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Beyond the Banks: The Influence of a Subterranean River on the Cave Invertebrate Community, A Case Study in Niquelândia, Goiás, Brazil

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RESUMO: Os cursos d'água presentes no interior de cavernas podem exercer influência significativa sobre a riqueza e a composição das comunidades de invertebrados terrestres. Neste estudo, investigamos se a proximidade com uma drenagem ativa afeta a diversidade de espécies em uma caverna calcária. Para isso, realizamos amostragens comparativas em dois ambientes distintos: as margens de um curso d'água e um conduto superior mais seco. Utilizando metodologia padronizada, delimitamos setores e quadrantes como unidades amostrais, registrando tanto os invertebrados terrestres quanto os substratos do piso da caverna. Os resultados revelaram diferenças marcantes entre os ambientes úmidos e secos: foram registradas 35 espécies próximas ao curso d'água e 27 nas áreas secas, com *Endecous* sp1 destacando-se como o morfotipo mais determinante na variação composicional. A diversidade beta total foi de 0,72, com predominância da substituição de espécies como principal componente. Nesse sentido, a presença dessa drenagem molda de maneira significativa a fauna associada, regulando a umidade local, influenciando padrões de oviposição e atuando como vetor de matéria orgânica para o meio subterrâneo. Esses achados ampliam a compreensão sobre a dinâmica dos ecossistemas subterrâneos e fornecem subsídios relevantes para estratégias de conservação e manejo de ambientes cavernícolas.
Palavras-chave: Drenagem, Invertebrados, Cavernas, Estrutura da Comunidade, Temperatura, Umidade.

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ABSTRACT: Watercourses inside caves can exert significant influence on the richness and composition of terrestrial invertebrate communities. In this study, we investigated whether proximity to an active drainage affects species diversity in a limestone cave. For this purpose, we conducted comparative sampling in two distinct environments: the margins of a watercourse and a drier upper conduit. Using standardized methodology, we delimited sectors and quadrants as sampling units, recording both terrestrial invertebrates and the substrates present on the cave floor. The results revealed marked differences between humid and dry environments: 35 species were recorded near the watercourse and 27 in the dry areas, with *Endecous* sp1 standing out as the morphotype most determinant in compositional variation. Total beta diversity was 0.72, with species replacement as the predominant component. In this sense, the presence of this drainage significantly shapes the associated fauna, regulating local humidity, influencing oviposition patterns, and acting as an important vector of organic matter into the subterranean environment. These findings broaden our understanding of the dynamics of subterranean ecosystems and provide relevant support for conservation and management strategies of cave environments.
Key-words: Drainage, Invertebrates, Caves, Community Structure, Temperature, Humidity.

1. INTRODUCTION

Subterranean ecosystems represent exceptional “natural laboratories” due to their structural simplicity and reduced biodiversity compared to surface environments (Poulson & White, 1969; Mammola, 2019). These ecosystems are typically associated with caves, aquifers, wells, and other subterranean habitats, which are often partially isolated from external influences such as weather fluctuations and anthropogenic disturbances. This degree of isolation gives rise to distinct and stable environmental gradients that are rarely observed in surface systems (Badino, 2010; Souza-Silva et al., 2021; Reis-Venâncio et al., 2024).

One of the most pronounced gradients in subterranean environments is light availability. Proximal to cave entrances or skylights, sufficient light may penetrate to support limited photosynthetic activity, permitting the growth of phototrophic organisms such as vascular plants, lichens, and algae (Monro et al., 2018). However, light intensity decreases sharply with distance from these openings, and the deeper zones are typically completely aphotic, rendering them unsuitable for photoautotrophic life (Souza-Silva & Ferreira, 2022; Reis-Venâncio et al., 2024). In these lightless zones, energy inputs are derived primarily from allochthonous organic matter transported from the surface, supporting communities of heterotrophic organisms (Souza-Silva & Ferreira, 2022). These environments are often classified as oligotrophic due to their low nutrient availability (Simon et al., 2007). Nevertheless, exceptions exist in systems where autochthonous energy sources, such as chemoautotrophic production, sustain specialized faunal assemblages (Sarbu et al., 1996).

Another defining feature of subterranean ecosystems is their pronounced thermal stability. Temperatures within these environments remain relatively constant throughout the year, with minimal fluctuations typically not exceeding a few degrees Celsius (Cardoso et al., 2024). Consequently, subterranean habitats often harbor unique and endemic species, many of which exhibit structures and behaviors shaped by the subterranean environment, including reduced pigmentation, diminished or absent vision, and enhanced non-visual sensory modalities (Howarth, 2023). These traits reflect strong selective pressures imposed by the darkness, high humidity, and environmental constancy characteristic of subterranean ecosystems.

