(B+C)) | Nestedness Proportion (C/(B+C)) | Global Change |
|---|---|---|---|---|---|
| 0.4309 | 0.2814 | 0.7123 | 0.6049 | 0.3951 | - |

B) **t-test**

| Statistic | Mean (C - B) | t-value | p.param | p.perm | p <= 0.05 |
|---|---|---|---|---|---|
| Paired t-test | -0.1494 | -2.7357 | 0.0105 | 0.01 | ✓ |

Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 07 de agosto de 2025. Aceito: 12 de dezembro de 2025. Publicado: 23 de dezembro de 2025.

Spatial β-diversity analysis during the wet season revealed a significant negative relationship with distance from the entrance ($\chi^2 = 4.267$; $p < 0.05$; Figure 7A), while temperature had no significant effect ($\chi^2 = 2.216$; $p = 0.136$). In the dry season, distance also had a significant negative effect on βsør-diversity ($\chi^2 = 7.177$; $p < 0.01$; Figure 7B), whereas temperature exhibited a significant positive effect ($\chi^2 = 5.458$; $p < 0.05$; Figure 7C). Partitioning of βsør revealed that species turnover was the dominant component of total β-diversity in both seasons, with highly significant effects in the wet season ($\chi^2 = 24.905$; $p < 0.001$; Figure 7D) and dry season ($\chi^2 = 106.153$; $p < 0.001$; Figure 7E).

