

Species Turnover of Bryophytes Driven by Rare Species and Geomorphology in Neotropical Siliciclastic Caves

Rafael Costa Cardoso (1), Rodrigo Lopes Ferreira (1)

(1) Center of Studies in Subterranean Biology, Federal University of Lavras, Lavras, Brazil, ucarafael@gmail.com

Abstract

Caves harbor unique and specialized biodiversity, playing a critical ecological role within their ecosystems. Despite this, research on cave-dwelling plant communities, especially in tropical regions, remains limited compared to studies on cave fauna. Light, humidity, and temperature significantly influence plant growth within the different plant groups. In caves Bryophytes often dominate due to their adaptability to low-light and high-humidity conditions. These plants are essential in regulating water, influencing soil formation, and facilitating the establishment of other plant groups. This study aimed to explore the bryophyte communities associated with Brazilian caves, focusing on the effects of geomorphological features, altitude, and entrance distances using the Zeta diversity approach. Conducted at 13 cave entrances in Ibitipoca State Park (PEIB), a region known for its large quartzite caves and rich bryophyte diversity, the research identified 70 species, including 14 new records for PEIB. Bryophytes were predominantly rupicolous, terricolous, or corticolous, with leafy, mat, tuft, and weft forms being the most common life-forms. Zeta diversity analysis revealed that species turnover is primarily driven by rare species, with entrance dimensions, slope, and colonization depth significantly predicting diversity patterns. These findings underscore the ecological importance of caves as genetic reservoirs and refuges for rare species, emphasizing the need for conservation strategies to protect these unique environments.

1. Introduction

The distribution and intensity of light at cave entrances directly influence the composition and distribution of plant communities, making light the primary limiting factor for flora in these environments (Dobat, 1998; Abdulin, 2011; Mazina et al., 2023). Cave entrances, often situated in diverse landscapes with varying phytogeographic contexts, create unique ecological zones that bridge external ecosystems and the oligotrophic subterranean conditions. These ecotonal areas, while well-studied for faunal communities (Prous et al., 2015; Mammola & Isaia, 2018), can also play a critical role in cave flora varying factors like its entrance dimensions, geographic orientation, and soil composition (Alves & Kolbek, 1993; Badia et al., 2021; Monro et al., 2018). Plants adapted to low-light, high-humidity conditions, such as sciophytes and ombrophiles, are more likely to thrive in these habitats (Carmo et al., 2016; Puglisi et al., 2019).

Bryophytes, with their remarkable adaptability, dominate cave ecosystems due to their resilience to low-light and high-humidity

conditions (Puglisi et al., 2018, 2019; 2024; Cong et al., 2023). They play a crucial ecological role by shaping water dynamics, serving as bioindicators, supporting vegetational succession, and promoting habitats for diverse fauna. (Rodrigues et al., 2016; Ren et al., 2021). Furthermore, bryophyte diversity at cave entrances may serve as an indicator of overall plant community diversity, suggesting their importance as ecological architects (Ren et al., 2021). However, these plants are highly sensitive to climatic changes, and caves may serve as refuges for rare or threatened bryophytes, highlighting their conservation value amid global warming threats (Gabriel et al., 2004; Mammola et al., 2019a, 2019b).

This study explores the ecology of bryophytes at cave entrances in Brazil, examining how geomorphological features, altitude, colonization depth, and entrance distance shape their diversity. We hypothesize that rare species are more affected by distance due to limited dispersion, while common species respond to structural features. Insights from this research aim to inform conservation efforts to protect these unique ecosystems.

2. Materials and methods

Study Area

Ibitipoca State Park (PEIB) is a protected area located in the southeastern region of Minas Gerais, Brazil, within the municipality of Lima Duarte. Spanning 1,923.5 hectares (Fig. 1), PEIB is renowned for its large quartzite caves within a relatively small area (Corrêa-Neto, 1997; Willems et al., 2008; Wray & Sauro, 2017). Notably, it includes the largest and the third-largest quartzitic caves in Brazil: Martimiano II and Bromélias caves (Rubbiolli et al., 2019; Oliveira et al., 2024). The PEIB is known for its significant diversity of bryophytes nationwide. Over 300 bryophyte species have been recorded in Ibitipoca State Park (Amorim et al., 2011; Luiz-Ponzo et al., 2013; Yano & Luiz-Ponzo, 2014; Machado et al., 2016), of which 209 belong to liverworts (Marchantiophyta), a significant proportion of the total species reported for Brazil (Machado et al., 2016).