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Despite their apparent simplicity, subterranean ecosystems encompass a wide range of microhabitats, each providing distinct ecological niches that can be exploited by different invertebrate species (Souza-Silva et al., 2021, da Rocha Melo et al., 2025). These microhabitats may vary considerably in substrate type, moisture levels, and organic matter content, creating a complex interplay of factors that shape species distribution and community dynamics (Reis-Venâncio et al., 2022; da Rocha Melo et al., 2025).

Understanding how substrate availability and composition influence the associated fauna has become an increasingly important focus in contemporary ecological research, particularly in the Neotropics. This line of inquiry is highly relevant to the conservation of speleological heritage, as it helps elucidate the ecological processes that sustain subterranean life. Substrates such as guano, plant debris, sand, silt, and clay not only determine which organisms can persist in these environments but also regulate nutrient cycles and contribute to ecosystem stability (Souza-Silva et al., 2012). By clarifying the intricate relationships among substrate characteristics, moisture, nutrient availability, and biodiversity, researchers can support more effective conservation strategies aimed at safeguarding these fragile ecosystems, which often harbor high levels of endemism (Simões et al., 2014).

Research in subterranean environments not only advances the understanding of these systems but also provides valuable insights into evolutionary and ecological processes applicable to more complex ecosystems (Poulson & White, 1969; Mammola, 2019). Factors such as dispersal limitations, climatic variables, and habitat heterogeneity exert strong influences on both alpha and beta diversity, shaping species replacement and loss (turnover and nestedness) in cave-dwelling invertebrate communities (Calderón-Patrón et al., 2016; Souza-Silva et al., 2021; Reis-Venâncio et al., 2022, 2024). In this context, several factors have been recognized as drivers of invertebrate community structure in Neotropical caves, including the presence of drainage systems (Simões et al., 2015). Water bodies play a particularly important role in shaping patterns of dispersal and distribution across multiple animal groups. Flooding events, for instance, can generate disturbances that deeply alter community composition (Simões et al., 2015).

Drainage systems also enhance local humidity in both air and soil, thereby influencing faunal distribution (Simões et al., 2015). Moreover, river margins accumulate large amounts of transported and deposited organic matter, which serve as critical resources for cave-dwelling species (Souza-Silva et al., 2012). These processes highlight the potential importance of rivers in structuring invertebrate assemblages within caves, underscoring the need for detailed investigations to subsidize conservation and management strategies for these ecosystems.

In this context, the present study examines how proximity to a riverbank affects the composition and species richness of terrestrial invertebrates in a limestone cave. Specifically, we test two hypotheses: (i) species richness differs significantly between the regions analyzed, with greater richness expected in areas closer to the drainage; and (ii) faunal composition varies between regions, as distinct environmental conditions act as ecological filters, favoring species able to establish under the conditions of each habitat.

2. MATERIAL AND METHODS

Study site

Terrestrial invertebrates were sampled during a single field campaign conducted in the dry season of 2021. The study was carried out in Gruta da Lapa, located in the municipality of

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Niquelândia, northeastern Goiás state, Brazil (Figure 1), within the Cerrado biome, recognized as one of the world's biodiversity hotspots (Myers et al., 2000). The region is classified as having a tropical "Aw" climate under the Köppen–Geiger system, with a pronounced dry season extending from March to October (Álvares et al., 2013).