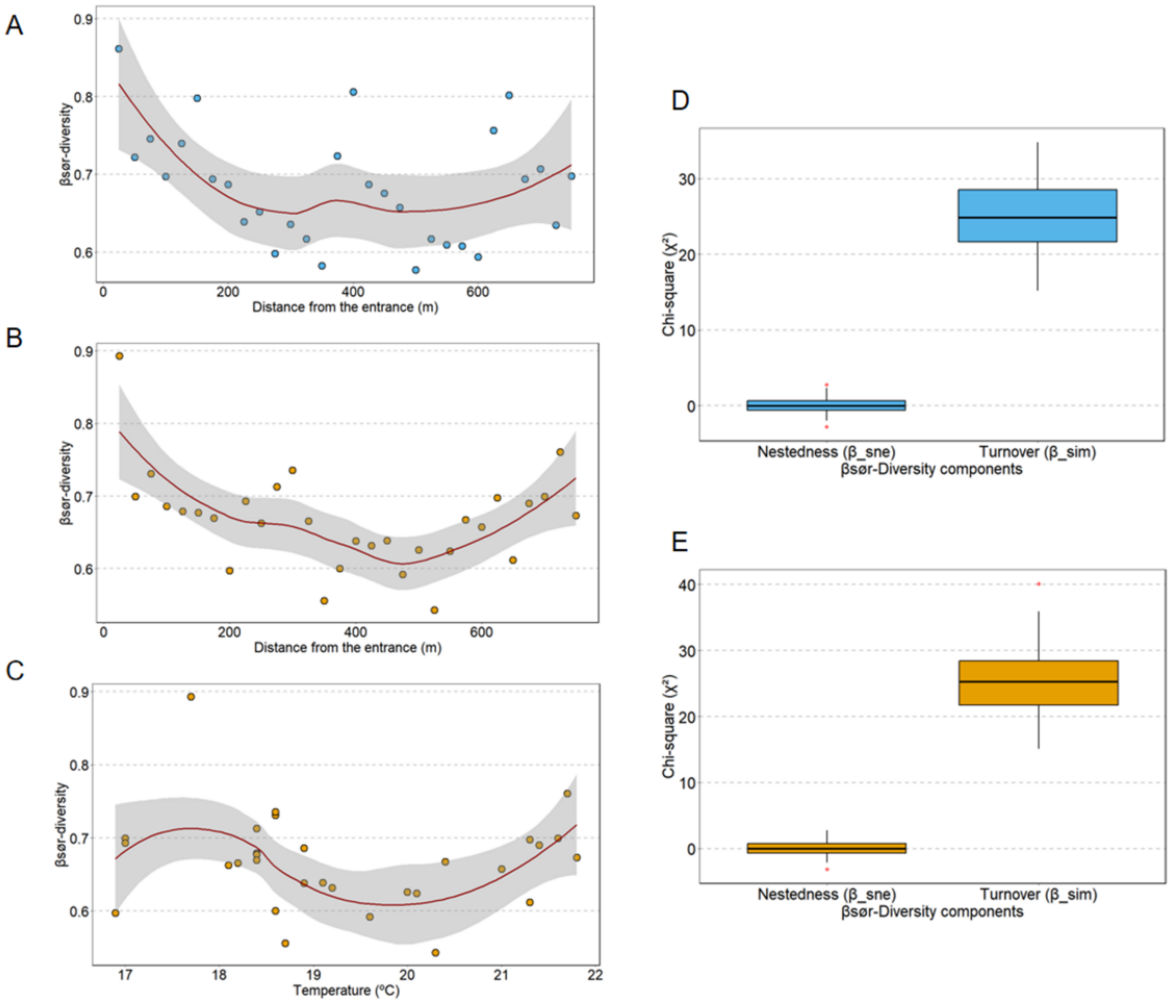


*Figure 7. Patterns of β-diversity in relation to environmental gradients and the contribution of its components. (A-C) Relationships between β-diversity and environmental variables during the wet season (blue) and dry season (yellow): (A) β-diversity as a function of distance from the cave entrance (meters) in the wet season; (B) β-diversity as a function of distance from the cave entrance in the dry season; and (C) response of β-diversity to temperature (°C)in the dry season. Lines represent model fits with 95% confidence intervals (shaded areas). (D-E) Contribution of turnover and nestedness to overall β-diversity in each season: (D) wet season and (E) dry season. Boxplots represent the distribution of chi-square values ($\chi^2$) from model comparisons.*

## 4. DISCUSSION

This study demonstrates that species richness was higher during the wet season and in sectors located closer to the cave entrance, suggesting that microclimatic conditions are key determinants in the structuring of subterranean invertebrate communities. Temperature exhibited

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a positive effect on species richness, whereas relative humidity primarily influenced species composition. Temporal β-diversity varied significantly between seasons and was predominantly driven by species turnover, indicating that temporal replacement, rather than nestedness, is the principal mechanism underlying community dynamics. Spatially, distance from the cave entrance had a consistent negative effect on βsør-diversity across both seasons, while temperature was a significant predictor only during the dry season. Partitioning of βsør-diversity further confirmed species turnover as the dominant component driving spatial differentiation among cave sectors.

***Seasonal variations influencing cave fauna***

Salitre Cave experiences seasonal water flow (Silva & Simões, 2002), which, during the wet season, may facilitate the transport of organic matter into the cave, thereby enhancing the availability of trophic resources (Souza-Silva et al. 2011; Venarsky et al. 2012). This influx benefits subterranean invertebrates, which often exhibit increased abundance and reproductive activity during this period, a pattern also observed in other karst systems (Bento et al., 2016). Consequently, the observed increase in species richness during the wet season may be attributed to enhanced food availability, which promotes habitat colonization and intensifies foraging activity (Schneider et al. 2011; Souza-Silva et al. 2012).

Seasonal variation also influenced temporal β-diversity, with species turnover emerging as the primary mechanism underlying compositional change. This indicates that community shifts are driven largely by species replacement in response to environmental fluctuations. During the dry season, more restrictive microclimatic conditions may lead certain species to reduce their activity levels or seek refuge in more stable microhabitats, such as rock crevices or shallow subterranean zones (Ledesma et al. 2020; Novak et al. 2012). Such behavioral and spatial shifts may result in the exclusion of less tolerant taxa and the appearance of others better adapted to drier conditions, promoting seasonal turnover in the subterranean fauna.

Although deep and shallow subterranean habitats are relatively buffered from surface conditions, they are not entirely stable and can exhibit seasonal fluctuations in temperature and humidity, often with a delayed response to external climatic changes (Tobin et al., 2013). Moreover, surface environments exert a strong influence on subterranean ecosystems, with abiotic factors such as precipitation positively affecting cave species richness, particularly in regions where dry-season rainfall is higher (Mendes Rabelo et al., 2020).