Sampling Design

Thirteen cave entrances within Ibitipoca State Park were studied between March and June 2022. At each entrance, all bryophytes plant species were surveyed and collected, starting from the speleometric closure point. Geographic data, including X and Y coordinates and altitude, were obtained using a Garmin GPSMAP 64s. Cave entrance dimensions (height, width, and slope) were measured using a handheld compass and laser rangefinder, with dimensions analyzed as height-to-width ratios.

Bryophyte samples were dried and identified by specialists at the Bryophytes Laboratory of the Federal University of Juiz de Fora (UFJF). Identification involved microscopic analysis using an Olympus SZ040 or Zeiss Stemi-200C stereoscopic microscope and Olympus BX41 or Zeiss Primo Star light microscope, following taxonomic guidelines by

Goffinet et al. (2009), Frey & Stech (2009), and Crandall-Stotler et al. (2009). Voucher specimens were deposited in the Herbarium Professor Leopoldo Krieger (CESJ) at UFJF.

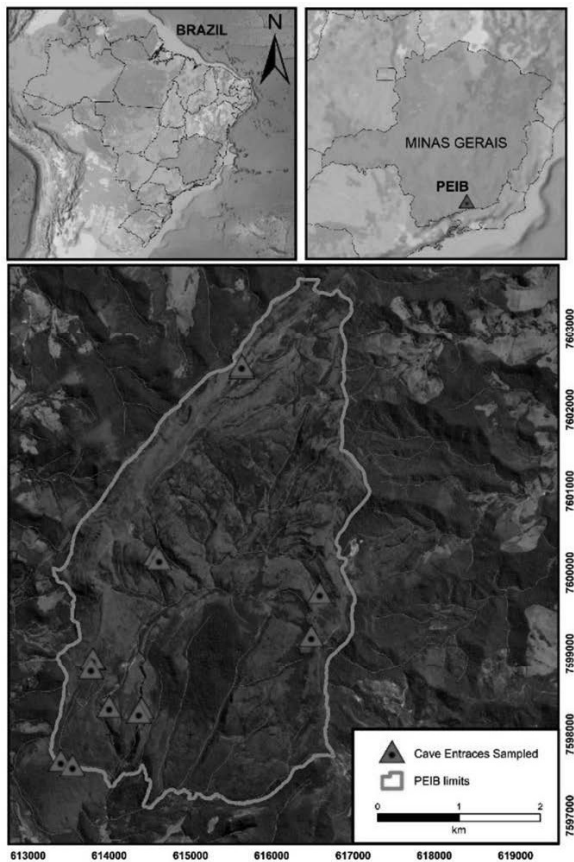


Figure 1: A - Ibitipoca State Parque limits and the distribution of cave entrances sampled Ibitipoca State Parque, located in Minas Gerais state, Brazil.

3. Results

Our study documented 14 bryophyte species previously unrecorded in Ibitipoca State Park (PEIB), including seven liverworts and seven mosses. The liverworts, belonging to five families, included *Riccardia hymenophytoides* (Aneuraceae), *Cephalozia crossii*, *Odontoschisma brasiliense* (Cephaloziaceae), *Heteroscyphus marginatus*, *Lophocolea heterophylla* (Lophocoleaceae), *Symphyogyna leptothelia* (Pallaviciniaceae), and *Plagiochila aerea* (Plagiochilaceae). The mosses represented six families: *Rhynchostegium serrulatum* (Brachytheciaceae), *Syrrophodon gardneri* (Calymperaceae), *Fissidens serratus*, *F. submarginatus* (Fissidentaceae), *Campylopus thwaitesii* (Leucobryaceae), *Lepidopilidium nitens* (Pilotrichaceae), and *Sphagnum magellanicum* (Sphagnaceae).

Interestingly, 11 of the 13 species previously reported by Yano &

Data Analysis

To access the life-forms and substrate preferences intrinsic to each bryophyte species, we used the information available in the Flora do Brasil database (REFLORA, 2024). To check previous records of each species in PEIB, we consulted publications on PEIB bryoflora by Yano & Luiz-Ponzo (2014) and Machado et al. (2016) and the scientific collections database SpeciesLink (SpeciesLink, 2024).