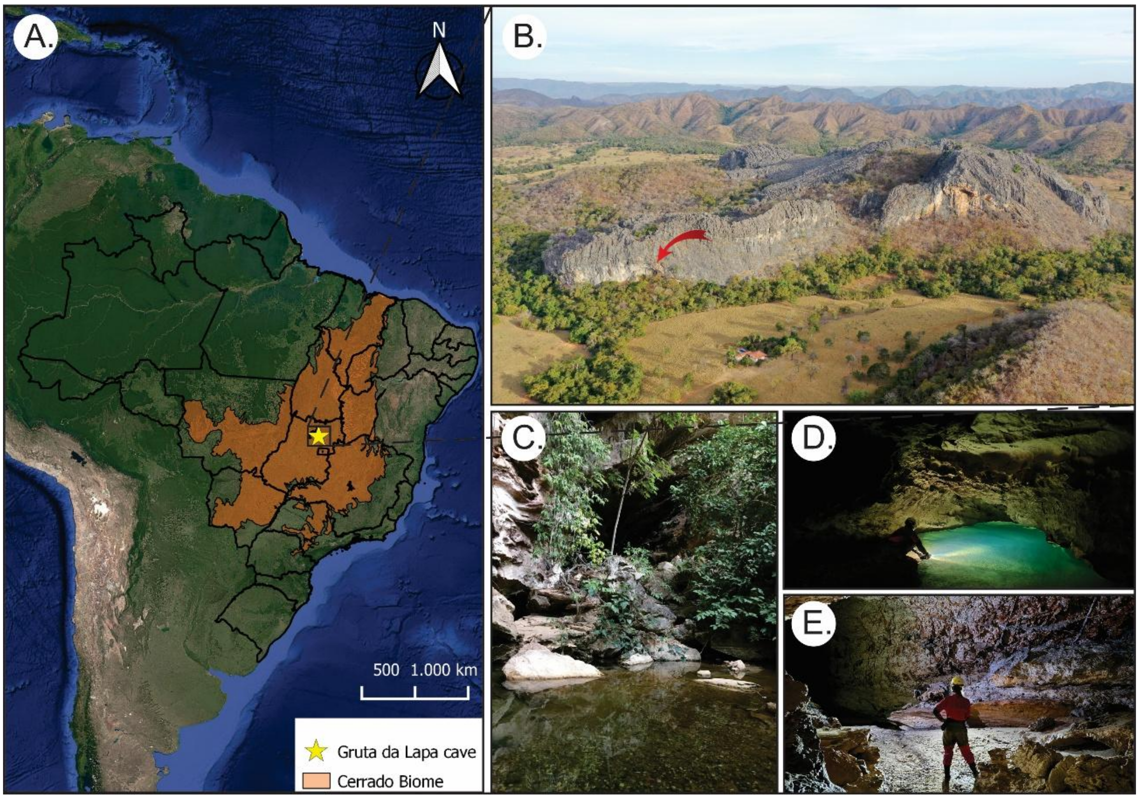

Figure 1. Location of Gruta da Lapa in the state of Goiás, Brazil (A); carbonate outcrop hosting the cave, with a red arrow indicating the cave's entrance (B); cave entrance at the upper portion, with the drainage at its base (C); drainage inside the cave (D); and internal cave conduit (E).

Gruta da Lapa contains an active autogenic drainage system that flows continuously throughout the year. This drainage emerges just below the main cave entrance, forming a spring. The cave has no skylights or secondary entrances, only the principal one. No established bat colonies were observed inside the cave, although small amounts of guano were recorded. The cave features linear conduits with few recesses: a lower conduit running adjacent to the river, and an upper conduit that is completely dry, with no direct contact with the drainage. In the vicinity of the entrance, local residents have constructed a dam to supply water to the surrounding community.

Sampling design

Invertebrate sampling was conducted at two spatial scales: sectors of 30 m² and quadrants of 1 m. Within each sector, three quadrants were evenly distributed on the cave floor - two positioned at the extremities and one centrally - as illustrated by Vaz et al. (2025). Along the entire cave, six sectors (totaling 18 quadrants) were established: three located along the drainage margin, approximately 25m, 60m, and 94m from the entrance, and three situated in a drier upper conduit, at about 120m, 65m, and 60m from the entrance (Figure 2). Sectors were used for compositional analyses and to enhance the cave's faunistic inventory by increasing species detectability. Species composition within each sector was determined by the specimens collected and by aggregating the

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species recorded across its three quadrants.

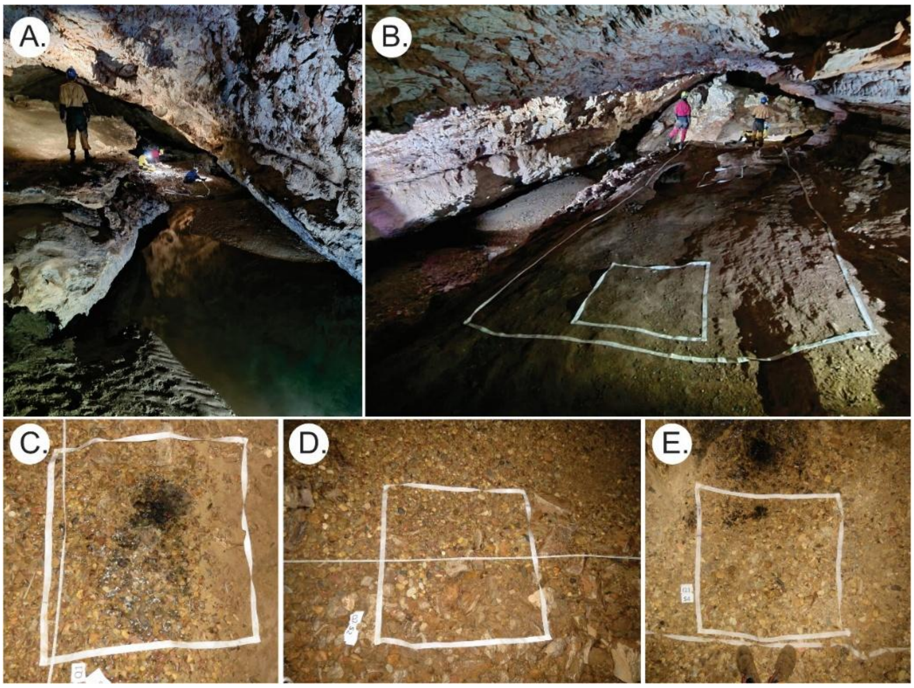

Figure 2. (A) Lower conduct along the drainage margin, highlighting one of the sampling points; (B) Upper passage in the dry-area of the cave, with one of the sampling points indicated; (C–E) Examples of sampling quadrats, illustrating the different substrates measured in the study.

