UNIVERSIDADE FEDERAL DE LAVRAS

GABRIELLE SOARES MUNIZ PACHECO

COMO OS ATRIBUTOS AMBIENTAIS AFETAM E LIMITAM AS COMUNIDADES DE INVERTEBRADOS EM CAVERNAS TROPICAIS E SUAS ÁREAS ADJACENTES?

LAVRAS - MG
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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas para a obtenção do título de Doutor.

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"Poucos são aqueles que veem com seus próprios olhos e sentem com seus próprios corações."

Albert Einstein

RESUMO

Ambientes subterrâneos desempenham um papel crucial como ecossistemas complexos, oferecendo refúgio para invertebrados e vertebrados que desempenham serviços ecológicos na superfície. No Brasil, a conservação da fauna cavernícola enfrenta desafios devido à falta de metodologias eficazes. O interesse minerário em regiões com alta incidência de cavernas, permitida por legislações recentes, apresenta desafios para conciliar preservação e exploração. A legislação utiliza o conceito de "área de influência" para se referir as áreas adjacentes às cavernas, mas a falta de métodos padronizados para sua determinação dificulta sua definição quando se objetiva a preservação de espécies de invertebrados terrestres que habitam essas áreas. Estudos indicam a importância não apenas da proteção da cavidade, mas também de seu entorno para a conservação eficaz. Esta tese então contribui par ao conhecimento das relações entre os invertebrados terrestres de ambientes subterrâneos e de superfície, a fim de guiar a definição de áreas de influência em cavernas de diferentes litologias. Composta por dois manuscritos, o primeiro busca compreender os fatores essenciais para a manutenção de comunidades de invertebrados nos ambientes subterrâneo e epígeo em áreas cársticas de diferentes litologias ao longo das estações chuvosa e seca, enquanto o segundo investiga os fatores limitantes para a similaridade da fauna entre os ambientes subterrâneo e epígeo em diferentes litologias e estações do ano.

Palavras-Chave: ambientes cársticos; fauna de invertebrados; ecossistemas subterrâneos; fatores ambientais; similaridade de espécies; micro-habitats; conservação; conectividade de cavernas; área de influência; condições climáticas.

ABSTRACT

Subterranean environments play a crucial role as complex ecosystems, providing refuge for invertebrates and vertebrates that perform ecological services on the surface. In Brazil, the conservation of cave fauna faces challenges due to the lack of effective methodologies. Mining interest in regions with a high incidence of caves, permitted by recent legislation, poses challenges in reconciling preservation and exploitation. The legislation employs the concept of "influence area" to refer to areas adjacent to caves, but the lack of standardized methods for its determination complicates its definition when the aim is to preserve terrestrial invertebrate species inhabiting these areas. Studies indicate the importance of protecting not only the cavity itself but also its surroundings for effective conservation. This thesis contributes to the understanding of the relationships between terrestrial invertebrates in subterranean and surface environments to guide the definition of influence areas in caves of different lithologies. Comprising two manuscripts, the first seeks to understand the essential factors for maintaining invertebrate communities in subterranean and epigeal environments in karst areas of different lithologies throughout the rainy and dry seasons. The second manuscript investigates the limiting factors for the similarity of fauna between subterranean and epigeal environments in different lithologies and seasons of the year.

Keywords: karst environments; invertebrate fauna; subterranean ecosystems; environmental factors; species similarity; microhabitats; conservation; cave connectivity; influence area; climatic conditions.

INDICADORES DE IMPACTO

Os ambientes subterrâneos podem desempenhar o papel de ecossistemas complexos, oferecendo refúgio a uma variedade de invertebrados e vertebrados que desempenham serviços ecológicos nos ecossistemas de superfície. Além disso, esses ambientes frequentemente exibem uma notável riqueza de espécies que são estritamente adaptadas ao ambiente cavernícola, sendo muitas vezes endêmicas. No entanto, a conservação da fauna cavernícola no Brasil enfrenta desafios devido à carência de metodologias eficazes para compreender e proteger essa biodiversidade, visando atenuar os impactos da atividade humana sobre esses ecossistemas. Por outro lado, a atividade de mineração em áreas próximas a cavernas é permitida pela legislação brasileira, desde que siga as diretrizes e parâmetros estabelecidos. Entretanto, apesar de preservação das áreas ao redor das cavernas (áreas de influência) ter sido incluída na legislação brasileira, o setor minerário tem se deparado com questões que dificultam a expansão de suas atividades em locais com cavernas pelo fato de que as legislações pertinentes se utilizam do conceito sem que existam métodos padronizados que permitam definir, com segurança, estas áreas. Diante disso, a necessidade de estudos que auxiliem na definição de metodologias de determinação de área de influência é essencial. Portanto, esta tese teve como principal objetivo produzir resultados que possam contribuir no conhecimento fundamental das relações entre a fauna de invertebrados das cavernas e seus ambientes externos adjacentes, a fim de embasar e auxiliar a criação de métodos padronizados e políticas para a delimitação de áreas de influência em ambientes de cavernas inseridas em diferentes tipos de rocha (Carbonáticas, Ferruginosas e Quartzíticas). Ela é composta por dois manuscritos que visam compreender a relação entre os ambientes epígeo e hipógeo, do um ponto de vista biológico, tendo como objeto de estudo os invertebrados terrestres. O primeiro manuscrito tenta elucidar quais os fatores essenciais para a manutenção das comunidades de invertebrados de superfície e subterrâneos em áreas cársticas de diferentes litologias, ao longo das diferentes estações do ano. Já o segundo capítulo objetiva determinar quais são os fatores limitantes para a similaridade da fauna de invertebrados terrestres das cavernas de diferentes litologias e suas áreas adjacentes ao longo das diferentes estações do ano.

IMPACT INDICATORS

Underground environments can play the role of complex ecosystems, offering refuge to a variety of invertebrates and vertebrates that perform ecological services in surface ecosystems. Furthermore, these environments often display a remarkable richness of species that are strictly adapted to the cave environment, and are often endemic. However, the conservation of cave fauna in Brazil faces challenges due to the lack of effective methodologies to understand and protect this biodiversity, aiming to mitigate the impacts of human activity on these ecosystems. On the other hand, mining activity in areas close to caves is permitted by Brazilian legislation, as long as it follows established guidelines and parameters. However, although the preservation of areas around caves (areas of influence) has been included in the legal framework, the mining sector has been faced with issues that make it difficult to expand its activities in places with caves due to the fact that the relevant legislation uses concept without there being standardized methods that allow these areas to be defined safely. Given this, the need for studies that help define methodologies for determining the area of influence is essential. Therefore, the main objective of this thesis was to produce results that could contribute to the fundamental knowledge of the relationships between the cave invertebrate fauna and their adjacent external environments, in order to support and assist the creation of standardized methods and policies for the delimitation of areas of influence. in cave environments inserted in different types of rock (Carbonatic, Ferruginous and Quartzite). It is composed of two manuscripts that aim to understand the relationship between epigean and hypogean environments, from a biological point of view, with terrestrial invertebrates as the object of study. The first manuscript attempts to elucidate which factors are essential for the maintenance of surface and underground invertebrate communities in karst areas of different lithologies, throughout the different seasons. The second chapter aims to determine what are the limiting factors for the similarity of the terrestrial invertebrate fauna of caves of different lithologies and their adjacent areas throughout the different seasons of the year.

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PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Os ambientes cavernícolas consistem de ecossistemas únicos, que oferecem refúgio a uma variedade de invertebrados e vertebrados que desempenham serviços ecológicos tanto nos ambientes subterrâneos quanto nos ecossistemas de superfície. Além disso, esses ambientes frequentemente exibem uma notável riqueza de espécies que são estritamente adaptadas ao ambiente cavernícola, sendo muitas vezes endêmicas.

A relação entre cavernas e os ambientes de superfície torna-se aparente ao considerar que a maioria da fauna cavernícola consiste de animais que transitam entre os ambientes de superfície e subterrâneo, com diversos níveis interdependência destes ambientes. Além disso, a fauna de cavernas em regiões tropicais constitui um subconjunto do pool de espécies regionais, destacando a intrincada interconexão entre os ecossistemas subterrâneos e de superfície (Gibert e Deharveng, 2002; Mendes-Rabelo et al., 2020).

No entanto, a relação entre os ambientes de superfície e subterrâneo é complexa, pois pode ser influenciada por diversos fatores dentro da paisagem de superfície. Esses fatores incluem variações na composição litológica das cavernas, vegetação associada, status de conservação, padrões de uso da terra e o pool regional de espécies de superfície (Souza-Silva et al., 2011a; Pellegrini et al., 2016; Mammola et al., 2017; Jaffé et al., 2018; Mendes-Rabelo et al., 2020; Cardoso et al., 2022).

Muitos desses fatores influenciam significativamente os padrões climáticos locais, e quaisquer mudanças em um ou mais desses fatores podem potencialmente perturbar o equilíbrio ambiental característico das cavernas (Barker & Genty, 1998). Essas variações, especialmente aquelas relacionadas ao clima, podem afetar negativamente as espécies cavernícolas, principalmente aquelas restritas a esse ecossistema específico, pois dependem diretamente de temperaturas estáveis e alta umidade para sua sobrevivência (Howarth, 1993; Gillieson, 1996; Gibert & Deharveng, 2002).

Nos ecossistemas de cavernas, a penetração restrita da luz em áreas mais profundas e a consequente ausência de produtividade primária direta por meio da fotossíntese destacam a importância dos recursos orgânicos do ambiente de superfície para sustentar a fauna (Schneider et al., 2011; Souza-Silva et al., 2011b; Smrž et al., 2015). Dentro desses ambientes, a fonte de energia fundamental para a cadeia alimentar é predominantemente heterotrófica e alóctone (Souza-Silva et al., 2011b). Esse recurso abrange vários componentes vegetais, como raízes, folhas, troncos e frutos; animais, incluindo carcaças, fezes e materiais regurgitados; e microrganismos, todos provenientes do ambiente de superfície adjacente (Ferreira et al., 2015;

Smrž et al., 2015). Consequentemente, determinar áreas de superfície para a conservação da fauna cavernícola é imperativo para manter as condições ambientais e seus recursos tróficos.

Na legislação brasileira, as áreas epígeas adjacentes às cavernas são denominadas “áreas de influência”. Apesar de a preservação dessas áreas de influência ter sido incluída no arcabouço jurídico, as legislações pertinentes (BRASIL, 2008, MMA, 2017) utilizam-se deste conceito sem que existam ainda métodos padronizados que permitam definir, com segurança, estas áreas. Diante disso, a necessidade de estudos que auxiliem na definição de metodologias de determinação de área de influência é essencial.

Foi publicado um documento técnico pelo Centro Nacional de Pesquisa e Conservação de Cavernas (CECAV) indicando três critérios bióticos para a determinação desta área. São eles: conectividade do sistema subterrâneo através da distribuição de espécies troglóbias; avaliação das espécies de morcegos que aportam recursos (guano) para o interior da caverna; e estudos sobre a contribuição de sistemas radiculares de plantas e de animais acidentais para as cavernas (CECAV, 2022). Apesar da relevância dos critérios propostos, eles não contemplam especificamente as demais variáveis ambientais que influenciam o sistema cárstico, nem a maior parte da fauna que habita o ambiente subterrâneo. Além disso, estão susceptíveis a alto nível de subjetividade de acordo com a interpretação do responsável pelo estudo e/ou análise ambiental.

Ademais, há outros indicadores biológicos que deveriam ser considerados. Entre eles, podemos destacar os fatores ambientais (manutenção da estabilidade ambiental, nível de luminosidade e importação de recursos tróficos) e ecológicos (comunidade e espécies troglófilas e troglóxenas obrigatórias). Diferentes estudos têm mostrado que a conservação eficaz do ambiente subterrâneo não se limita à proteção apenas da cavidade, mas também de seu entorno (Hildreth-Werker & Werker 2006, Xiao & Weng 2007, Elez et al 2013). Porém, A maioria dos estudos realizados consideram fatores físicos (ex. Sánchez et al 2007) e cênicos/rupestres (ex. Xiao & Weng 2007), mas não os biológicos. Os poucos trabalhos avaliaram as relações entre fauna externa e subterrânea foram desenvolvidos abordando apenas as zonas ecotonais da entrada das cavernas (Prous et al 2004 e 2015; Bento et al., 2021; Oliveira & Ferreira, 2024).

Embora seja reconhecida a importância do ambiente externo para o subterrâneo, não há estudos que indiquem os métodos ou elementos a serem considerados no tocante à delimitação desta área epígea associada à manutenção da dinâmica biológica dos ambientes subterrâneos. Faz-se assim necessária e urgente a proposição de metodologias que visam delimitar, do ponto de vista biológico, as áreas epígeas para conservação no entorno das cavidades, de forma a garantir a proteção da fauna subterrânea.

Sendo assim, esta tese tem como principal avaliar as relações entre a fauna de invertebrados das cavernas e seus ambientes externos adjacentes, em ambientes de cavernas inseridas em diferentes tipos de rocha (Carbonáticas, Ferruginosas e Quartzíticas). Ela é composta por dois manuscritos que visam compreender a relação entre os ambientes epígeo e hipógeo, do um ponto de vista biológico, tendo como objeto de estudo os invertebrados terrestres. O primeiro manuscrito tenta elucidar quais os fatores essenciais para a manutenção das comunidades de invertebrados de superfície e subterrâneos em áreas cársticas de diferentes litologias, ao longo das diferentes estações do ano. Já o segundo capítulo objetiva determinar quais são os fatores limitantes para a similaridade da fauna de invertebrados terrestres das cavernas de diferentes litologias e suas áreas adjacentes ao longo das diferentes estações do ano.

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SEGUNDA PARTE: ARTIGOS

ARTIGO 1

Different rocks, different weathers: How environmental attributes affect invertebrate communities in caves and their surrounding areas?