Zeta diversity (ζ) quantifies species shared across multiple assemblages, providing a framework for assessing biological diversity and species turnover patterns (Hui and McGeoch 2014; McGeoch et al. 2019). The zeta order represents the number of assemblages analyzed: ζ_1 corresponds to alpha diversity, ζ_2 to pairwise beta diversity, and higher orders assess species shared across more sites. We used this method to evaluate bryophyte diversity across sites, focusing on spatial variations in assemblages. Typically, zeta diversity decreases as the number of sites increases, with steep declines suggesting turnover driven by rare species, and gradual declines indicating turnover by common species. Retention rates, which measure species persistence across zeta orders, were compared across regions to understand the roles of rare and common species (Latombe et al., 2017, 2018).

To assess general diversity patterns, we calculated zeta diversity values (ζ_2 to ζ_6) and alpha diversity (ζ_1), using normalized zeta values to address site richness differences (McGeoch et al., 2019). Simpson-equivalent zeta (ζ_{ij}/S_j) and Sørensen-equivalent zeta (ζ_{ik}/S_{0k}) were employed to analyze nestedness and turnover (Baselga 2010). Zeta declines were modeled using the 'Zeta.decline' function from the 'zetadiv' R package (Latombe et al., 2018).

For environmental drivers of species turnover, we applied generalized dissimilarity models (GDM) using MS-GDM to evaluate spatial and environmental influences on zeta diversity across orders. This method accounts for non-linear environmental effects and spatial distances, exploring their impacts on turnover for both rare and common species. The analyses considered zeta orders 2 to 6, incorporating five environmental variables and inter-site distances, following Latombe et al. (2017, 2018).

Ponzo (2014) in cave environments were absent in our study, including *Brachymenium consimile*, *Rhodobryum beyrichianum* (Bryaceae), *Holomitrium olfersianum* (Dicranaceae), *Chryso-hypnum elegantulum* (Hypnaceae), *Lepidopilum brevipes* Mitt., *L. scabrisetum* (Schwägr.) Steere (Bryophyta: Pilotrichaceae), *Leptoscyphus amphibolius* (Nees) Grolle (Marchantiophyta: Geocalycaceae), *Saccogynidium caldense* (Ångstr.) Grolle (Marchantiophyta: Geocalycaceae), *Syzygiella trigonifolia* (Steph.) Herzog, *Hedwigia* (Marchantiophyta: Jamesoniellaceae).

Regarding bryophyte life forms, leafy forms were the most prevalent among cave bryophytes, followed by mats, tufts, and wefts. Substrate preferences predominantly included rupicolous, terricolous, and corticolous types.

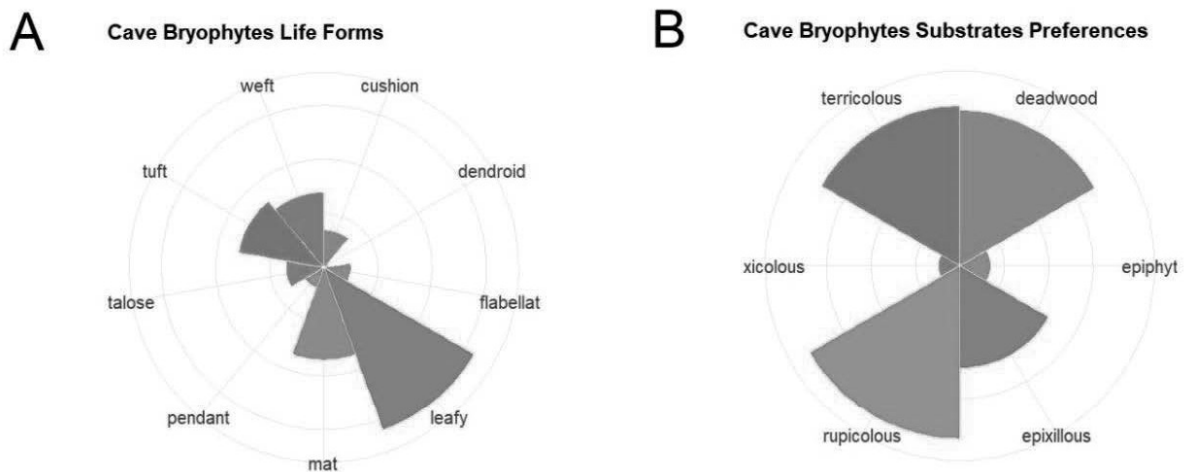


Figure 2: A) Life Forms and B) and substrate preferences of the species collected at the entrances of the caves studied.

Zeta diversity values declined rapidly to zero, with retention rates increasing sharply, reflecting a consistent pattern across both Sørensen and Simpson analyses (Fig. 5A, C). The slightly steeper decline in Sørensen at lower zeta orders indicates minimal nestedness effects. Retention rates dropped at higher zeta orders, suggesting that even the most common species are less likely to persist as more sites are added, emphasizing the turnover driven by rare or site-specific species.