Invertebrate sampling and identification

Terrestrial invertebrates were collected and recorded through visual searches and active manual collection using tweezers and brushes, following adapted methodologies from Ferreira (2004) and Wynne et al. (2019). Four experienced researchers conducted exhaustive sampling, including direct capture and in situ abundance recording within the predefined sectors and quadrants.

All specimens were preserved in labeled containers with 70% ethanol. In the laboratory, they were identified to the highest possible taxonomic level using stereomicroscopes and identification keys, then grouped into distinct morphotypes (Oliver & Beattie, 1966a, b). Finally, all specimens were deposited in the Collection of Subterranean Invertebrates of Lavras (ISLA), affiliated with the Center for Studies in Subterranean Biology at the Federal University of Lavras, Brazil (https://www.biologiasubterranea.com.br/en/).

Habitat structure measurement

To qualitatively and quantitatively characterize soil substrate components, digital photographs of each quadrant were taken prior to collection (several examples are shown in Figure S1), following Souza-Silva et al. (2021). Images were captured with the camera held at chest height and perpendicular to the soil surface to minimize distortion.

In the laboratory, images were analyzed using ImageJ software (Ferreira & Rasband, 2012) to calculate the area occupied by each substrate type within the quadrants. The total image area was standardized to 1, enabling determination of relative substrate proportions ranging from 0 to 1. Substrates were classified into the following categories: guano, leaf litter, thin and medium branches, water, matrix rock, small and medium blocks, coarse and fine gravel, sand, and silt.

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Data Analysis

Influence of Habitat Structuring on Species Richness

Substrate diversity was calculated using the Shannon index (H') (Magurran, 2004), based on the relative proportions of all substrate categories identified per quadrat. In addition, the diversity of organic resources and shelters was estimated separately, also using the Shannon index. Organic resources included guano, branches, and leaf litter, whereas shelters comprised branches, blocks, and gravel (Souza-Silva et al., 2021; Reis-Venâncio et al., 2024; Vaz et al., 2025).

Analyses of species richness were performed exclusively at the quadrat scale. Richness was estimated as the total number of morphospecies recorded per quadrat. To assess the influence of substrate, resource, and shelter diversities on species richness, we applied two independent Generalized Linear Models (GLMs) (Zuur, 2009). The first model included the river-margin quadrats, while the second included only dry-area quadrant. Both models assumed Poisson distribution, appropriate for count data.

Model fit was evaluated in two steps. First, we tested for overdispersion using the *testDispersion()* function in the "DHARMa" package (Harting, 2022). Subsequently, the *check_model()* function from the "performance" package (Lüdecke et al., 2021) was applied to assess homoscedasticity, agreement between predicted and observed values, residual normality, multicollinearity among predictors, zero inflation, and potential outliers.

Differences in mean species richness between river-margin and dry-area regions were tested using the Mann–Whitney U test (Mann & Whitney, 1947). To further explore substrate structure, we performed a cluster analysis based on the Whittaker Association Index (Clarke et al., 2014). Sampling units were grouped using the average linkage method and Euclidean distance, after fourth-root transformation of the data (Figure 3).

Faunal Similarity Between Assemblages

To compare faunal composition between river-margin and dry-area assemblages, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed on a Bray–Curtis similarity matrix constructed from Hellinger-transformed data (Legendre & Gallagher, 2001). Additionally, a Similarity Percentage (SIMPER) analysis was applied to determine the species contributing most to the dissimilarities between the two groups.

Beta diversity between regions was estimated using the *beta()* function of the "BAT" package (Cardoso et al., 2015), based on an abundance matrix at the sector level. This metric was partitioned into two components: β-replacement, representing compositional turnover between regions, and β-nesting, reflecting species loss (Baselga, 2010).

Species diversity within each region was further assessed using Hill numbers, which incorporate a sensitivity parameter (q) to differentially weight rare versus common species. The parameter varied from 0 to 3, in increments of 0.1. Low values (q = 0–1) emphasize rare species, whereas higher values ($q > 1$) progressively highlight common species. This approach provides a continuous framework for diversity assessment, unifying traditional indices such as species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$). Calculations were performed with the *hill_taxa()* function from the "hillR" package in R (Chao et al., 2014).