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ABSTRACT

The intricate interplay between surface and subterranean ecosystems significantly influences the diversity and composition of terrestrial invertebrate communities. This study delves into the relationships within and between these environments across different lithologies and seasons. Analyzing limestone and quartzitic caves in southeastern Brazil, we explore species richness, composition, and the impact of environmental variables on invertebrate communities. Our study revealed a notable diversity of invertebrate species, with significant variations in richness and composition between subterranean and surface environments. The DistLM models, demonstrated that climatic variables, particularly humidity and temperature, significantly influence species composition, with variations observed between lithologies and environments. The stability of microclimatic conditions within cave systems emerges as a critical factor influencing the subterranean fauna. The dissimilarities in invertebrate composition between surface and subterranean environments underscore the selective pressures imposed by caves, challenging species to overcome such environmental filters. Despite surface environments offering greater variability in conditions and trophic resources, our findings highlight the importance of local environmental context and specific conditions in shaping invertebrate communities. Furthermore, spatial variability within caves emphasizes the necessity for a nuanced approach to conservation, considering the heterogeneity of habitats within each cave system. Overall, this study contributes to a comprehensive understanding of subterranean ecosystems and their surrounding areas, emphasizing the need for tailored conservation strategies that account for both regional and cave-specific factors in the context of global environmental changes.

Key words. influence areas; subterranean biology; ecosystem ecology.

1 INTRODUCTION

The relationship between caves and the surface environments becomes apparent when considering that the majority of cave fauna consists of troglophiles and trogloxenes (Tobin et al., 2013; Deharveng & Bedos, 2018). The former refers to species adapted to living in both environments, while the latter depends on the surface compartment to complete their life cycle (Sket, 2008; Howarth & Moldovan, 2018). These species exhibit a closer relationship with the surface when compared to the troglobites, which are the ones that live exclusively in the subterranean habitat (Sket, 2008; Howarth & Moldovan, 2018). Moreover, the cave fauna many times consists in a subset of the regional species pool, underscoring the interconnection between underground and surface ecosystems, as observed in the neotropical region (Gibert and Deharveng 2002; Mendes-Rabelo et al., 2020).

Nonetheless, the relationship between surface and subterranean environments is intricate, as it can be influenced by diverse factors within the surface landscape. These factors include variations in the lithological composition of the caves, associated vegetation, conservation status, land use patterns, and the regional pool of surface species (Souza-Silva et al., 2011a; Pellegrini et al., 2016; Mammola et al., 2017; Jaffé et al., 2018; Mendes-Rabelo et al., 2020; Cardoso et al., 2022). Many of these factors significantly influence local climatic patterns, and any changes in one or more of these factors may potentially disrupt the characteristic environmental equilibrium of caves (Barker & Genty, 1998). These variations, particularly those related to climate, can negatively affect cave-dwelling species, especially those restricted to this specific ecosystem, as they depend directly on stable temperatures and high humidity for their survival (Howarth, 1993; Gillieson, 1996; Gibert & Deharveng, 2002).

In cave ecosystems, the absence of light into deeper areas and the resulting absence of direct primary productivity through photosynthesis underscore the significance of organic resources from the surface environment for sustaining the fauna (Schneider et al., 2011; Souza-Silva et al., 2011b; Smrž et al., 2015). Within these environments, the foundational energy source for the food chain is predominantly heterotrophic and allochthonous (Souza-Silva et al., 2011b). This resource encompasses various plant components such as roots, leaves, trunks, and fruits; animals including carcasses, feces, and materials regurgitated by owls; and microorganisms, mostly sourced from the adjacent surface environment (Ferreira et al., 2015; Smrž et al., 2015). Consequently, determining surface areas for the conservation of cave fauna is imperative to uphold environmental conditions and their trophic resources.

It is important to highlight that subterranean environments operate as ecosystems, providing refuge for a diverse array of invertebrate and vertebrate species, many of which play vital roles in delivering environmental services to both subterranean and surface ecosystems (Kuns et al., 2011). Numerous studies seek to unravel the primary biotic and abiotic factors that significantly influence the species richness and composition of cave invertebrates (Christman & Culver, 2001; Simões et al., 2015; Lunghi et al., 2017; Pacheco et al., 2020; Souza-Silva et al., 2021). However, our understanding of the invertebrate fauna in the surface environments adjacent to caves, as well as its relationship with cave invertebrates, remains limited (Oliveira, 2020).

Therefore, this study aims to address the following research questions: (i) How similar are invertebrate species composition between the surface and subterranean environments across different lithologies during different seasons? (ii) What are the primary factors influencing the composition of invertebrate fauna in both surface and subterranean environments across different lithologies during different seasons?

Based on the stated research questions, we proposed the following hypotheses: (i) The faunal similarities would be greater within the same environment, and lower when comparing across the surface and subterranean environments. Furthermore, that the seasonality would have a different influence on the faunal similarities among the different environments; (ii) The variables that drive the invertebrate fauna composition would vary across environments, as well as across lithologies and seasons.

2 METHODS

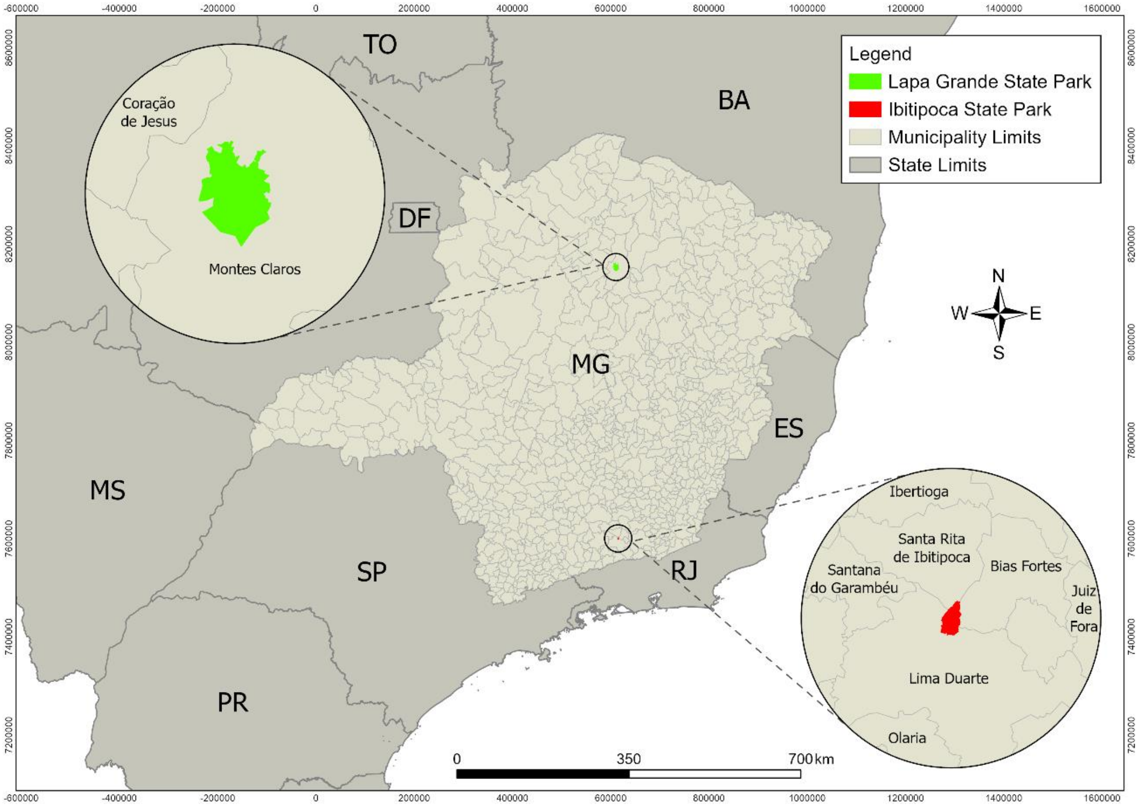
2.1 Study area

The caves examined in this study are located at two State Parks, classified as Integral Protection Conservation Units (BRASIL, 2000), both in the state of Minas Gerais. The first is the Lapa Grande State Park (hereafter referred to as LGSP), situated in a significant Brazilian karst region (IEF, 2014) (northern Minas Gerais state, in the municipality of Montes Claros). The second is the Ibitipoca State Park (hereafter referred to as ISP), in the municipality of Lima Duarte, southern Minas Gerais, renowned for the presence of quartzitic caves (IEF, 2007) (Figure 1).

The region of LGSP sits within the São Francisco River basin, one of the major rivers in Brazil (CBHSF, 2023). The climate is categorized as Hot Central Tropical and Semi-arid, marked by high average annual temperatures exceeding 18 °C, and dry period of at least six months each year (IDE-Sisema, 2023). Furthermore, this area is part of the Cerrado biome, where the predominant phytophysiognomies include Cerrado *Strictu Sensu*, Deciduous Seasonal Forest (Dry Forest) associated with rocky outcrops, and Semideciduous Seasonal

Forest along watercourses (Hoffman, 2012). Elevations range from 600 to 1000 m above sea level in the region, characterized by rugged terrain with prominent limestone outcrops and other karst formations. The limestone rocks found in the park are part of the São Francisco Carbonate Supergroup, specifically the Bambuí Group, which includes the Lagoa da Jacaré and Serra da Saudade formations (CPRM/RIGEO, 2014; IEF, 2014; IDE-Sisema, 2023).

Figure 1 – Location of study areas



Source: from the authors (2023)

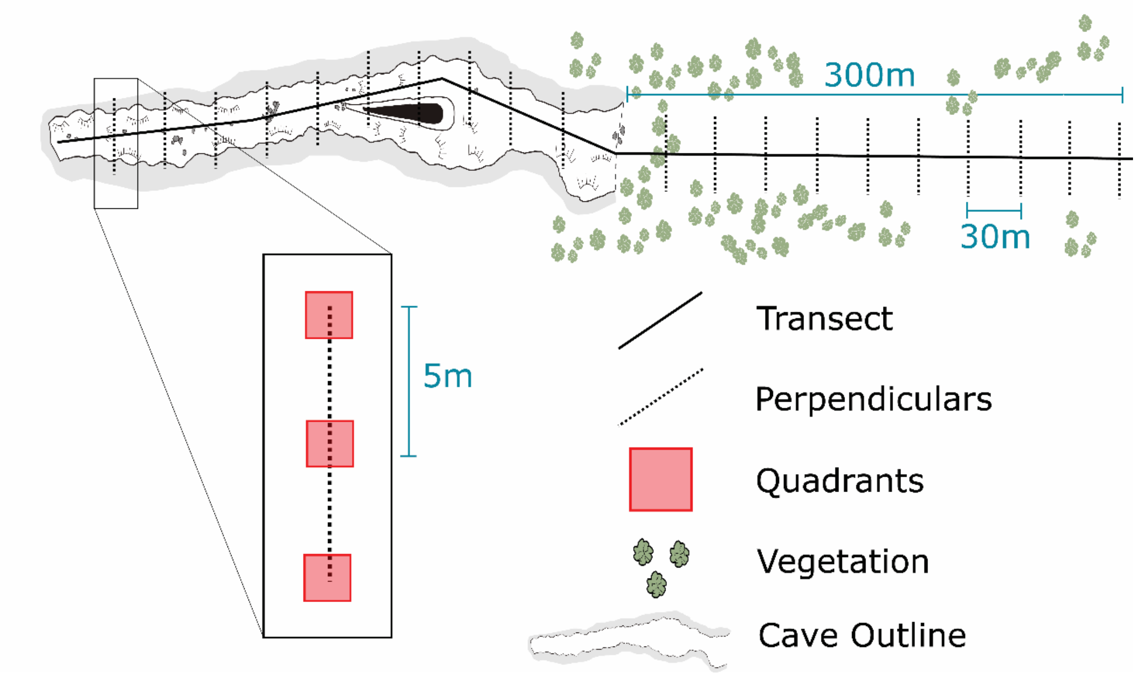
On the other hand, ISP region lies within the Paraíba do Sul River basin, and the Rio Grande River basin defines its western border (IDE-Sisema, 2023). The climate is mild and humid mesothermal, characteristic of Central Brazil Tropical, with average annual temperatures ranging between 10 and 15 °C and up to two dry months per year (IDE-Sisema, 2023). The climate of the park is significantly influenced by the local mountainous landscape (IEF, 2007). The park belongs to the Atlantic Forest biome, although the region exhibits a diverse range of phytophysiognomies, including prominent ones like Altitude Grasslands, Rocky Grassland, Montane Semideciduous Seasonal Forest, and patches of Montane Rainforest (cloud forest) (IDE-Sisema, 2023; IEF, 2007). The Grassland phytophysiognomies dominate the park, while the forested phytophysiognomy occurs in smaller proportions, often linked to valley and drainage areas (IEF, 2007). The Ibitipoca Ridge stands as one of the highest elevations in the region, with average elevations ranging from 1000 to 1400 m. Additionally, the terrain is rugged, marked by steep escarpments (IEF, 2007). The geomorphological formation in which the park is located is a quartzitic unit referred to as the Andrelândia Plateau (IDE-Sisema, 2023; IEF, 2007).

2.2 Sampling design

Three caves were chosen in each of the study areas, and biotic data collection occurred during two consecutive seasons: dry and rainy, resulting in two field campaigns for each area. We took into account intrinsic cave characteristics as well as the surrounding conditions for cave selection process, as data collection extended to the surface environment. Consequently, caves with less than 300 m of linear projection and those situated in excessively rugged terrain not included.

A transect crossing each cave and its adjacent surface environment was delineated. Consequently, the transect stretched both inwards and outwards from the cave entrance, covering 300 meters in each direction. Then, 20 collection points were designated within the transect, with 10 located inside the cave and 10 in the surface environment. A 10m perpendicular segment was established at each point, where three subsamples were collected from one-square-meter quadrants. This procedure ensured that the subsamples were taken with a minimum distance of 5 meters between them. Lastly, the sampling effort was standardized as10 minutes per square meter (10min/m^2) (Figure 2).

Figure 2 – Ilustration of the methodology used in the study



Source: from the authors (2023)

2.3 Data collection

We measured ground-level temperature and humidity at each of our sampling points using a digital thermo-hygrometer (AKSO AK-625, with an accuracy of ± 0.8 °C and ± 4 % relative humidity). A photograph was taken at chest height in each quadrant, at a right angle to the ground to analyze substrate types and organic resources quantitatively. These photographs underwent analysis using Image-J software (Schneider et al., 2012), where the areas occupied by each type of substrate were measured and recorded. The specific substrate types and organic resources assessed in the quadrants were outlined in Table 1. Subsequently, substrate diversity was evaluated using the Shannon index.