4. Discussion

Tropical regions, known for their rich biodiversity, face significant anthropogenic threats, including in cave ecosystems (Myers et al., 2000; Ferreira et al., 2022). While considerable conservation efforts focus on subterranean biology, the study of cave-dwelling flora in tropical areas remains underexplored. Brazil, with its vast karst systems and caves across biomes like the Cerrado and Atlantic Forest, provides an opportunity to study such ecosystems. Ibitipoca State Park (PEIB), notable for its quartzite caves and exceptional bryophyte diversity, exemplifies this potential. Our study, focusing on 13 cave entrances, identified 70 bryophyte species, including 14 not previously recorded in PEIB. This expands the known checklist of cave bryophytes, highlighting caves as vital genetic reservoirs and habitats for endemic flora (Gabriel et al., 2004; Cong et al., 2023).

Bryophyte diversity at PEIB reflects substrate availability and environmental conditions. Liverworts are typically the most diverse group in the park, but in cave habitats, mosses were slightly more diverse in our study. Substrates in cave entrances, such as tree trunks and decomposing matter, are scarce, influencing species distribution and reducing diversity differences between liverworts and mosses compared to external environments (Yano & Ponzo, 2014). Thalloid liverworts often colonize terrestrial substrates, while leafy liverworts and mosses adapt to varied substrates, with mosses showing greater habitat generalism and tolerance for low light (Shaw & Goffinet, 2000; Herrero-Borgoñón, 2024).

Subterranean conditions filter bryophyte communities, favoring specific life forms like leafy, turf, weft, and mat forms, which reflect adaptations to environmental challenges. Dense forms like cushions or turfs store water but receive less light, while mats and wefts thrive in shady, humid environments typical of caves (Vittoz et al., 2010; Bates, 1998). These functional traits underscore the ecological strategies of bryophytes in adapting to the oligotrophic, low-light, and high-humidity conditions of cave entrances.

Spatial distance emerged as a key driver of turnover for rare species ($\zeta_{2,3}$), while common species (ζ_{4-6}) were influenced primarily by slope and depth of colonization. For ζ_2 , entrance ratio, slope, and colonization depth were significant, whereas slope was the dominant factor for ζ_3 . The MS-GDM models explained variances of 42.9% (ζ_2), 59.7% (ζ_3), 62.5% (ζ_4), 56.1% (ζ_5), and 41.7% (ζ_6), highlighting the distinct environmental and spatial variables affecting turnover across different zeta orders.

Turnover Patterns

Zeta diversity analyses revealed a rapid decline from the second to higher zeta orders, highlighting the dominance of rare species in the cave bryophyte communities of PEIB. This exponential decline, consistent in both Sørensen and Simpson analyses, indicates minimal nestedness effects and suggests that species retention across sites is largely stochastic (Latombe, 2017; Fonte et al., 2021). The retention rate patterns, where rates initially rise but then decrease at higher zeta orders, emphasize the influence of rare species on turnover, with even common species becoming less likely to persist across multiple sites.

These findings point to a small core of common species widely distributed and a larger pool of rare species restricted to specific locations. The unique environments of caves, shaped by geographic isolation and distinct microhabitats, foster this pattern by serving as refuges for rare, endemic, and relict species (Culver & Pipan, 2019; Oliveira & Ferreira, 2024; Gabriel et al., 2004; Monro et al., 2018; Cong et al., 2023).

Drivers of Turnover

MS-GDM models highlighted spatial distance as a critical factor driving turnover for rare species (ζ_{2-3}) but less influential for common species (ζ_{4-6}). Entrance dimensions significantly affected turnover at lower zeta orders, indicating lower phylogenetic distances when species overlap increases. As zeta orders rose, factors like slope and colonization depth gained importance, particularly for common species.

Steeper slopes at cave entrances were associated with higher nutrient and moisture inputs from surface environments, creating favorable substrates for colonization. These conditions align with the requirements of bryophytes, which depend on water for metabolic processes and gamete motility during reproduction (Lemos-Michel, 2001). Thus, environmental factors at cave entrances drive the compositional differences observed between rare and common species, reflecting the critical ecological role of these unique habitats.