3. RESULTS

A total of 51 invertebrate species were recorded, distributed across 16 orders (Figure 2).

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Mean species richness per quadrat was higher in river-margin areas (3.22 ± 1.20 SD) compared with dry, more distant areas (1.80 ± 1.09 SD). The most species-rich orders were Araneae, Diptera, Coleoptera, and Hemiptera (Figure 3). In sectors near the river margin, 228 individuals representing 35 species were recorded, whereas 180 individuals belonging to 27 species were sampled in the dry portion of the cave. Photographs of several sampled species are shown in Figure 4.

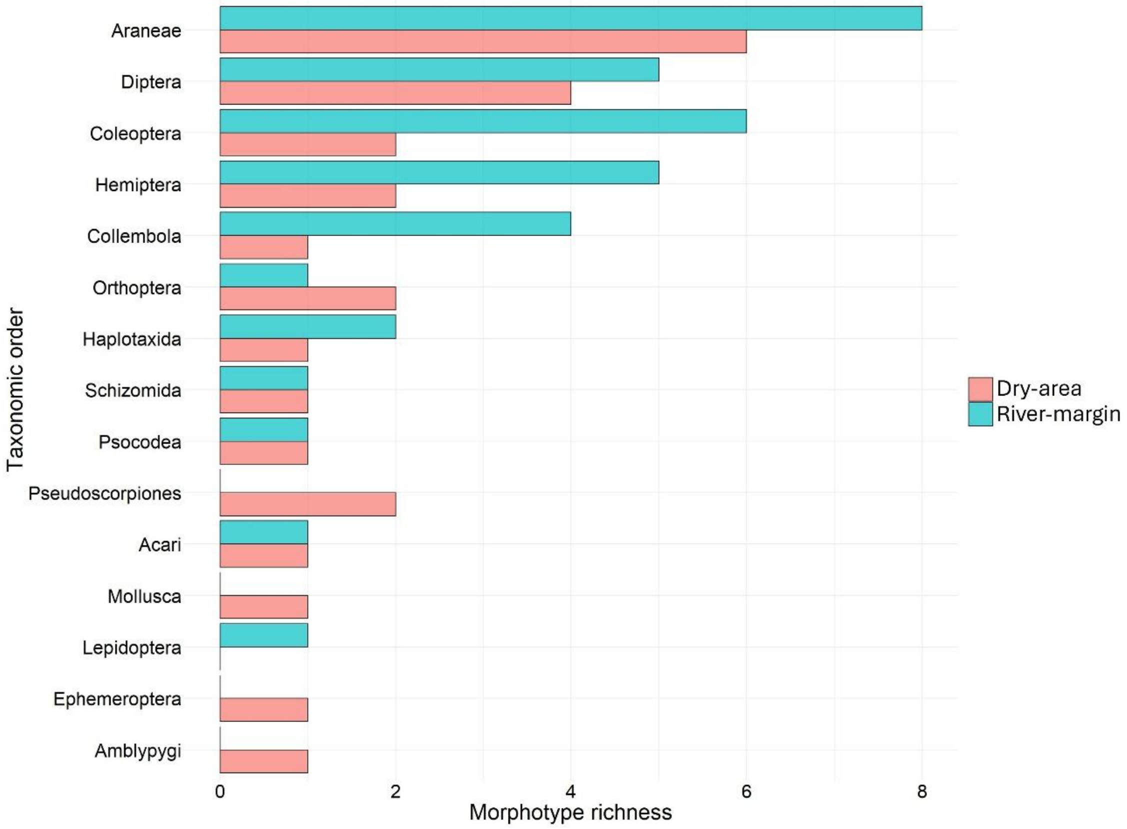

Figure 3. Morphospecies richness by taxonomic order recorded in each of the investigated areas, the river-margin and the dry-area, in Gruta da Lapa Cave, Niquelândia, northeastern Goiás, Brazil.