Table 1 - Description of the substrate type and organic resources variables that were measured in the quadrants

(Continues)

Variable	Description
Guano	Feces from flying animals such as bats and birds
Plant Organic Matter	Plant debris, fallen branches of any diameter, leaf litter, and other organic substrates of vegetal origin

Table 2 - Description of the substrate type and organic resources variables that were measured in the quadrants

(Conclusion)

Variable	Description
Fine Substrate	Substrate with fine grain size, less than 2mm, including sand, silt, clay, and mud
Gravel	Substrate with grain size ranging from 2mm to 65mm
Rocks	Substrate with grain size ranging from 66mm to 500mm.
Blocks	Substrate with grain size ranging from 501mm to 4,000mm
Bedrock	Rocks larger than 4,000mm
Compacted	Fine-grained substrate, less than 2mm, densely compacted
Water body	Streams, water puddles, and active drips
Vegetation	Living vegetation, encompassing phanerogams, cryptogams, and algae

Source: from the authors (2023)

Invertebrates were collected using the Direct Intuitive Search method (Wynne et al., 2019) within the quadrants. This approach involved gathering the invertebrate fauna from the leaf litter and other potential microhabitats, including areas beneath stones, blocks, and logs, utilizing a tray, forceps, and brush. The collected invertebrates were then preserved in a 70% alcohol solution and subsequently categorized into morphospecies in the laboratory, with the assistance of a stereomicroscope, following the protocols outlined in Oliver and Beattie (1996) and Derraik et al. (2002).

2.4 Data analysis

2.4.1 Species richness and similarity comparisons

We generated Boxplot graphs to compare the average species richness between the samples of the subterranean and surface cave areas at the different seasons. Furthermore, we applied the Wilcoxon-Mann-Whitney tests to evaluate any observed differences. This non-parametric test is especially well suited for comparing data distributions from two independent sample groups, making it a preferred tool when the data does not adhere to the assumptions of normality. For the creation of the graph and the execution of this analysis, we utilized the R software (R Core Team, 2022).

Then, we built Multidimensional Scaling (MDS) graphs along with Analysis of Similarities (ANOSIM) in order to investigate the similarities and dissimilarities of the fauna composition from the different lithologies (limestone and quartzite), during both seasons (dry and rainy) in the different environments (epigean and hypogean). MDS graphs allowed the visual understanding of differences between groups and the ANOSIM showed if such differences were significant.

2.4.2 Influence of environmental variables on the composition of invertebrates

Eight Distance-Based Linear Models (DistLMs) were built to evaluate the relative significance of environmental variables in elucidating variations in species composition among invertebrate communities in the different lithologies and different seasons. The eight models and plots correspond to the different environments (subterranean and surface) at the different lithologies (limestone and quartzite) during different seasons (wet and dry). For model construction, Bray-Curtis resemblance matrices were employed, which are acknowledged as one of the most appropriate method for examining species composition data and making comparisons between biological communities (Ricotta & Podani, 2017). Furthermore, this approach is responsive to relative abundances and remains robust even in situations with a substantial amount of missing data(Ricotta & Podani, 2017).

The Forward approach was chosen for model selection, which begins with an empty model and progressively incorporates predictor variables one by one, selecting those that make a significant contribution to enhancing model fit (Andersen & Bro, 2010). Additionally, the Adjusted R-squared coefficient served as the model selection criterion. This coefficient quantifies the proportion of total variability in the response variable that the model can account for. It considers model complexity by excluding variables that do not substantially contribute to explaining the data. A higher Adjusted R-squared value indicates a better-fitting model, taking into consideration parsimony (Johnson & Omland, 2004).

The environmental variables incorporated into the models encompassed the substrate and organic resource variables (outlined in Table 1), as well as substrate diversity, temperature, and humidity at the time of sampling, along with the distance from the cave entrance (considered solely for sampling spots within the cave environment). Substrate variables were aggregated into *indicators* in the DistLM models to enhance model fitting and aid interpretation. Specifically, the variables "fine substrate", "bedrock," and "compacted substrate" were consolidated under "homogeneous substrates". Furthermore, the variables "gravel," "rocks," and "blocks" were combined as "shelter availability."

3 RESULTS

A total of 4,863 invertebrates were collected, comprising 2,110 from LGSP and 2,753 from ISP. We identified 31 invertebrate orders, with 27 present in LGSP and 29 in ISP. LGSP yielded 415 invertebrate morphospecies (72 subterranean, 363 from surface and 19 shared), while ISP revealed 553 morphospecies (105 subterranean, 469 from surface and 49 shared). In LGSP, the most diverse invertebrate orders were Araneae, Coleoptera and Hymenoptera, with respectively 75, 95 and 62 species. In ISP, on the other hand, the most diverse orders were Araneae, Coleoptera and Acari, with species richness of 90, 83 and 71, respectively (Table 3).

Table 3 - List of orders found in each of the study locations with their respective species richness (LGSP = Lapa Grande State Park; ISP = Ibitipoca State Park; Subterr. = Subterranen environment; Surface = Surface environment; Shared = Species shared between both environments; S= Species richness; N = Abundance of individuals)

(Continues)

	LGSP					**ISP**				
	Subterr.		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**
	S	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**
Arachnida										
Acari	7	18	24	130	2	12	23	50	185	6
Araneae	15	79	61	197	1	25	173	80	426	16
Opiliones	1	4	-	-	-	1	7	5	8	1
Palpigradi	1	3	-	-	-	1	2	-	-	-
Pseudoscorpiones	2	3	4	31	1	2	4	5	71	-
Scorpiones	-	-	-	-	-	-	-	1	1	-
Chilopoda	-	-	2	9	-	2	2	7	18	1
Symphyla	1	2	-	-	-	-	-	2	2	-
Diplopoda	3	16	4	47	1	6	11	3	5	-
Entognatha										
Collembola	3	23	12	114	-	10	46	29	177	6
Diplura	-	-	-	-	-	1	1	1	1	-
Malacostraca										
Isopoda	1	1	1	1	-	3	11	4	68	1
Insecta										

Table 4 - List of orders found in each of the study locations with their respective species richness (LGSP = Lapa Grande State Park; ISP = Ibitipoca State Park; Subterr. = Subterranen environment; Surface = Surface environment; Shared = Species shared between both environments; S= Species richness; N = Abundance of individuals)

(Conclusion)

	LGSP					**ISP**				
	Subterr.		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**
	S	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**
Archaeognatha	-	-	-	-	-	-	-	6	11	-
Blattodea	-	-	7	118	-	6	130	17	132	4
Coleoptera	15	33	85	205	4	8	14	76	169	4
Dermaptera	-	-	3	3	-	-	-	3	4	-
Diptera	5	20	17	32	1	11	21	17	34	4
Embioptera	-	-	1	5	-	-	-	2	3	-
Gastropoda	-	-	1	1	-	-	-	1	2	-
Hemiptera	4	16	31	91	4	5	7	45	97	3
Hymenoptera	2	2	62	398	2	3	5	64	742	-
Lepidoptera	3	9	21	33	-	2	2	14	23	-
Mantodea	-	-	1	1	-	-	-	-	-	-
Neuroptera	1	1	1	3	1	-	-	1	1	-
Oligochaeta	2	33	1	1	-	-	-	2	3	-
Orthoptera	1	21	7	27	-	2	24	3	34	1
Phasmatodea	-	-	-	-	-	-	-	1	2	-
Psocodea	5	119	12	248	2	5	7	11	23	-
Thysanoptera	-	-	3	9	-	-	-	9	21	-
Zygentoma	-	-	2	3	-	-	-	-	-	-
Total	**72**	**403**	**363**	**1707**	**19**	**105**	**490**	**459**	**2263**	**49**

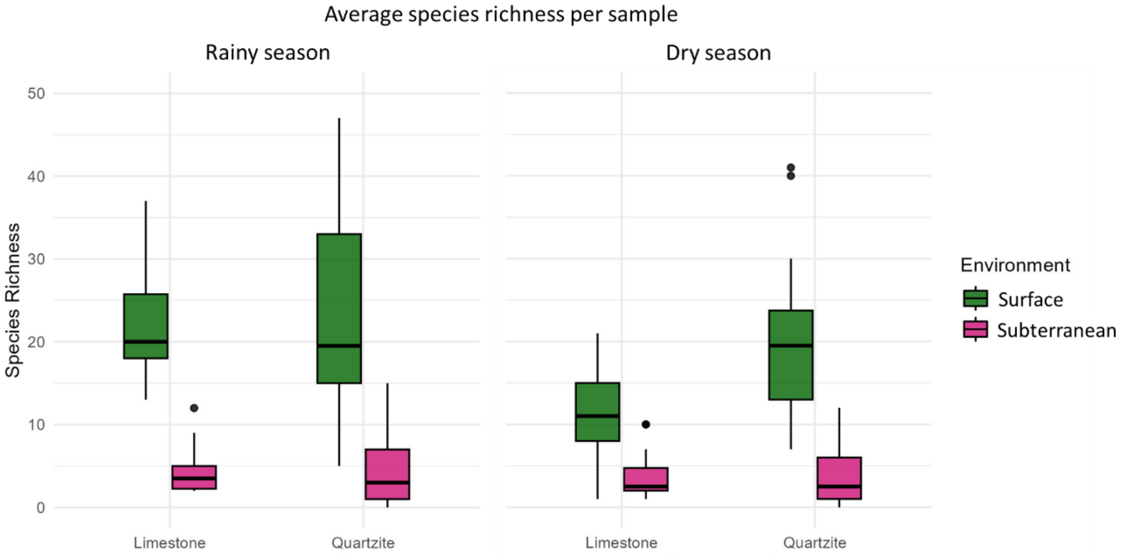
Source: from the authors (2023)

3.1 Species richness comparisons

Differences in total species richness between the two parks were not statistically significant (rainy season: W=1885; p=0.657; dry season: W=1470; p=0.083). However, when comparing the subterranean and surface cave regions, richness on surface was significantly higher in both areas (rainy season: W=55.5; p<0.01; dry season: W=183; p<0.01).

Furthermore, when considering the different lithologies separately, we observed that for limestone, the average total species richness was different among seasons (W=2359; p=0.003) while for quartzite it was not (W=1880.5; p=0.674). Lastly, when considering the fauna from the different environments during the different seasons, the species richness was higher during the rainy season for the surface environment when compared to the dry season (W=2590; p<0.01), while for the subterranean environment it was not (W=1994; p=0.305) (Figure 3).

Figure 3 – Average species richness registered in the sampling spots



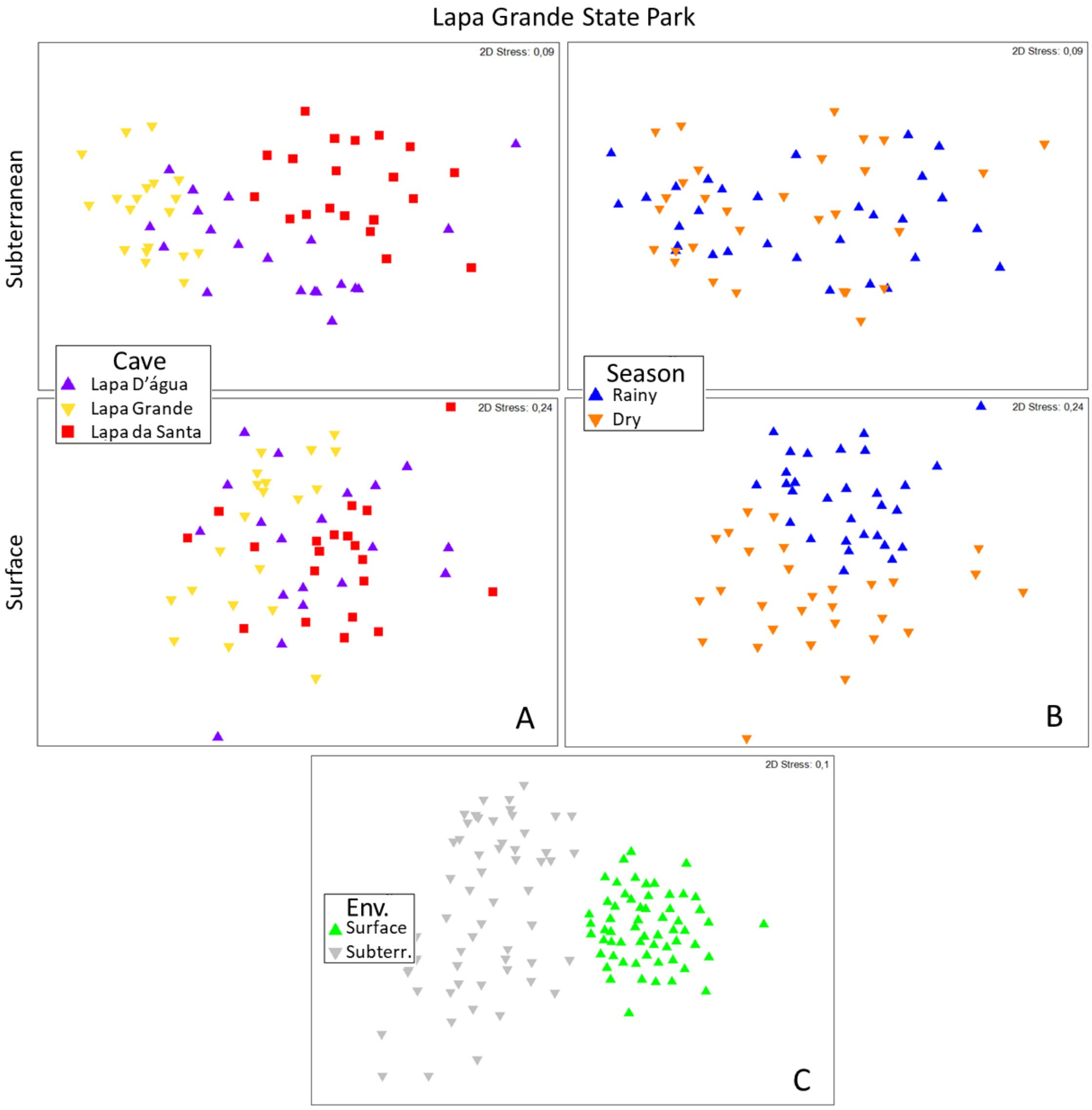
Source: from the authors (2023)

3.2 Community similarities

3.2.1 Limestone (Lapa Grande State Park)

Examining the MDS plots, we observed a clear differentiation in the fauna composition of different caves for the subterranean environment (Figure 4). For the surface environment, even though such differences are not that clear in the MDS plots, they present statistically significant differences according to the ANOSIM (Table 5). Nevertheless, the fauna from the surface environment differed between seasons, contrarily to the subterranean fauna (Figure 4; Table 5).