Despite recent advances in understanding subterranean community responses to seasonal variability, significant knowledge gaps remain. Long-term, high-resolution monitoring of community structure (particularly with comprehensive humidity data across cave zones) is essential to deepen our understanding of these dynamics (Tobin et al., 2013). Furthermore, assessing the impacts of extreme climatic events will be critical for developing more effective conservation and management strategies aimed at safeguarding subterranean biodiversity under increasing global environmental change (da Rocha Melo et al., 2025).

***Temperature variations influencing cave fauna***

Temperature had a significant positive effect on species richness, suggesting that higher temperatures promote increased activity and diversity among cave-dwelling invertebrates. Previous studies have shown that thermal variation can modulate the behavior of subterranean organisms, influencing ecological interactions and shaping community structure (Souza-Silva et al. 2021;

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Mammola, 2019). Our findings are consistent with earlier research demonstrating a positive association between temperature and species richness in subterranean systems (Souza-Silva et al. 2021; Tobin et al. 2013; Junta et al. 2025; Mendes Rabelo et al. 2020). In general, average annual temperature plays a key role in subterranean ecosystems, particularly in Neotropical regions, where species richness tends to be higher in areas with elevated minimum temperatures (Mendes Rabelo et al., 2020).

Conversely, Vaz et al. (2025) did not detect a significant relationship between temperature and species richness, likely due to the presence of a perennial stream running through the entire length of the cave analyzed in their study, which may buffer thermal variability along the subterranean gradient. This contrasts with the conditions in Salitre Cave, where the watercourse is intermittent, allowing for greater thermal amplitude and thereby amplifying the influence of temperature on community structure.

The effect of temperature on βsør-diversity was significant only during the dry season, suggesting that in the wet season, other factors (such as increased humidity and resource availability) may exert a stronger influence on community composition. During the wet season, temperature remained relatively stable (20°C to 22°C), while in the dry season, a broader thermal range (17°C to 22°C) was observed. This increased variability likely contributed to spatial differentiation in community structure, as reflected by elevated βsør-diversity driven by species turnover. Species less tolerant to lower temperatures may have shifted toward warmer microhabitats, while cold-adapted species may have occupied cooler sectors. This redistribution likely reduces interspecific competition for resources and facilitates species coexistence along the thermal gradient, thereby enhancing species turnover and spatial βsør-diversity during the dry season.

***Influence of distance from the cave entrance on cave fauna***

Distance from the cave entrance was a key factor influencing the structure of the invertebrate community, affecting species richness, β-diversity, and species composition. The entrance zone represents a more ecologically heterogeneous environment, characterized by greater variability in humidity, temperature, and light availability. This environmental complexity promotes the formation of diverse microhabitats, which in turn supports higher species richness (Tamme et al. 2010; Mammola, 2019; Reis-Venâncio et al. 2024). In addition, the entrance region receives a more substantial influx of organic matter from the surface, resulting in increased availability of trophic resources for subterranean fauna (Souza-Silva et al., 2021).

As distance from the entrance increases, the observed decline in βsør-diversity and its effect on species composition indicate a trend toward faunal homogenization in the deeper cave zones. This pattern suggests that reduced environmental heterogeneity and the persistence of oligotrophic conditions limit local diversity, favoring a restricted set of species adapted to these stable, resource-poor environments (Tobin et al., 2013). Similar findings have been reported in previous studies, which have shown that cave communities in deeper sectors typically exhibit lower species richness and greater structural predictability due to limited resource input and reduced environmental variability (Moseley, 2008, 2009).

In addition to reduced connectivity with surface ecosystems, other factors may constrain colonization of deeper cave areas. The progressive loss of light, lower availability of organic material, and the presence of physical barriers hinder both the dispersal of fauna and the transport

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of trophic inputs via gravity, water flow, or air currents (Prous et al. 2015; Souza-Silva et al. 2021). Consequently, there is a marked decline in species richness along the cave depth gradient, an ecological pattern widely documented in subterranean systems across the globe (Culver et al. 2000; Prous et al. 2015; Souza-Silva et al. 2021).