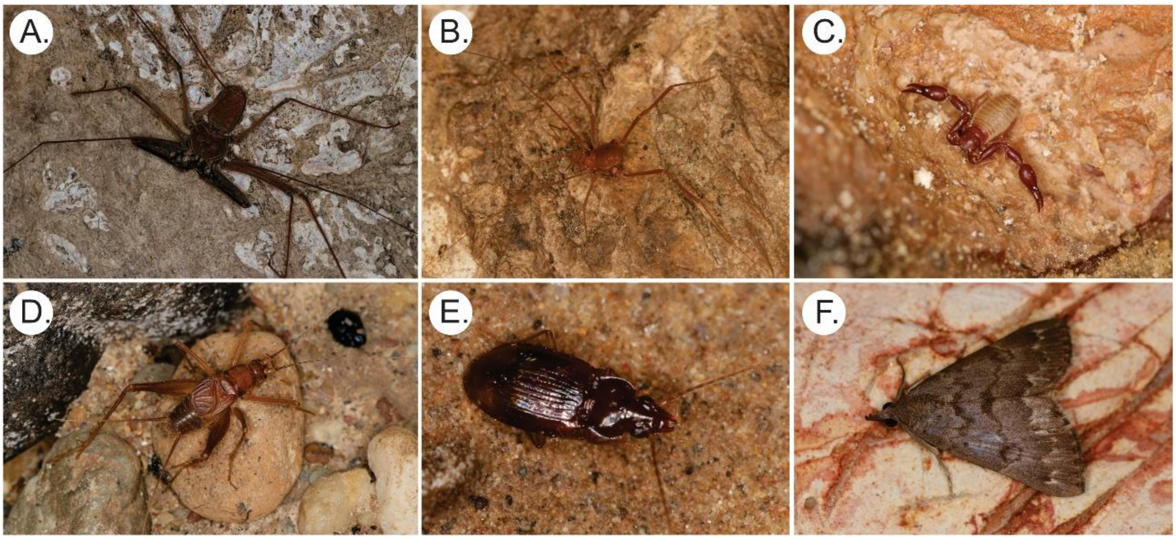

Figure 4. Representative species recorded during the study: (A) Heterophrynus (Amblypygi: Phrynidae); (B) an opilionid Eusarcus (Opiliones: Gonyleptidae); (C) a pseudoscorpion (Chernetidae); (D) Endecous (Orthoptera: Phalangopsidae); (E) a beetle from the subfamily Pterostichini (Carabidae); (F) Hypena (Lepidoptera: Erebidae).

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No significant relationships were detected between the diversity variables tested and morphospecies richness. However, the Mann–Whitney U test revealed a significant difference in mean richness between the two regions (W = 15.5; p = 0.026).

The Whittaker's Association Index indicated that the greatest guano concentration (GA) occurred in quadrat one of sector two (river-margin). The dendrogram revealed a relationship between distance from the entrance and blocks (Figure 5).

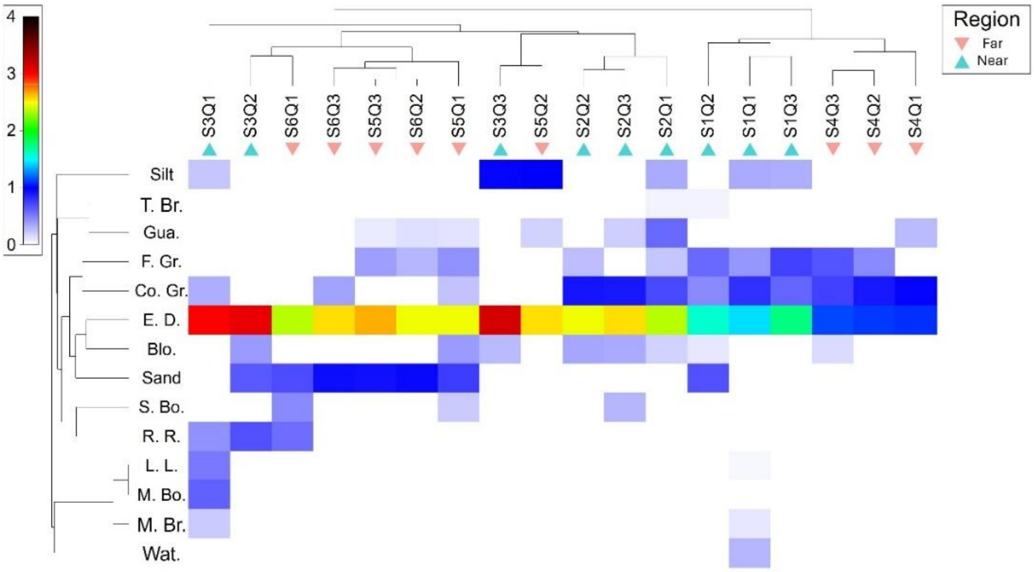

Figure 5. Whittaker Association Index showing the relationships between the quantities of different substrates and the distance from the cave entrance (D.E.). Substrates: T.Br., thin branch; Gua., guano; F.Gr., fine gravel; Co.Gr., coarse gravel; Blo., blocks; S.Bo., small boulder; R.R., rough rock; L.L., leaf litter; M.Bo., medium boulder; M.Br., medium branch; Wat., water.

Faunal composition differed significantly between river-margin and dry-area assemblages ($R^2 = 0.114$; $F = 2.06$; $p = 0.039$). SIMPER analysis identified *Endecous* sp. 1 ($p = 0.001$) as one of the main contributors to this dissimilarity, with preferential occurrence along the river margin. Beta diversity between regions was βtotal = 0.72, with species turnover contributing most (βreplacement = 0.57) and nestedness playing a smaller role (βnesting = 0.15).