Figure 4 – MDS graphs highlighting the main differences in the invertebrate fauna composition from Lapa Grande State Park by environments and seasons. (A) Comparisons among caves for each environment; (B) comparisons between seasons for each environment and (C) comparison between subterranean and surface environments.



Source: from the authors (2023)

The ANOSIM unveiled significant differences in fauna composition driven by both environmental variations and seasonal fluctuations. Notably, the subterranean and surface environments displayed considerable dissimilarities among caves, especially in the rainy season. Furthermore, the surface environment exhibited differences in species compositions between rainy and dry seasons, while the subterranean environment did not (Table 5).

Table 5 - ANOSIM analysis investigating the dissimilarities on the invertebrate fauna from Lapa Grande State Park species composition under different approaches (R= Global R statistics)

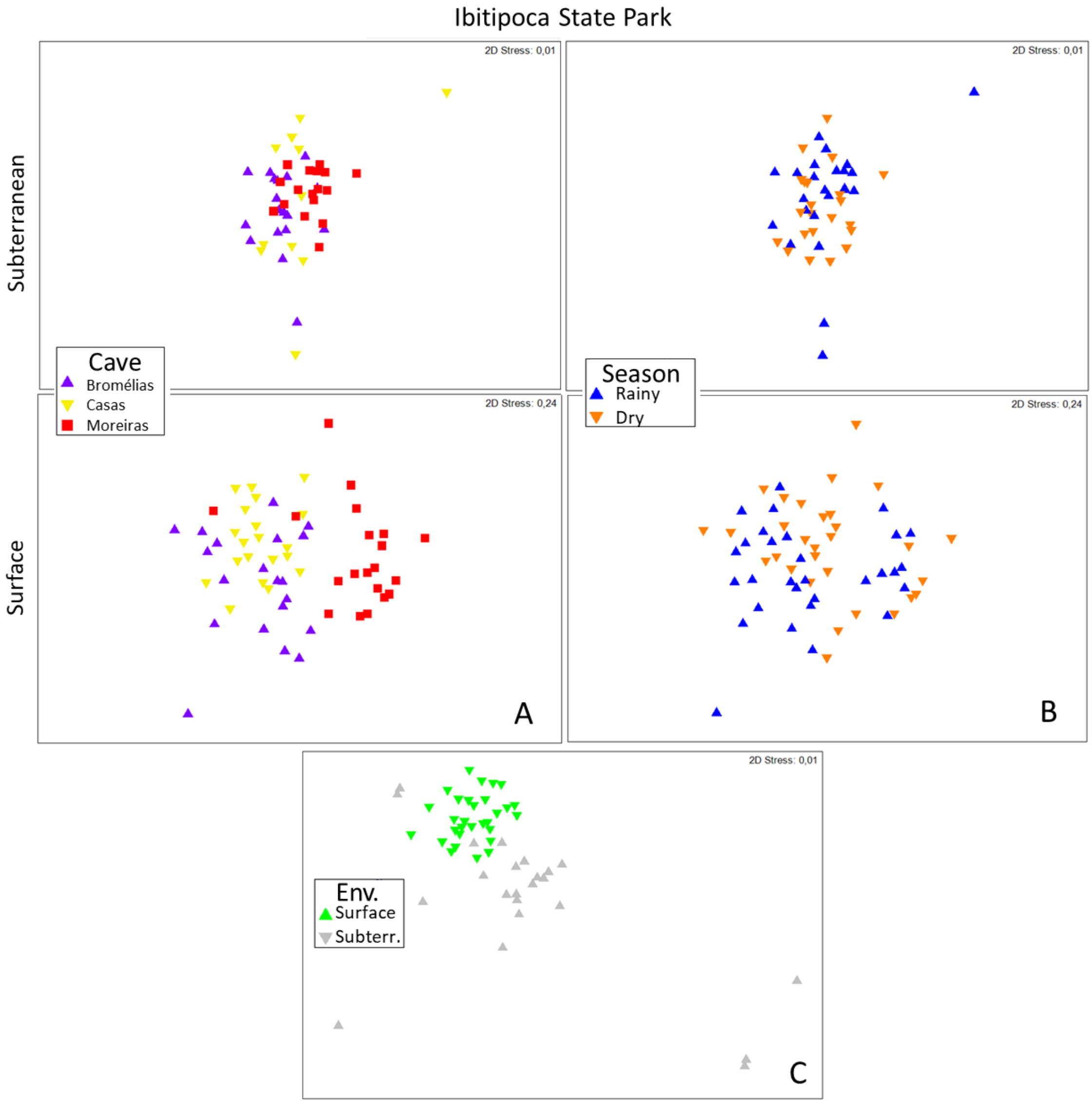
Approach		R	p
Environment	**Season**		
Subterranean (among caves)	Rainy	0.506	0.01*
	Dry	0.345	0.01*
Surface (among caves)	Rainy	0.513	0.01*
	Dry	0.296	0.01*
Subterranean x Surface (among environments)	Rainy	0.62	0.01*
	Dry	0.485	0.01*
Subterranean	Rainy x Dry (among seasons)	-0.006	0.58
Surface		0.264	0.01*

Source: from the authors (2023)

3.2.2 Quartzites (Ibitipoca State Park)

In the MDS plots, we observed a more pronounced distinction in fauna composition between different caves when comparing the surface and subterranean environments (Figure 5). Conversely, although not as conspicuous for the subterranean environment in the MDS plots, differences were significant as evidenced by ANOSIM (Table 6). Furthermore, while the surface fauna displayed distinct patterns between seasons, there was no such differentiation in the subterranean habitats (Figure 5; Table 6).

Figure 5 - MDS graphs highlighting the main differences in the invertebrate fauna composition from Ibitipoca State Park by environments and seasons. (A) Comparisons among caves for each environment; (B) comparisons between seasons for each environment and (C) comparison between subterranean and surface environments.



Source: from the authors (2023)

The ANOSIM revealed significant differences in fauna composition based on both environmental factors and seasons. Notably, the subterranean and surface environments exhibited significant dissimilarities among caves, but those were more balanced among the different seasons. Furthermore, the surface environment also displayed variations between rainy and dry seasons (Table 6).

Table 6 - ANOSIM analysis investigating the dissimilarities on the invertebrate fauna from Ibitipoca State Park species composition under different approaches (R= Global R statistics)

Approach		**R**	**p**
Environment	**Season**		
Subterranean (among caves)	Rainy	0.361	0.01*
	Dry	0.321	0.01*
Surface (among caves)	Rainy	0.549	0.01*
	Dry	0.34	0.01*
Subterranean x Surface (among environments)	Rainy	0.549	0.01*
	Dry	0.5	0.01*
Subterranean	Rainy x Dry (among seasons)	-0.002	0.49
Surface		0.057	0.02*

Source: from the authors (2023)

3.3 Influence of environmental variables on the invertebrate community composition

3.3.1 Limestone (Lapa Grande State Park)

The DistLM model analysis revealed that the selected predictor variables have a significant impact on species composition in all studied scenarios. However, the variables with the highest explanatory power and the strength of this relationship varied significantly between environments among limestone caves.

In LGSP, models considering subterranean and surface cave environments during the rainy season explained 49.83% and 29.04% of the variations in species composition, respectively. However, when it comes to the dry season, models explaining species composition accounted for 29.26% and 11.76% of the observed variations in the subterranean and surface cave environments (Table 5).

The model that exclusively considered the subterranean environment during rainy seasons exhibited the highest capacity to account for variations in species composition. This emphasizes the significant influence of the cave's specific conditions on its fauna. Humidity, the presence of homogeneous substrates, substrate diversity, and shelter availability emerged as the primary environmental factors influencing species composition variations in this environment during the rainy season. In contrast, during the dry season, the key variables influencing invertebrate species composition were humidity, temperature, and the presence of guano.

Finally, in the surface environment, during the rainy season, the dominant factors influencing variations in species composition were the presence of homogeneous substrates, vegetation, plant organic matter, temperature, and humidity. In the dry seasons, variations in species composition were primarily influenced by humidity and temperature (refer to Table 5).

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Finally, in the surface environment, during the rainy season, the dominant factors influencing variations in species composition were homogeneous substrates, vegetation, plant organic matter, temperature, and humidity. In the dry season, variations in species composition were primarily influenced by humidity and temperature (refer to Table 5).

Table 7 - Summary of Distance-Based Linear Models (DistLMs) best models after the sequential tests used to analyze the relationship between predictor variables and species composition in the subterranean and surface cave environments of Lapa Grande State Park during different seasons (Adj. R^2 = Adjusted R-squared; Prop = Proportion of variable explanation within the model; Cumul. Prop. = Cumulative proportion of model explanation; * = statistically significant variables)

Approach			Predictor Variables	Adj. R^2	Pseudo-F	Prop. (%)	Cumul. Prop. (%)	p-value
Response variable	**Season**	**Environment**						
Species composition	Rainy	Subterranean	Humidity	0.1672	6.8242	19.59	19.59	0.001*
			Homogeneous substrates	0.2155	1.574	12.77	32.37	0.026*
			Substrate diversity	0.2589	2.4641	6.29	38.66	0.009*
			Shelter availability	0.3072	1.5584	11.16	49.83	0.026*
		Surface	Homogeneous substrates	0.0459	1.6987	11.17	11.17	0.001*
			Vegetation	0.0680	1.6398	5.26	16.44	0.013*
			Plant organic matter	0.0872	1.5481	4.87	21.31	0.04*
			Temperature	0.0892	1.0547	3.31	24.63	0.393
			Humidity	0.1053	1.4306	4.41	29,04	0.05*
	Dry	Subterranean	Humidity	0.1462	5.9668	17.56	17.56	0.001*
			Temperature	0.1836	2.2833	6.42	23.99	0.01*
			Guano	0.2110	1.9383	5.27	29.26	0.021*
		Surface	Humidity	0.0194	1.5743	5.32	5.32	0.022*
			Temperature	0.0523	1.9724	6.44	11.76	0.001*

Source: from the authors (2023)

In general, models regarding the surface fauna showed lower level of explanatory power when compared to the models developed for the subterranean ones. However, it is important to highlight that many of the most influential variables on the fauna were shared by the models, albeit with varying degrees of significance.

Humidity emerged as the most significant variable explaining variations in species composition within LGSP. It featured in all models and acted as the primary explanatory variable in three of them. The second most influential factor was temperature, playing a crucial role in elucidating the variations in fauna composition in three out of the four scenarios considered (see Table 2).

3.3.2 Quartzites (Ibitipoca State Park)

Within the ISP, the DistLM analyses revealed that the predictor variables indeed had a noteworthy impact on species composition within the cave environments. Parallel to LGSP, the strength of this relationship varied across these environments. Nonetheless, there was a notable distinction in the overall pattern compared to the other region: the surface environments demonstrated a higher percentage of model explanation compared to the subterranean environments in both seasons.

In the subterranean environments of ISP caves, the models exhibited lower explanatory power when compared to the surface environments, accounting for 19.21% and 8.17% of the variation in species composition during the rainy and dry seasons, respectively. The surface environment models, on the other hand, explained 31.49% and 16.93% of the variations in species composition during the rainy and dry seasons, respectively (Table 8).

In the subterranean environment, the variables with the greatest explanatory power were humidity and temperature during the rainy season and only humidity during the dry season. For the surface environment, the most important variables were the presence of homogeneous substrates, vegetation and shelter availability during the rainy season and the presence of homogeneous substrate and substrate diversity during the dry season (Table 8).

Table 8 - Summary of Distance-Based Linear Models (DistLMs) sequential tests used to analyze the relationship between predictor variables and species composition in the subterranean and surface cave environments of Ibitipoca State Park during different seasons (Adj. R² = Adjusted R-squared; Prop = Proportion of variable explanation within the model; Cumul. Prop. = Cumulative proportion of model explanation; * = statistically significant variables)

Approach			**Predictor Variables**	**Adj. R²**	**Pseudo-F**	**Prop. (%)**	**Cumul. Prop. (%)**	**p-value**
Response variable	**Season**	**Environment**						
Species composition	Rainy	Subterranean	Humidity	0.0873	3.29	12.53	12.53	0.001*
			Temperature	0.1187	1.81	6.68	19.21	0.003*
		Surface	Homogeneous substrate	0.0910	1.9683	18.5	18.5	0.001*
			Vegetation	0.1131	1.647	5.03	23.54	0.002*
			Shelter availability	0.1362	1.3341	7.94	31.49	0.039*
	Dry	Subterranean	Humidity	0.0401	1.9586	8.17	8.17	0.001*
		Surface	Homogeneous substrate	0.0471	1.7179	11.28	11.28	0.003*
			Substrate diversity	0.0734	1.7666	5.64	16.93	0.001*

Source: from the authors (2023)

When considering the subterranean environments, the most significant variable for the models was humidity, which explained 12.53% of the variation in species compositions during the rainy season and 8.17% of the variations during dry season, being the only variable that was selected by the model (Table 8).

In the surface cave environments, the most influential variable was the presence of homogeneous substrates, which explained 18.5% of the variation in species composition during the rainy season and 11.28% during the dry season (Table 8).