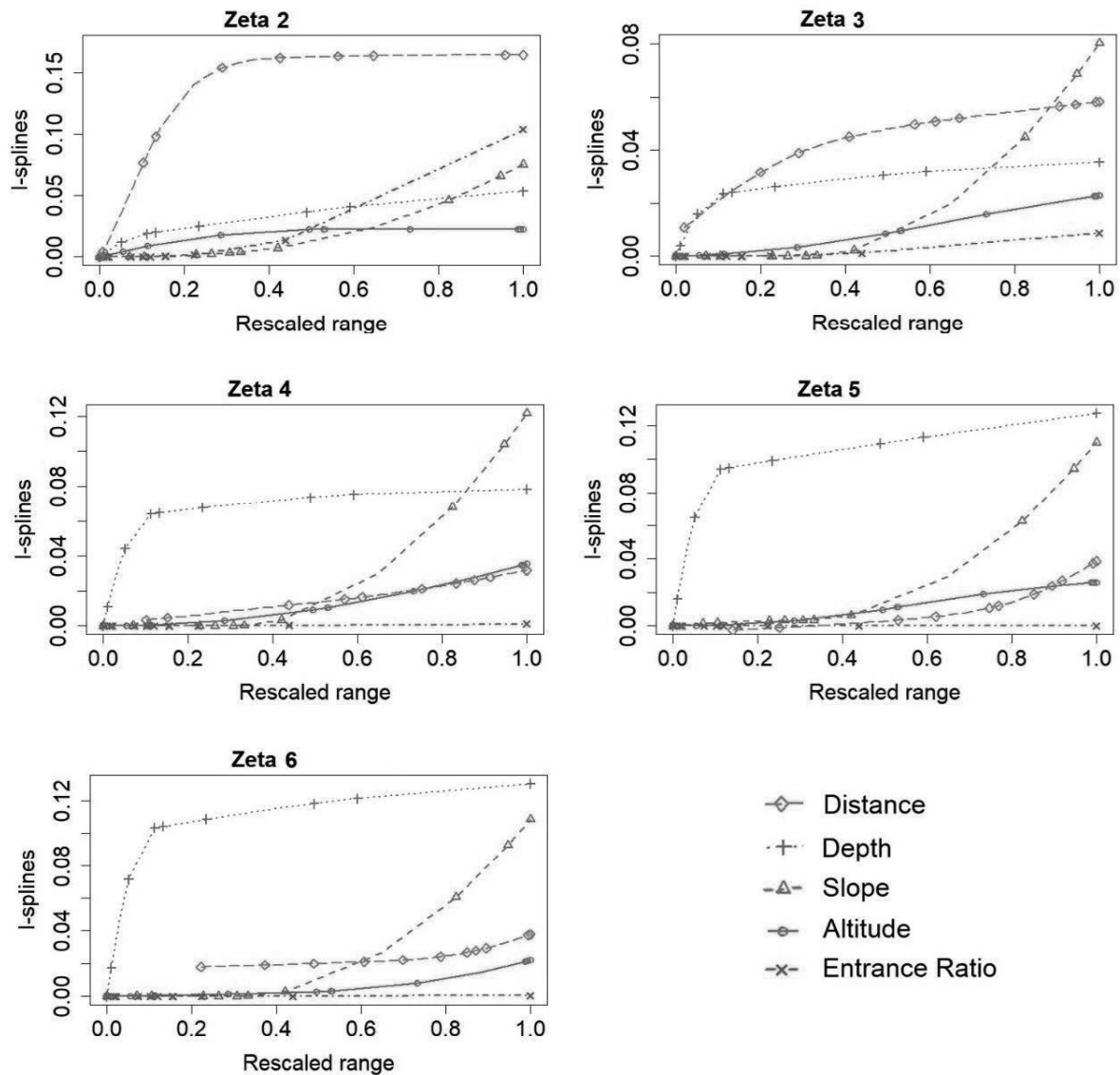


Figure 3: MS-GDM analyses for zeta orders 2-6 using environmental features and straight-line distances between sites based on their geographic coordinates of the cave entrances bryoflora communities sampled.

5. Conclusion

In conclusion, our study underscores that, similar to findings in non-tropical caves, some Brazilian caves serve as important habitats for bryophyte communities, supporting highly diverse and unique assemblages. Our research in Ibitipoca State Park identified 70 bryophyte species, including 14 new records, and highlighted that cave geomorphological features (such as entrance dimensions and slope) as well as geographic

distance, are significant factors in predicting bryophyte diversity and phylogenetic similarity among subterranean habitats. Furthermore, rare species appear to play a key role in driving species turnover. This research provides valuable insights into the ecology of cave flora in tropical regions and supports ongoing conservation efforts aimed at protecting cave habitats and their associated flora.

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