Hill number analysis showed that for *q* values between 0 and 1, diversity was greater in river-margin sectors, indicating the predominance of rare species. For $q > 1$, however, diversity was higher in the dry-areas, reflecting the dominance of more widespread and relatively abundant species across sampling points (Figure 6).

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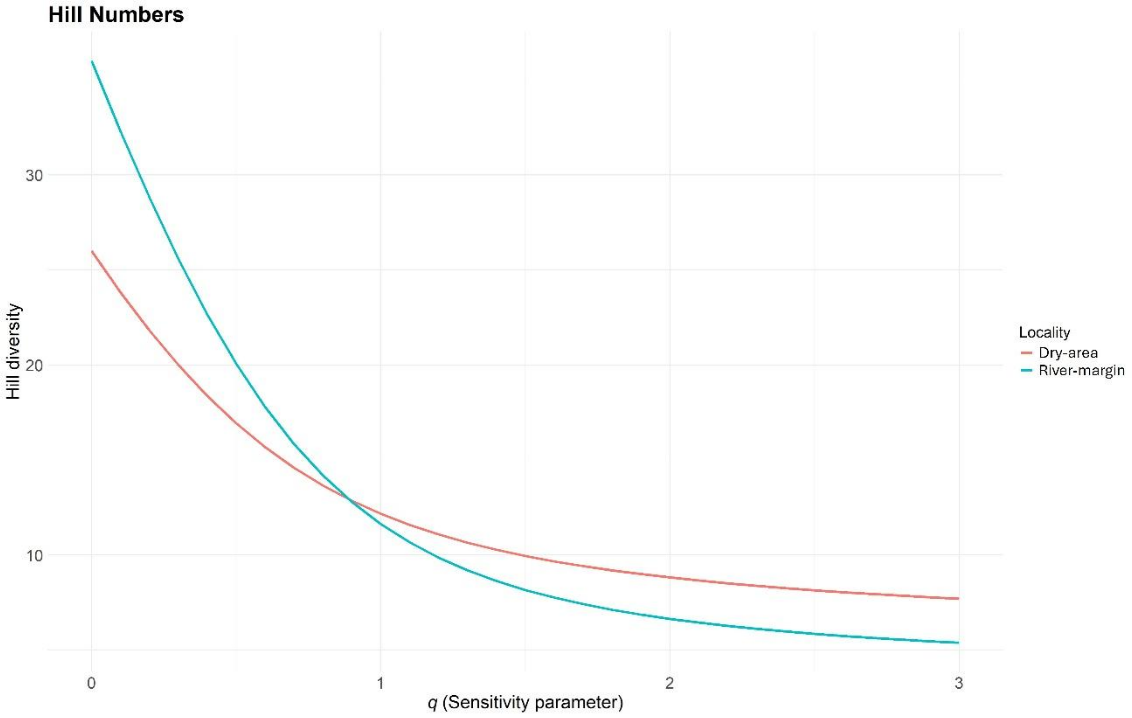

Figure 6. Hill number curve illustrating the variation in Hill diversity as a function of the sensitivity parameter (q). Values of q between 0 and 1 place greater emphasis on rare species, whereas values of q > 1 give more weight to the most frequent and/or abundant species.

4. DISCUSSION

Our findings, demonstrates that assemblages associated with different regions – "river-margin" and "dry areas" - differ significantly in both species' richness and composition. As expected, richness was greater in river-margin and lower in the dry areas. Community composition also varied, reflecting differences in ecological conditions and habitat structure, which appear to filter species according to their affinity for these environments and the specific niches they provide.

Variation in habitat structure is a key factor shaping invertebrate communities in subterranean ecosystems, and several structural parameters have previously been shown to play an important role in determining both species richness and community composition (Reis-Venâncio et al., 2024; da Rocha Melo et al., 2025). In the case of Gruta da Lapa, however, none of the parameters tested as proxies for habitat structure were related to richness or composition. This result may be attributable to the limited number of sampling units within the cave, as well as to the pronounced heterogeneity between the two sampled areas (river-margin and dry areas).

Our results indicate that proximity to the drainage exerts a significant influence on the composition of terrestrial invertebrate species within the cave. The drainage enhances both atmospheric and soil moisture, thereby creating favorable microhabitats that support the establishment of species adapted to such conditions (Chown et al., 2011). The homeostasis of these organisms is primarily regulated by thermoregulatory mechanisms and water balance, and environmental shifts in temperature or water availability commonly trigger adaptive responses (Chown et al., 2011). Notably, some invertebrates possess the ability to absorb water vapor directly from the environment through specialized hygrosensory mechanisms, enabling them to maintain water balance and homeostatic stability (Chown et al., 2011).