4 DISCUSSION

A remarkable diversity of terrestrial invertebrate species was revealed for both seasons in Lapa Grande and Ibitipoca State Park caves and sorroundings. Although there were no statistically significant differences in species richness between the two areas, we observed significant variations in both species richness and composition of invertebrates between the cave environments and their respective adjacent areas in both regions. In the limestone area, species richness was notably higher during the rainy season, whereas such trend was not observed in the quartzite region. Moreover, our findings emphasize the diverse environmental variables that influence the invertebrate fauna in both areas, with climatic factors emerging as the most influential drivers of species composition.

When investigating the relationship between surface and subterranean environments, we observed significant differences between them in regards of species richness and composition, which varied across both lithologies and seasons. As anticipated, invertebrate species richness was higher in surface environments compared to subterranean environments (Cardoso, 2012; Mendes-Rabelo et al., 2020). Furthermore, species richness in subterranean environments exhibited a more tightly clustered distribution around the average, whereas in the surface environment, there was notably greater data variation. The consistent distribution pattern around the average through both study sites highlights the sensitivity of subterranean fauna to environmental variations. The stability in subterranean species richness may stem from the relatively constant environmental conditions found within caves, which can act as a selective filter favoring species pre-adapted to such specific conditions (Poulson & White, 1969; Prous et al., 2004; 2015; Mendes-Rabelo et al., 2019).

The seasonal variations of species richness improve our understanding of the influence of seasonality on the terrestrial invertebrate fauna. During the rainy season, surface environments exhibited higher species richness when compared to the dry season. The increased resource availability and productivity in the surface environment during the rainy period most likely explains this factor (Silva et al., 2011). Nevertheless, similar to what happens for surface environments, subterranean environments also tend to have an increase in the organic matter input during the rainy season (Souza-Silva et al., 2007, 2011b, 2012), what was expected since a significant part of organic matter input in caves occurs through water (Simon et al., 2007; Souza-Silva et al., 2011b). Although seasonal differences in subterranean species richness have already been previously reported in the literature (Bento et al., 2016; Lunghi et al., 2017), subterranean environments did not show differences in species richness across the different seasons in our study. Schneider et al. (2011) also found that subterranean species richness does not increase with the increase of organic matter input in an ecosystem-level manipulation study. The lack of response from species richness variations to the seasonality in our study areas reinforces the importance of environmental stability for subterranean ecosystems and its invertebrate fauna.

Our investigation into the invertebrate community similarities revealed that both lithologies exhibited similar trends, with the subterranean environment displaying stability in species composition across seasons, in contrast to the surface environment. Such stability in the subterranean environment species composition between seasons underlines once more the importance of the consistent environmental conditions characteristic of caves. This stability provides a refuge for species adapted to cave conditions, shielding them from the pronounced seasonal variations experienced by surface fauna (Mammola, 2018).

Moreover, the observed dissimilarities in surface fauna composition between rainy and dry seasons resonate with studies highlighting the impact of seasonal fluctuations on surface environments (Tonkin et al., 2017) and its invertebrate fauna (Frith & Frith, 1990; Kai & Corlett, 2002). Seasonal variations influence factors such as temperature, humidity, precipitation, and resource availability in the surface ecosystems, contributing to their dynamic nature. In contrast, subterranean ecosystems have a more stable nature across seasons, with such factors fluctuating less around the annual average observed for the surface environment (Badino, 2004, 2010; Mejía-Ortíz et al., 2020, 2021).

Another interesting pattern was the distinct invertebrate fauna compositions found among different caves when considering only the subterranean environment. Similarly, there were statistically significant dissimilarities among the surface environments, although less prominent than on subterranean environment. This nuanced response might be linked to the moderating effect of cave microclimates, which provide a more stable and buffered environment when compared to the surface. Likewise, Simões et al. (2015) found dissimilar invertebrate fauna among caves, however in a larger sampling scale. Therefore, this intricate interplay between community similarities underscores the need for larger scale studies, because some invertebrate community properties only emerge at larger scales analysis and are often masked at restricted analysis scales, as is the case in this study (Moseley, 2009; Mammola, 2018; Reis-Venâncio et al., 2022).

Distinct patterns mark the ecological relationships between subterranean and surface environments for invertebrate communities. Subterranean ecosystems exhibit stability in species composition across seasons due to consistent temperature and humidity levels, creating a refuge for species adapted to cave conditions. In contrast, surface environments experience pronounced seasonal variations, particularly evident in the dissimilarities in fauna composition between rainy and dry seasons, emphasizing their dynamic nature influenced by seasonal fluctuations.

The intensity of the relationship between environmental variables and species composition exhibited variations across the studied environments and seasons. Broadly, the variables measured in the limestone environment provided a more robust explanation for species composition variation in contrast to the quartzitic environment. For limestone, the influence of environmental variables on species composition depends on the environment and season, and is more pronounced inside the caves for the rainy season. Many studies define cave environments as "natural laboratories", precisely due to the more simplified and stable biotic and abiotic conditions present in these environments (Poulson & White, 1969; Mammola et al., 2014; Mammola, 2018; Sánchez-Fernández, 2018).

The fact that our model for the subterranean environment explained a much larger percentage of the variation in fauna composition compared to the surface region is consistent with such assumptions. The inherent stability of cave environments, with relatively constant temperature and high humidity levels, creates a more predictable and less dynamic setting for invertebrate communities. This stability likely explains the increased explanatory power of models, as the limited external influences over subterranean environment (compared to the surface) further contributes to the efficacy of models, as it becomes more effective in capturing the intricate relationships between environmental factors and invertebrate communities.

Regarding the quartzitic lithology, the predictor variables have a modest impact on species composition variations, when compared to limestone. Furthermore, the strength of this relationship varies between different environments, with an increased influence of predictor variables on the surface environment when compared to the subterranean one. This unexpected result suggests that such caves might be more susceptible to the epigean environmental factors when compared to limestone, indicating a complex interplay of lithological and microclimatic factors that require further investigation to better comprehend the dynamics of species composition in quartzitic areas.

The consistency of climatic factors, i.e. humidity and temperature, being more crucial for subterranean environments across both lithologies aligns with existing literature emphasizing the significance of such variables in structuring subterranean ecosystems (Mammola et al., 2015; Simões et al., 2015; Lunghi et al., 2017). This consistency supports the idea that these climatic variables play a fundamental role in shaping the subterranean community structure by providing a stable habitat, buffered from the high environmental variations occurring in the surface ecosystem.

While a heightened influence of the vegetation, shelter availability and substrate diversity were observed for the surface invertebrate communities, such findings might suggest that these communities are using these microhabitats as refuges from the high fluctuations typically observed for surface environments. Our study methodology measured the temperature and humidity at the sampling spots at ground level. Due to the greater complexity of the variables that influence surface communities, the direct effect of temperature and humidity may not have been evident, but the presence of vegetation and shelter availability, for example, indirectly reflects an animal preference for milder climatic conditions (Kolasa & Picket, 1991; Ficetola et al., 2020).

Regardless of the type of environment, lithology or season, climatic variables stood out when explaining species composition variations in the studied environments. Temperature inside the cave tends to fluctuate around the average when compared to the microclimate found in local surface habitats. On the other hand, humidity inside the cave tends to be higher than that observed in surface areas (Badino, 2004, 2010; Mejía-Ortíz et al., 2020, 2021). This climatic dynamic suggests the presence of relatively constant and moderate conditions in the deeper parts of the cave, providing an environment with less fluctuation in environmental conditions, which can influence the fauna inhabiting this subterranean space (Raschmanova et al. 2018; Pallarés et al. 2020; Colado et al., 2021, 2022). This stability in environmental conditions within cave systems is a critical factor influencing the adaptation and persistence of fauna inhabiting caves, highlighting the importance of subterranean habitats as possible refuges in the face of surface environmental fluctuations, as the ones observed in the current concerning scenario of global warming (Mammola & Isaia, 2017).

4.1 Concluding remarks

Previous studies assume a strong relationship between the surface and subterranean fauna (Mendes-Rabelo et al., 2020; Oliveira, 2020). Still, the high differentiation found between surface and subterranean environments in our study reinforces the idea that cave environments impose significant selective pressures on the fauna that inhabit them, which must overcome severe environmental filters to colonize these environments in long term (Chapman, 1982; Sket, 1999; Romero, 2009). This highlights the role of local environmental context and the specific environmental conditions found in each specific compartment of the environment in structuring invertebrate communities.

This study provides valuable insights into the ecological relationships of invertebrate communities in environments with caves, emphasizing the significance of considering both caves and their surrounding areas an interactive ecosystem, rich in biodiversity. The observed differences in species richness and composition between the study areas reflect the complexity of the relationship between these ecological environments. Furthermore, the pronounced influence of climatic variables on fauna composition from both the subterranean and surface environments suggests conservation strategies aiming to maintain such microclimatic conditions might succeed in providing a greater connection between the subterranean and surface environments. These findings contribute to a deeper understanding of subterranean systems and their surroundings, emphasizing the importance of considering both regional and cave-specific factors in conservation strategies for these environments, especially considering a scenario of global warming (Rachmanova et al., 2018; Pallarés et al., 2020).

In conclusion, recognizing the ecological patterns in both surface and subterranean environments is crucial for comprehending the connections between these ecosystems. The stability observed in subterranean environments, along with their potential role as refuges amidst global environmental fluctuations, such as those associated with climate change, underscores the importance of integrating subterranean ecology into broader ecological frameworks.

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ARTIGO 2

Beyond borders: factors limiting the similarity of terrestrial invertebrates between caves and their surrounding areas

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ABSTRACT

Karst environments, characterized by interactions between soluble bedrock, water, soil, and biotic elements, host unique ecosystems, including caves. Caves exhibit unique environmental characteristics when compared to surface environments, but a level of connectivity is known between them. This study explores the influence of environmental factors on the similarity of terrestrial invertebrate fauna between subterranean cave environments and their adjacent surface areas in diverse lithologies and seasons. Three State Parks in Minas Gerais, representing distinct lithologies (limestone, iron ore, and quartzite), were studied. The analysis revealed 30 invertebrate orders and a total abundance of 7,661 individuals. As expected, surface environments exhibited higher species richness than subterranean environments across all lithologies, while the higher similarity between environments was observed for ferruginous lithology. Humidity emerged as the main factor influencing faunal similarity in all areas, with different quantitative breakpoints. In Lapa Grande State Park (limestone), temperature, humidity, and water bodies positively influenced similarity during the rainy season, while shelter availability played a crucial role in the dry season. In Serra do Rola Moça State Park (iron ore), humidity was a key factor in both seasons. In Ibitipoca State Park (quartzite), humidity and substrate diversity influenced similarity during the rainy season. These findings highlight the importance of microhabitats and climatic conditions in shaping terrestrial invertebrate communities in both subterranean and surface environments. The study provides valuable insights into the ecological interactions between subterranean and surface environments, emphasizing the need for conservation strategies that consider the geological, biological, and climatic connectivity between caves and their surrounding areas.

Keywords: karst environments; invertebrate fauna; subterranean ecosystems; species similarity; microhabitats; conservation.

1 INTRODUCTION

Karst areas comprise complex, dynamic, and interactive landscapes consisting of soluble bedrock, water, soil, biotic elements, and atmospheric factors. Among the most common karst features are natural subterranean hollow spaces known as caves. Caves exhibit unique environmental characteristics when compared to surface environments, including the permanent absence of light and a tendency towards stable environmental conditions, such as temperature and humidity (Poulson & White, 1969; Culver, 1982; Sket, 1999; Badino, 2004; Sebela & Turk, 2011; Culver & Pipan, 2019). These conditions are essential for the establishment of populations living in the subterranean environment and allow the presence of a distinctive fauna, often comprised of species specialized for subterranean life, such as troglobites (obligatory cave animals) and troglophiles (facultative cave animals) (Sket, 2008; Howarth & Hoch, 2012). On the other hand, some invertebrate and vertebrate species spend part of their life cycle inside caves (trogloxens), with some species usually residing in areas near the cave entrances (Culver & Pipan, 2014). The entrance and twilight zones of caves exhibit higher humidity and shading compared to surface environments, serving as refuges against extreme surface climate variations (Prous et al., 2004, 2015; Culver & Pipan, 2014; Howarth & Wynne, 2022).

Underground connectivity between caves allows gene flow among species and directly depends on the landscape's integrity in which these caves are inserted. In ferruginous environments, for example, large caves function as "attractive" for fauna because they offer various trophic resources (e.g., deposits of plant organic matter or guano) that do not exist in small fissures and interstitial spaces between large caves (Souza-Silva et al., 2011; Ferreira et al., 2015). This network of small fissures, in addition to serving as "connections" between large caves, may harbor specific fauna and promote species flow between caves and/or other compartments of the endokarst (Ferreira et al., 2015; Howarth & Wynne, 2022). In these underground meso-spaces, the primary resources available to the fauna are the roots of surface vegetation and microorganisms, especially fungi and bacteria (Ferreira et al., 2015).

While numerous studies explore the distinct relationships among different subterranean compartments (Novak et al. 2012; Tobin et al., 2013; Prous et al. 2015; Pellegrini & Ferreira, 2016; Reis-Venâncio et al., 2022) or between landscape features and subterranean fauna (Xiao & Weng 2007; Pellegrini et al., 2016; Lunghi et al., 2017; Jaffé et al., 2018; Mammola & Isaia 2018; Bento et al., 2021, Cardoso et al., 2022), there is a limited number of studies focusing on the connection between cave fauna and their corresponding surface communities. Such studies explored the connections between the subterranean and surface communities for aquatic (Death, 1989; Simon & Benfield, 2001; Pipan & Culver, 2007; Wood et al., 2008) and terrestrial (Prous 2004; 2015; Mammola et al., 2017; Oliveira, 2020) fauna.

Hence, the existence and functionality of surface connectivity between caves for terrestrial invertebrates remains mainly unexplored. Additionally, the potential effects of the matrix rock type influencing this interface between surface and subterranean communities remain unknown, despite its crucial significance for conservation purposes. Therefore, the main objectives of this study were to determine the primary factors influencing the similarity of fauna between subterranean cave environments and their adjacent surface areas in different lithologies during rainy and dry seasons. Additionally, we aimed to establish the extent to which these factors influence invertebrate faunal similarity.