***Humidity variations influencing cave fauna***

Humidity played a fundamental role in structuring the invertebrate community in Salitre Cave, significantly influencing species composition throughout the cave's spatial gradient. The critical importance of this variable for subterranean fauna has been well documented in the literature (Tobin et al. 2013; Prous et al. 2015; Souza-Silva et al. 2021; Reis-Venâncio et al. 2024; Junta et al. 2025). During the dry season, sectors near the entrance exhibited lower humidity levels, which may have constrained the persistence of hygrophilous taxa and favored species with greater desiccation resistance (Silveira et al., 2024). This microclimatic variability likely contributed to the observed pattern of species turnover, reinforcing turnover as the dominant driver of temporal β-diversity.

Numerous studies have shown that troglobitic species tend to be more abundant in cave sectors characterized by high and stable humidity, whereas taxa with greater desiccation tolerance typically occupy drier, more environmentally variable zones (Martins & Ferreira, 2020; Novak et al. 2021; Moseley, 2008; Souza-Silva et al. 2021). This distribution pattern highlights the role of humidity as a critical environmental filter, selectively favoring species based on their physiological tolerance thresholds. Furthermore, as humidity tends to increase with distance from the cave entrance, it is important to consider this gradient in conjunction with spatial variables when analyzing patterns of species richness and occurrence (Tobin et al. 2013; Prous et al. 2015; Souza-Silva et al. 2021).

The pronounced intolerance to desiccation observed among troglobitic invertebrates is largely attributed to traits such as reduced body size and thinner cuticles, which enhance cutaneous respiration but increase vulnerability to water loss. While these adaptations are advantageous in dark, humid environments, they impose physiological constraints that restrict these species to stable, high-humidity microhabitats. Such microhabitats are typically characterized by low thermal variability, creating narrow but stable ecological niches (Tobin et al. 2013; Lunghi et al. 2014, 2017; Kozel et al. 2019). As a result, troglobitic invertebrates are more frequently found in the deeper, climatically buffered regions of caves, avoiding entrance zones where abiotic conditions are more variable and potentially inhospitable (Novak et al. 2012; Tobin et al. 2013; Lunghi et al. 2017; Mammola & Isaia, 2018).

A clear gradient is also observed in the diversity of non-troglobitic species, which tends to decrease with increasing distance from the cave entrance. This pattern suggests the presence of ecological ecotones along the entrance-to-depth gradient. In the entrance zones, where environmental conditions are less extreme and organic matter input is higher, non-troglobitic species prevail. In contrast, as conditions become more oligotrophic, humid, and thermally stable deeper inside the cave, they increasingly favor the persistence of highly specialized troglobitic species that have evolved to thrive in these extreme subterranean conditions (Novak et al. 2012; Tobin et al. 2013; Kozel et al. 2019; Souza-Silva et al. 2021). This ecological gradient exemplifies how environmental filters and habitat specialization shape the distribution, composition, and coexistence of species in cave ecosystems.

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This study highlights the need for future research to explore the cave's ecological connectivity with its surrounding environments, including investigations of both surface and soil-dwelling fauna. Such studies would provide deeper insights into species interactions across habitats. Additionally, examining seasonal dynamics within these communities could help identify potential migration patterns and behavioral responses to environmental fluctuations.

## ACKNOWLEDGMENTS

We would like to thank Flávio Túlio, Tarsila Raposo, Mário César Laboissiérè, Maja Kraguljac, Xavier Prous, Cristiane Barros and Fábio Bondezan. We would also like to thank Maquinetur, Mario, Gilson, Tiola and Zé Luiz. Rodrigo Lopes Ferreira thanks the National Council for Scientific and Technological Development (CNPq grant no. 302925/2022-8), Dara Veiga thanks the Foundation for the Coordination of Improvement of Higher Education Personnel (CAPES) for the scholarship. We also thank Vale Company and the team at the Center for Studies in Subterranean Biology (CEBS/UFLA) for their support.