Beyond its role in elevating humidity, the river also functions as a key vector of organic

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matter into the subterranean environment, providing essential resources that sustain cave-dwelling communities. Similar dynamics have been documented in several cave systems worldwide (Weinstein, 1994; Souza-Silva et al., 2012). This process is ecologically significant, given that a substantial fraction of organic inputs in caves is of allochthonous origin, transported from external ecosystems. The continuous influx of moisture and resources from the river thus represents a critical driver of community structure.

Other critical environmental parameters, such as fluctuations in temperature and humidity levels, may play a significant role in shaping the distribution patterns of terrestrial invertebrate communities within caves (Souza-Silva et al., 2021). These factors may underline the differences in species richness observed between the analyzed sectors. Hill numbers revealed greater diversity of rare species in the river-margin areas, suggesting a measurable influence of the watercourse. Similarly, a recent study (Junta et al., 2025) demonstrated that habitat alterations can drive changes in species occurrence. The decline in non-troglobitic species (i.e., those not restricted to subterranean environments) with increasing distance from the entrance suggests that invertebrates not adapted to cave conditions are unable to persist due to a series of environmental filters. Taking together with other studies, these findings highlight the importance of watercourses as key structuring elements of subterranean ecosystems (Souza-Silva et al., 2021). The abrupt transition in humidity between the "margin river" and dry cave sectors may account for the high species turnover observed.

Humidity is a key environmental factor that directly influences the reproductive biology of many invertebrates. In females of crickets of the genus *Endecous*, oviposition site selection is strongly determined by substrate moisture (Farias-Martins et al., 2017). This preference likely accounts for the higher concentration of individuals in areas adjacent to rivers, where elevated humidity reduces the risk of desiccation (Castro-Souza et al., 2020). In addition, humidity can influence the acoustic signaling of males in stridulating species such as *Endecous* (Farias-Martins et al., 2017). The intense calls produced by males may serve as cues to females, indicating that the environment provides suitable conditions of moisture for oviposition (Hertl et al., 2001).

In contrast, some invertebrate species commonly recorded in cave environments were observed occupying microhabitats characterized by lower humidity levels, which may function as refuges. Groups such as Lepidoptera larvae, spiders of the family Filistatidae, and psocopterans of the family Psyllipsocidae were found predominantly in the drier cave sectors. Conversely, taxa such as *Endecous* sp.1, Carabidae (Coleoptera), and Veliidae (Hemiptera) were more abundant in moister areas, where high humidity is essential due to physiological constraints, increased foraging efficiency, or specific water requirements at certain stages of the life cycle.

These contrasting habitat preferences highlight the diverse adaptive strategies of cave invertebrates in meeting the demands of their ecological niches. Such patterns are shaped by the interplay between humidity (Souza-Silva et al., 2021) and resource availability (Simões et al., 2015).

In general, the presence of water bodies in caves is considered an important factor for increasing invertebrate richness, not only because they contribute to higher humidity but also because they function as pathways for the import of organic resources into subterranean ecosystems (Souza-Silva et al., 2012). Consequently, more humid environments are expected to harbor greater species richness (Simões et al., 2022). However, it is important to note that the drainage observed in this cave is of autogenic origin, with water flow beginning inside the cave and moving outward. This type of flow passes through multiple physical barriers that act as filters, preventing the passage of coarse organic material into the deeper portions. As a result, only fine

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particles or dissolved organic compounds are transported, which may be less attractive and/or accessible to many of the sampled invertebrates, or may not be detected by the methodology employed.

Overall, our findings highlight the central role of watercourses in shaping subterranean invertebrate communities, both by regulating humidity, influencing reproductive and behavioral patterns, and mediating the supply of organic matter. The marked differences between "river-margin" and "dry" cave sectors demonstrate how localized hydrological and microclimatic variation can strongly influence community assembly and species turnover. From a conservation standpoint, these results indicate that disturbances to natural hydrological regimes (such as groundwater extraction, alterations in surface drainage, or other human-driven impacts) can critically affect cave biodiversity. Safeguarding the natural dynamics of subterranean water systems is therefore essential to preserve the ecological processes that sustain species richness and functional diversity within cave ecosystems.

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Author Contributions

Rodrigo Lopes Ferreira was responsible for conceptualization, methodology, and English revision. Paulo César Reis-Venâncio conducted the statistical analyses, prepared the artwork, constructed the maps, and handled translation and revisions. Ana Laura Alves prepared the original draft. Ana Laura Alves, Paulo César Reis-Venâncio, Rodrigo Lopes Ferreira, and Marconi Souza Silva contributed to review and editing. All authors have read and approved the final 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 involvement that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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