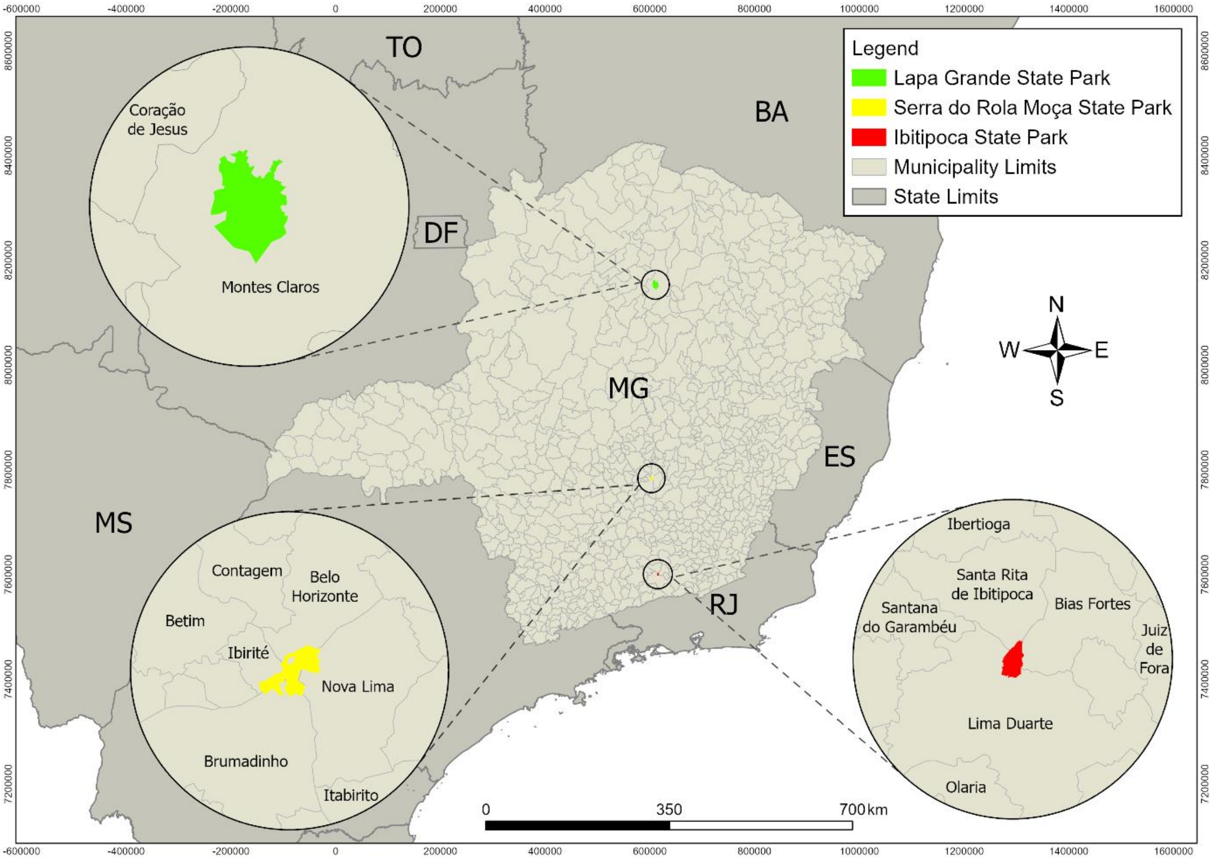
We hypothesized that environmental factors such as temperature, humidity, resource and microhabitat availability would significantly influence the similarity of invertebrate fauna in cave environments and their surrounding surface areas. More specifically, we further hypothesized that these effects might vary among caves located in different lithologies due to variations in the physical and chemical properties of the rocks. Lastly, we expected that the effects of environmental variables on species similarity would differ among different seasons of the year.

2 METHODS

2.1 Study area

The caves surveyed in this study are all inserted in three State Parks located in Minas Gerais State (Southeastern Brazil), each representing a different lithology. The Lapa Grande State Park (LGSP) is located in Northeastern Minas Gerais state, within the limits of the municipality of Montes Claros, protecting a significant karst area with several expressive limestone caves. The Serra do Rola Moça State Park (SRMSP) is situated in the municipality of Nova Lima, which is located at the Iron Quadrangle region (central Minas Gerais state), safeguarding iron-rich caves. Finally, the Ibitipoca State Park (ISP) is located at the municipality of Lima Duarte (Southern Minas Gerais state) encompassing a significant number of quartzitic caves (Figure 1).

Figure 1 – Location of study areas



Source: from the authors (2023)

Situated within the São Francisco River basin, an important watercourse in Brazil (CBHSF, 2023), the LGSP region experiences a Hot Central Tropical and Semi-arid climate. This climatic classification is characterized by elevated average annual temperatures surpassing 18°C, accompanied by an arid period lasting at least six months annually (IDE-Sisema, 2023). Additionally, the area falls under the Cerrado biome, featuring prevalent phytophysiognomies such as Cerrado *Strictu Sensu*, Deciduous Seasonal Forest (Dry Forest) linked with rocky formations, and Semideciduous Seasonal Forest along watercourses (Hoffman, 2012). The region boasts rugged topography, with elevations ranging from 600 to 1000 meters above sea level, the region boasts rugged topography, accentuated by prominent limestone outcrops and various karst formations. The limestone formations, integral to the São Francisco Carbonate Supergroup, specifically the Bambuí Group, encompass the Lagoa da Jacaré and Serra da Saudade formations within the park (CPRM/RIGEO, 2014; IEF, 2014; IDE-Sisema, 2023).

SRMSP is also within the São Francisco river basin (IDE-Sisema, 2023), which represents an important conservation area within the Atlantic Forest biome. The climate in this area is classified as tropical Brazil Central semi-humid, characterized by a mesothermal mild and humid profile with an average temperature ranging between 10 and 15°C (IDE-Sisema, 2023). The region experiences a dry period lasting four to five months annually. Multiple geomorphological groups compose the geology of SRMSP, including Itabira, Caraça, Piracicaba, Nova Lima, and Sabará (IDE-Sisema, 2023). Unfortunately, SRMSP is surrounded by iron ore mining activities, which pose potential risks to the conservation of the park's biodiversity.

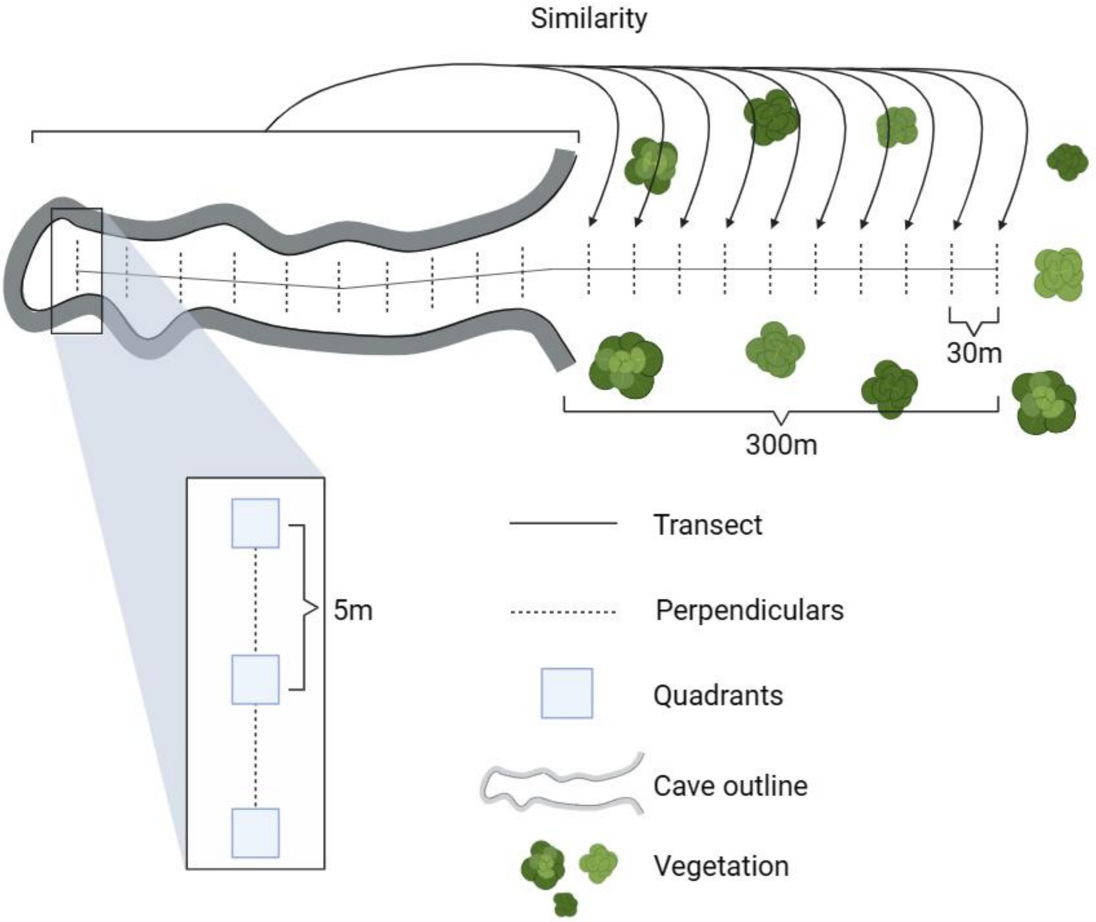
Lastly, nestled within the Paraíba do Sul River basin, the ISP region is defined by the Rio Grande River basin on its western boundary (IDE-Sisema, 2023). Displaying the characteristic climate of Central Brazil Tropical, it features a mild and humid mesothermal climate with average annual temperatures spanning 10 to 15°C and experiencing one to two dry months each year (IDE-Sisema, 2023). Notably, the park's climate is significantly shaped by the local mountainous topography (IEF, 2007). Falling within the Atlantic Forest biome, the region displays diverse phytophysiognomies, including Altitude Grasslands, Rocky Grassland, Montane Semideciduous Seasonal Forest, and patches of Montane Rainforest (cloud forest) (IDE-Sisema, 2023; IEF, 2007). The area of the park is predominantly dominated by Grassland phytophysiognomies, with forested phytophysiognomy occurring in smaller proportions, often associated with valleys and drainage areas (IEF, 2007). Elevations range from 1000 to 1400 meters, with the Ibitipoca Ridge standing as one of the highest points in the region. Steep escarpments mark the rugged terrain of the park (IEF, 2007). Geomorphologically, the park is situated in a quartzitic unit known as the Andrelândia Plateau (IDE-Sisema, 2023; IEF, 2007).

2.2 Sampling design and data assessment

Three caves were selected in each of the research sites, and biotic data were collected during both the dry and rainy seasons, thus involving two field campaigns for each location. When selecting the caves, we considered both the unique features of the caves and the environmental context in their surroundings, since our data collection extended to the surface environments. Consequently, we excluded from our selection process caves with a linear extent of less than 300 meters whenever possible, as well as those located in extremely challenging terrains. Furthermore, when feasible, we aimed to select caves with the most preserved surface habitats in their surroundings, since some of the areas were only recently converted into conservation units, still containing portions of altered areas such as pastures.

A transect traversing each cave and its surrounding surface environment was established. Starting from the cave entrance, the transect extended both inward and outward, covering a 300-meter distance in each direction. Along this transect, 20 sampling points were designated, with ten positioned in the subterranean and ten in the surface environment. At each of these points, a 10-meter perpendicular line was marked, and from each line, three subsamples were collected at one-square-meter quadrants. This systematic approach ensured that the subsamples were obtained with a minimum spacing of 5 meters between them and prevented bias from the expertise level of the collector at each quadrant (Figure 2). Furthermore, the sampling effort was standardized at 10 minutes per square meter (10min/m^2). In SRMSP, for the subterranean environment data collection, since all caves were smaller than 300m in linear extent (the most extensive cave was RM-39, with 72 meters), we performed an active search along the entire cave, instead of using the quadrants. This procedure aimed to ensure the obtainment of a representative sample of cave fauna while minimizing the potential effects of pseudo-replicates that could arise in the use of quadrants within such confined areas. The surface data collection was consistent throughout all the study sites.

Figure 2 - Sampling design illustrating the data collection methodology as well as the similarity approach used on the statistical models



Source: from the authors (2023)

In the quadrants, invertebrates were collected employing the Direct Intuitive Search method (Wynne et al., 2019). This technique entailed the systematic collection of invertebrate fauna from various microhabitats, including leaf litter and potential microhabitats beneath stones, blocks, and logs. This collection was made with the aid of forceps, and brush. In surface environments, when the litter was abundant, it was occasionally placed in a tray to facilitate the location and collection of invertebrates. The collected invertebrates were then stored in vials and preserved in a 70% alcohol solution. Later, they were analyzed in the laboratory and categorized into morphospecies with the aid of a stereomicroscope, following the established protocols as outlined in Oliver and Beattie (1996) and Derraik et al. (2002).

2.3 Description of the variables included in the analyses

To perform a quantitative analysis of substrate types and organic resources, a photograph was captured at chest height within each quadrant, positioned perpendicular to the ground. These photographs were subjected to analysis through Image-J software (Schneider et al., 2012), which enabled the measurement and documentation of the areas occupied by each specific substrate type. The distinct substrate types and organic resources assessed in the quadrants are outlined in Table 1. Following this, substrate diversity was assessed with the Shannon index.

At each of our designated sampling spots, the location was registered with a GPS (Garmin GPSMAP 64S). Then, we conducted ground-level measurements of temperature and humidity utilizing a digital thermo-hygrometer (AKSO AK-625, with a precision of ±0.8°C and ±4% relative humidity). Furthermore, canopy coverage was measured with a convex mirror spherical densitometer (Baudry et al., 2014). Lastly, the leaf litter depth was measured with a ruler three times in each quadrant and the average value for each quadrant was calculated afterwards.