**Funding**

During the preparation of this manuscript, Rodrigo Lopes Ferreira was supported by a research productivity grant from the National Council for Scientific and Technological Development (CNPq, grant nº 302925/2022-8), and Dara Veiga received a scholarship from the Coordination for the Improvement of Higher Education Personnel (CAPES, grant nº 001).

**Conflict of Interest**

The authors declare that they have no conflict of interest.

**Author contribution:** All authors contributed to the study conception and design. Material preparation and data collection were performed by Rodrigo Lopes Ferreira and statistical analysis were performed by Dara Veiga and Marconi Souza-Silva. The first draft of the manuscript was written by Dara Veiga and all authors commented on previous versions of the manuscript. All authors read and approved of the final manuscript.

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Revista Brasileira de Espeleologia – RBEsp
ISSN 2179.4952- V.02 – N° .14 – 2025.
Recebido: 07 de agosto de 2025. Aceito: 12 de dezembro de 2025. Publicado: 23 de dezembro de 2025.

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## Supplementary material

*Table S1. Turnover and nestedness components of beta diversity between wet and dry seasons for each sampling site, based on the Temporal Beta Diversity Index (TBI). Values represent turnover (B), nestedness (C), and total dissimilarity (D = B + C) standardized by the Sørensen dissimilarity denominator (2A + B + C). The column "Change" indicates the direction of species replacement: "+" for sites with more species gained than lost (C > B), "−" for more losses than gains (B > C), and "0" for equal turnover and nestedness (B = C).*

| Sector | Distance (m) | Turnover (B/(2A+B+C)) | Nestedness (C/(2A+B+C)) | Beta Total (D) |
|---|---|---|---|---|
| S1A | 25 | 0.6977 | 0.1628 | 0.8605 |
| S1B | 50 | 0.2632 | 0.3158 | 0.5789 |
| S1C | 75 | 0.1250 | 0.5000 | 0.6250 |
| S1D | 100 | 0.3125 | 0.1875 | 0.5000 |
| S2A | 125 | 0.3333 | 0.1333 | 0.4667 |
| S2B | 150 | 0.4706 | 0.1765 | 0.6471 |
| S2C | 175 | 0.5455 | 0.0909 | 0.6364 |
| S2D | 200 | 0.6471 | 0.1176 | 0.7647 |
| S3A | 225 | 0.3810 | 0.4286 | 0.8095 |
| S3B | 250 | 0.5556 | 0.2222 | 0.7778 |
| S3C | 275 | 0.5385 | 0.1538 | 0.6923 |
| S3D | 300 | 0.4444 | 0.4444 | 0.8889 |
| S4A | 325 | 0.5000 | 0.2000 | 0.7000 |
| S4B | 350 | 0.4545 | 0.1818 | 0.6364 |
| S4C | 375 | 0.5455 | 0.2727 | 0.8182 |
| S4D | 400 | 0.4667 | 0.4000 | 0.8667 |
| S5A | 425 | 0.3846 | 0.4615 | 0.8462 |
| S5B | 450 | 0.4375 | 0.3125 | 0.7500 |
| S5C | 475 | 0.3333 | 0.5000 | 0.8333 |
| S5D | 500 | 0.4444 | 0.2222 | 0.6667 |
| S6A | 525 | 0.4286 | 0.1429 | 0.5714 |
| S6B | 550 | 0.1818 | 0.4545 | 0.6364 |
| S6C | 575 | 0.6667 | 0.1111 | 0.7778 |
| S6D | 600 | 0.4545 | 0.0000 | 0.4545 |
| S7A | 625 | 0.4444 | 0.1111 | 0.5556 |
| S7B | 650 | 0.7241 | 0.1379 | 0.8621 |
| S7C | 675 | 0.3846 | 0.3846 | 0.7692 |
| S7D | 700 | 0.2000 | 0.6000 | 0.8000 |
| S8A | 725 | 0.4500 | 0.3500 | 0.8000 |
| S8B | 750 | 0.1111 | 0.6667 | 0.7778 |