To access the similarity between the caves and each of the surface sampling spots, we first combined the fauna collected in all of the quadrants from the subterranean environment (in SRMSP, since all caves were smaller than 300m in linear extent, instead of quadrants, we have performed an active search in the whole cave, as previously mentioned). Then, we built a Bray-Curtis similarity matrix comparing the species composition from the subterranean environment as a whole with each of the sampling points from the surface environment. The data that referred to the comparisons between the subterranean environment and each of the surface sampling point in the similarity matrix was then used as the “Similarity” variable when building the statistical models.

Table 1 - Description of the predictor variables used to build the statistical models

Variable	Type	Description	Unit
Plant Organic Matter	Substrate in the quadrants	Presence of plant debris, fallen branches of any diameter, leaf litter, and other organic substrates of plant origin	cm²
Homogeneous substrate		Substrate with a fine grain size, less than 2mm, including sand, silt, clay, mud, densely compacted substrate and bedrock	
Shelter availability		Substrate with a grain size ranging from 2mm to 4,000mm	
Water body		Streams, water puddles, and active drips	
Vegetation		Living vegetation, encompassing phanerogams, cryptogams, and algae	
Substrate Diversity	Index	Shannon index calculated from the substrate types in each quadrant	H'
Distance	Sample spot characterization	Distance between the sample spot and the cave entrance	m
Temperature		Temperature measured with the thermo-hygrometer	°C
Humidity		Humidity measured with the thermo-hygrometer	%
Canopy coverage		Percentage of canopy cover	%
Leaf litter depth		Depth of leaf litter inside the quadrant	cm

Source: from the authors (2023)

2.4 Data analysis

Boxplots were created to compare the average species richness between the subterranean and cave surrounding areas. Subsequently, to statistically evaluate any observed differences, the Wilcoxon-Mann-Whitney test was employed. This non-parametric test is particularly advantageous for comparing data distributions from two independent sample groups, making it the preferred method when the data does not conform to the assumptions of normality (MacFarlan & Yates, 2016).

To assess the influences of environmental variables on species similarity between surface and subterranean environments, we constructed Generalized Linear Mixed Models (GLMMs), with caves as the random factor. Gaussian distributions with log link functions were applied for the response variable in the analysis. Two models were developed for each study area, one corresponding to each season. The explanatory variables included in the statistical models are detailed in Table 1. Before constructing the models, Spearman correlation among the variables was tested using the chart.correlation function from the PerformanceAnalytics package. Variables with correlation values exceeding 70% were excluded from the analysis. We prioritized retaining variables that made ecological sense in addressing our research questions. Still, when in doubt, AICc values were compared between models with the model.sel function from the MuMin package (Burnham et al., 2011) to aid variable selection. Following the elimination of the highly correlated variables, non-significant predictors were progressively removed from the complete model, starting with those with the highest p values. Finally, the final model was tested for collinearity between predictor variables using the vif function from the car package.

Finally, to determine the quantitative breakpoints at which a variable ceases to influence faunal similarity, we employed segmented regressions with the significant continuous variables. These analyses were conducted using the segmented R package. All aforementioned analyses were performed using the R Software (R Core Team, 2022).

3 RESULTS

Our analysis, encompassing both rainy and dry seasons, unveiled 30 invertebrate orders and a total abundance of 7,661 invertebrates across the three parks (Table 2). The study did not include a comparison of morphotypes between each area, as the objective was not to assess compositions among them. Consequently, the total species richness including all study areas was not accessed. However, morphotype comparisons were conducted independently in each area, providing insights into the total number of morphospecies found in each. In LGSP, 416 morphospecies were identified (72 in the subterranean environment, 363 in the surface environment, and 19 shared – 4.56%). Similarly, in SRMSP, 467 morphospecies were observed (106 in the subterranean environment, 409 in the surface environment, and 48 shared – 10.27%). Finally, in ISP, 515 morphospecies were recorded (105 in the subterranean environment, 459 in the surface environment, and 49 shared – 9.51%). Particularly noteworthy in all areas were the orders Araneae, Coleoptera, and Hymenoptera, which exhibited the highest diversity and abundance in both subterranean and surface environments. Furthermore, the taxonomic groups that presented shared species across all lithologies were Acari, Araneae, Diptera and Hemiptera (Table 2).

Table 2 - List of orders found in each of the study locations with their respective species richness (LGSP = Lapa Grande State Park; SRMSP = Serra do Rola Moça State Park; ISP = Ibitipoca State Park; Subterr. = Subterranen environment; Surface = Surface environment; Shared = Species shared between both environments; S= Species richness; N = Abundance of individuals)

(Continues)

	LGSP					**SRMSP**					**ISP**				
	Subterr.		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**
	S	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**
Arachnida															
Acari	7	18	24	130	2	10	17	40	199	8	12	23	50	185	6
Araneae	15	79	61	197	1	10	91	56	296	5	25	173	80	426	16
Opiliones	1	4	-	-	-	5	15	8	16	2	1	7	5	8	1
Palpigradi	1	3	-	-	-	1	1	-	-	-	1	2	-	-	-
Pseudoscorpiones	2	3	4	31	1	2	31	4	35	1	2	4	5	71	-
Scorpiones	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Chilopoda	-	-	2	9	-	-	-	6	27	-	2	2	7	18	1
Symphyla	1	2	-	-	-	1	2	1	1	1	-	-	2	2	-
Diplopoda	3	16	4	47	1	3	19	4	44	3	6	11	3	5	-
Entognatha															
Collembola	3	23	12	114	-	14	32	22	148	6	10	46	29	177	6
Diplura	-	-	-	-	-	1	1	1	3	-	1	1	1	1	-
Malacostraca															
Isopoda	1	1	1	1	-	2	6	5	35	1	3	11	4	68	1

Table 3 - List of orders found in each of the study locations with their respective species richness (LGSP = Lapa Grande State Park; SRMSP = Serra do Rola Moça State Park; ISP = Ibitipoca State Park; Subterr. = Subterranen environment; Surface = Surface environment; Shared = Species shared between both environments; S= Species richness; N = Abundance of individuals)

(Continues)

	LGSP					**SRMSP**					**ISP**				
	Subterr.		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**
	S	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**
Insecta															
Archaeognatha	-	-	-	-	-	-	-	-	-	-	-	-	6	11	-
Blattodea	-	-	7	118	-	5	12	11	134	4	6	130	17	132	4
Coleoptera	15	33	85	205	4	9	42	96	245	-	8	14	76	169	4
Dermaptera	-	-	3	3	-	-	-	1	6	-	-	-	3	4	-
Diptera	5	20	17	32	1	4	14	20	54	3	11	21	17	34	4
Embioptera	-	-	1	5	-	-	-	1	1	-	-	-	2	3	-
Gastropoda	-	-	1	1	-	5	19	1	1	-	-	-	1	2	-
Hemiptera	4	16	31	91	4	9	18	45	114	3	5	7	45	97	3
Hymenoptera	2	2	62	398	2	9	79	50	822	6	3	5	64	742	-
Lepidoptera	3	9	21	33	-	4	6	8	18	1	2	2	14	23	-
Mantodea	-	-	1	1	-	-	-	1	1	-	-	-	-	-	-
Neuroptera	1	1	1	3	1	-	-	3	3	-	-	-	1	1	-
Oligochaeta	2	33	1	1	-	1	1	1	1	1	-	-	2	3	-

Table 4 - List of orders found in each of the study locations with their respective species richness (LGSP = Lapa Grande State Park; SRMSP = Serra do Rola Moça State Park; ISP = Ibitipoca State Park; Subterr. = Subterranen environment; Surface = Surface environment; Shared = Species shared between both environments; S= Species richness; N = Abundance of individuals)

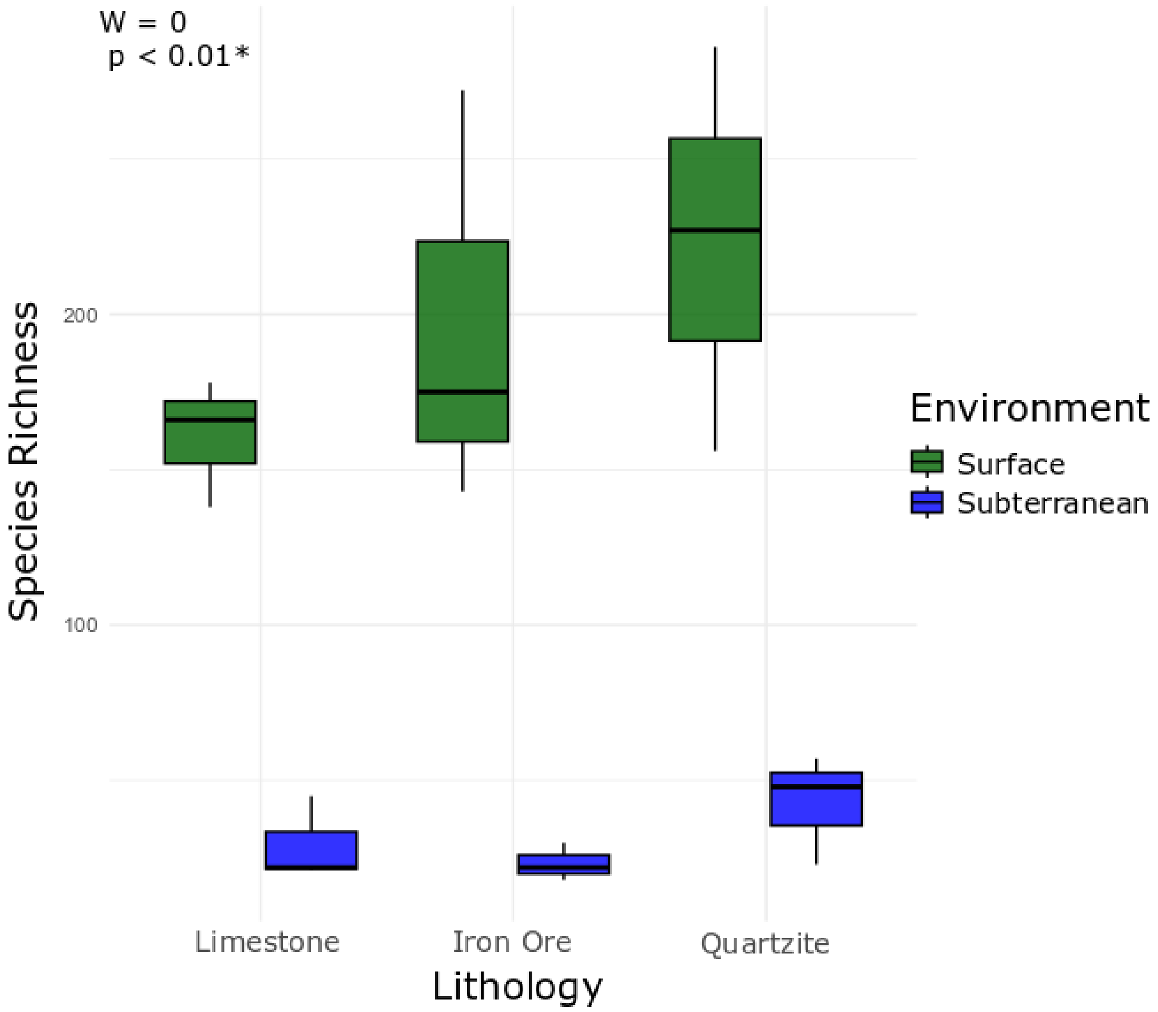
(Conclusion)

	LGSP					**SRMSP**					**ISP**				
	Subterr.		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**	**Subterr.**		**Surface**		**Shared**
	S	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**	**S**	**N**	**S**	**N**	**S**
Orthoptera	1	21	7	27	-	3	15	5	19	1	2	24	3	34	1
Phasmatodea	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-
Psocodea	5	119	12	248	2	4	38	11	42	2	5	7	11	23	-
Thysanoptera	-	-	3	9	-	1	1	5	12	-	-	-	9	21	-
Zygentoma	-	-	2	3	-	3	4	3	7	-	-	-	-	-	-
Total	**72**	**403**	**363**	**1707**	**19**	**106**	**464**	**409**	**2284**	**48**	**105**	**490**	**459**	**2263**	**49**

Source: from the authors (2023)

Furthermore, when considering the fauna from the different environments in the three lithologies, the species richness was higher on the surface environment when compared to the subterranean environment (W=0; p<0.01) (Figure 3).

Figure 3 – Comparison between the total species richness registered in the sampling areas



Source: from the authors (2023)

3.1 Limestone (Lapa Grande State Park)

The GLMM analysis investigating the variables influencing species similarity between subterranean and surface cave environments within Lapa Grande State Park (LGSP) revealed distinct patterns during different seasons. In the rainy season, the environmental variables temperature, humidity, and water bodies, showed a positive relationship with similarity (Table 5). On the other hand, during the dry season, shelter availability played a crucial role in influencing species similarity (Table 5).

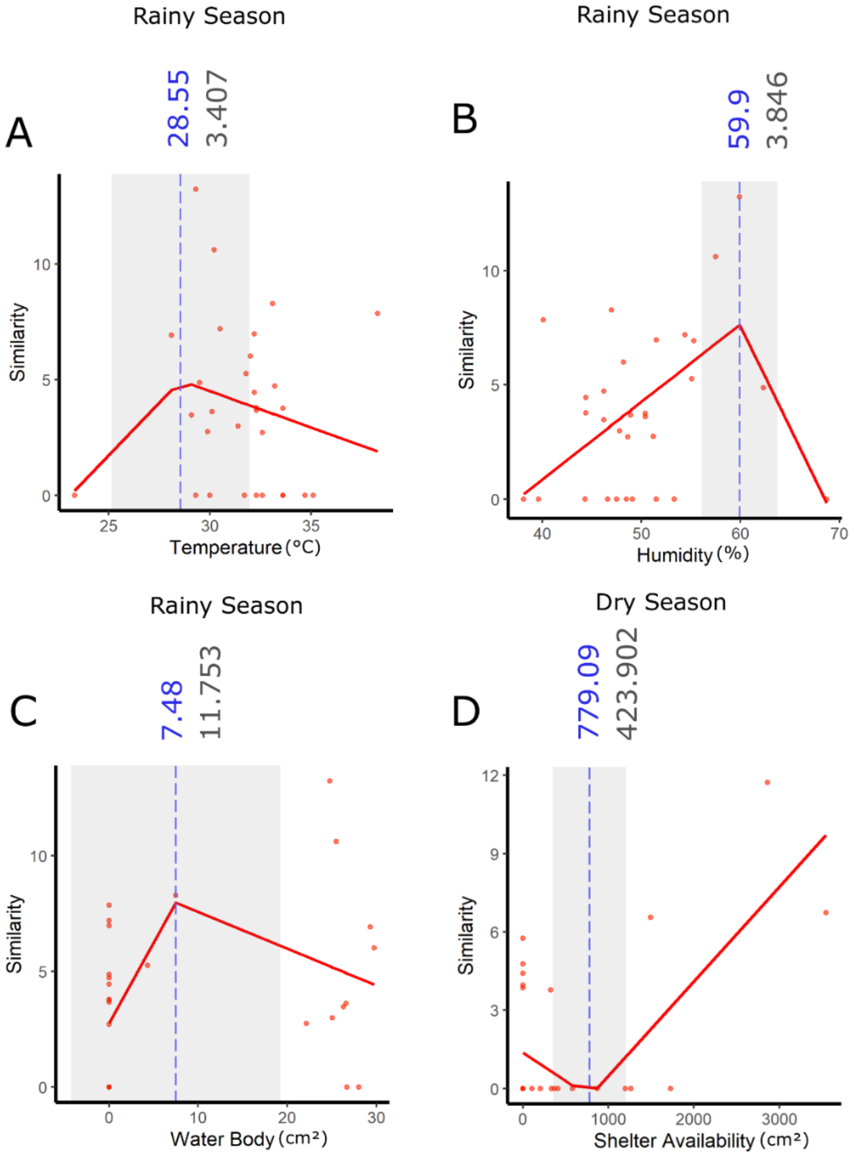
Table 5 - Summary of statistically significant sequential tests of Generalized Linear Mixed Models (GLMMs) used to analyze the relationship between predictor variables and species similarity in the subterranean and surface cave environments of Lapa Grande State Park during different seasons (Est = Estimate; Std Err = Standard Error)

Approach		**Predictor variables**	**Est**	**Std Err**	**t-value**	**p-value**
Response variable	**Season**					
Similarity	Rainy	Temperature	0.924	0.242	2.291	0.019*
		Humidity	0.392	0.140	2.786	0.009*
		Water Bodies	0.110	0.046	2.357	0.026*
Similarity	Dry	Shelter Availability	0.001	0.000	3.299	0.002*

Source: from the authors (2023)

Segmented regression models revealed that in the rainy season, the positive influence of temperature exhibited a breakpoint at 28.55°C (±3.40). In the case of humidity, the positive influence on the fauna similarity occurred through a breakpoint at 59.9% (±3.84). Regarding the presence of water bodies, a positive relationship with fauna similarity was observed up to a measure of 7.48m (±11.75) inside the sampling points. Furthermore, during the dry season, shelter availability began to influence the species similarity positively from 779.9 cm^2 onwards (Figure 4).

Figure 4 - Summary of best models describing the similarity between subterranean and surface fauna in Lapa Grande State Park. The values of ΔAICc of segmented regression in relation to the linear one are informed. The blue dashed line indicates the breakpoint and the grey area represents the standard error. A) Relationship between the species similarity and temperature during rainy season; B) Relationship between the species similarity and humidity during rainy season, C) Relationship between the species similarity and water bodies during rainy season and D) Relationship between the species similarity and shelter availability during dry season.



Source: from the authors (2023)

3.2 Iron Ore (Serra do Rola Moça State Park)

In Serra do Rola Moça State Park (SRMSP), the analysis of species similarity between subterranean and surface cave environments indicated a pronounced influence of humidity during both rainy and dry seasons (Table 6).

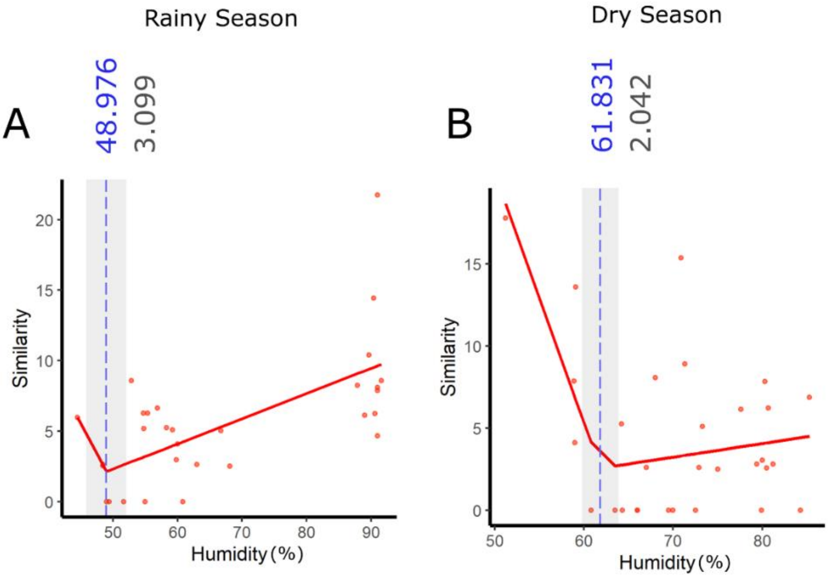
Table 6 - Summary of statistically significant sequential tests of Generalized Linear Mixed Models (GLMMs) used to analyze the relationship between predictor variables and species similarity in the subterranean and surface cave environments of Serra do Rola Moça State Park during different seasons (Est = Estimate; Std Err = Standard Error)

Approach		**Predictor variables**	**Est**	**Std Err**	**t-value**	**p-value**
Response variable	**Season**					
Similarity	Rainy	Humidity	0.157	0.039	4.010	<0.001*
Similarity	Dry	Humidity	0.163	0.039	4,194	<0.001*

Source: from the authors (2023)

The segmented regression analysis revealed that humidity had different quantitative breakpoints for the rainy and dry season, staying at 48.98% (±3.09) on the former and at 61.83% (±2.04) for the latter (Figure 5).

Figure 5 - Summary of best models describing the similarity between subterranean and surface fauna in Serra do Rola Moça State Park. The values of ΔAICc of segmented regression in relation to the linear one are informed. The blue dashed line indicates the breakpoint and the grey area represents the standard error. A) Relationship between the species similarity and humidity during rainy season and B) Relationship between the species similarity and humidity during dry season.



Source: from the authors (2023)

3.3 Quartzite (Ibitipoca State Park)

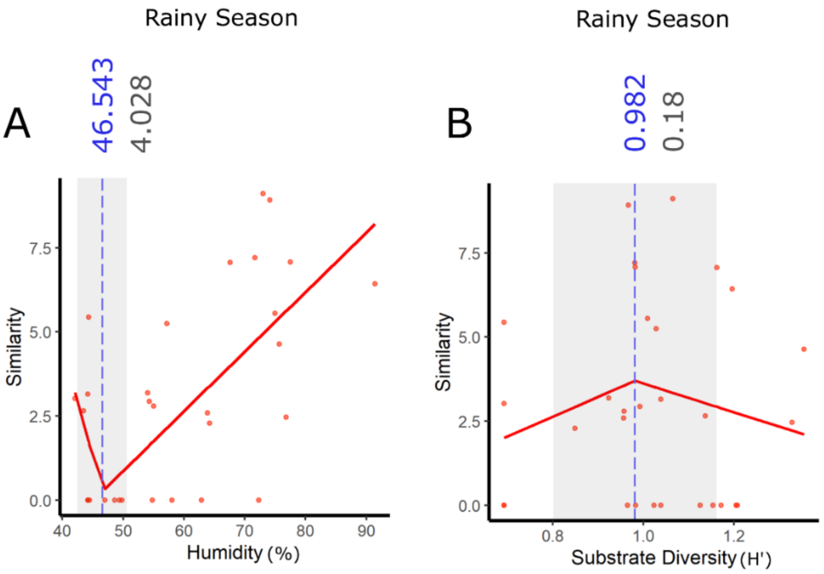
The analysis in Ibitipoca State Park (ISP) showed that the relationship between environmental variables and species similarity during the rainy season is mainly shaped by humidity and substrate diversity, while there were no statistically significant relationships during the dry season. Humidity exhibited a positive relationship with species similarity, suggesting that higher humidity conditions favored a more similar species composition in the subterranean and surface environments. Substrate diversity, on the other hand, had a negative influence on species similarity during the rainy season (Table 7).

Table 7 - Summary of statistically significant sequential tests of Generalized Linear Mixed Models (GLMMs) used to analyze the relationship between predictor variables and species similarity in the subterranean and surface cave environments of Serra do Ibitipoca State Park during different seasons (Est = Estimate; Std Err = Standard Error)

Approach		**Predictor variables**	**Est**	**Std Err**	**t-value**	**p-value**
Response variable	**Season**					
Similarity	Rainy	Humidity	0.157	0.054	2.866	0.009*
		Substrate Diversity	-7.053	3.000	-2.351	0.026*

Source: from the authors (2023)

Figure 6 - Summary of best models describing the similarity between subterranean and surface fauna in Ibitipoca State Park. The values of ΔAICc of segmented regression in relation to the linear one are informed. The blue dashed line indicates the breakpoint and the grey area represents the standard error. A) Relationship between the species similarity and humidity during rainy season and B) Relationship between the species similarity and substrate diversity during rainy season.



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Source: from the authors (2023)

Segmented regression models illustrated that humidity exhibited a quantitative breakpoint at 46.55% (±4.02), while substrate diversity had a breakpoint at 0.92 (±0.18), with the similarity decreasing as the substrate diversity gets higher (Figure 5).

4 DISCUSSION

Our sampling revealed a rich diversity of invertebrate fauna, encompassing 30 orders and a total abundance of 7,661 individuals. When comparing subterranean and surface environments, the richness of species was consistently higher on the surface, emphasizing the distinct ecological dynamics of these two habitats. Additionally, each park exhibited unique patterns of environmental variables influencing species similarity. Still, the primary factor influencing the similarity between subterranean and surface environments in all lithologies in our study was humidity. However, the presence of water bodies, substrate diversity, and shelter availability were also crucial factors influencing fauna similarity in the studied areas.

Humidity is a well-known influential factor in invertebrate fauna, both in subterranean (Peck, 1988; Tobin et al., 2013; Simões et al., 2015; Howarth & Wynne, 2022) and surface (Ivask et al., 2008; Babchenko et al., 2020; Zhukov et al., 2021) environments. In our study, it emerged as the primary factor influencing invertebrate fauna similarity across all areas. However, this influence varied among different areas. In LGSP, the relationship between species similarity was positive until around 60%, after which it began to decrease. In SRMSP and ISP, on the other hand, similarity only began to increase from 50-60% humidity values. This disparity may be a consequence of the drier climate present in LGSP compared to other regions (IDE-SISEMA, 2023), resulting in most humidity measurements from the surface environment being lower than 60%. Nevertheless, the consistent influence of humidity across different lithologies and seasons underscores its paramount importance in shaping terrestrial invertebrate faunal similarity.

In LGSP during the rainy season, aside from humidity, positive relationships were also observed between invertebrate similarity and temperature, as well as the presence of water bodies. The positive relationship with the presence of water bodies found in this area reinforces the importance of humidity for the similarity of the fauna in such environments (Prous et al., 2015). Furthermore, temperature conditions up until 28.55°C favored higher similar species composition between subterranean and surface environments. Beyond this point, the similarity diminishes with increasing temperature, as higher temperatures are known to negatively affect terrestrial invertebrate communities (Sinclair, 2002; Pakhomov et al., 2019; Figueroa et al., 2021). Moreover, higher temperatures favor plant evapotranspiration, which culminates in lower humidity (Kimball & Bernacchi, 2006).

In the dry season, shelter availability played a crucial role in influencing species similarity in LGSP. Similarly, the analysis in ISP revealed that, in addition to humidity, substrate diversity also influenced species similarity during the rainy season, highlighting the importance of microhabitats in structuring these communities, both inside and outside the cave environment (Zepon et al., 2017; Pacheco et al., 2020; Howarth & Wynne, 2022). The role of shelter availability in influencing faunal similarity during the dry season highlights the need to consider seasonal variations in conservation planning. Microhabitats can act in several ways to promote invertebrate diversity and, consequently on our case, faunal similarity. They can promote a diversity of physical habitats for the fauna to inhabit, as well as a diversity of microclimatic conditions, such as the maintenance of stable humidity and temperature, which are known key factors for structuring cave invertebrate fauna (Simões et al., 2015; Culver & Pipan, 2019). The identification of breakpoints for these microhabitats offers practical guidelines for land management practices, reinforcing the interconnectedness of surface and subterranean environments.

The connection between subterranean and surface environments is clear when observing the amount and proportion of shared species between them. The proportion of shared species was expected to be higher in the ferruginous lithology due to the high rock porosity and the extensive presence of *canaliculi* in such environments (Souza-Silva et al., 2011; Ferreira et al., 2015). While the similarity was indeed higher in the ferruginous lithology, the quartzitic lithology also presented a high proportion of shared species between environments, which was an unexpected outcome. These differences in shared species proportions may reflect ecological dynamics that are still not fully elucidated in the available scientific literature. Considering the fact that quartzitic rocks do not present the same level of structural interconnection of ferruginous rock (Souza-Silva et al., 2011), the high proportion of shared species might indicate that in this lithology, invertebrate species do transit between surface and subterranean environments using superficial pathways.

From a conservation point of view, this brings attention to the need of further understanding the biological connection between surface and subterranean environments and including such environments in conservation strategies. These results points out to the potential use of shared species proportions as an indicator of habitat conservation status and opens opportunities for targeted conservation strategies, providing practical insights for conservation practitioners. As an example, the most significantly altered areas in the external vicinity of the caves were noted in the LGSP where the pristine vegetation has been historically replaced by pastures near the cave entrances. Even after decades, pasturelands continue to dominate the surroundings of the caves in this region. In contrast, within the ISP and SRMSP, the external vegetation surrounding the caves remains well preserved. Hence, this preservation of the external environments seems to be a key factor contributing to the higher number of shared species between the caves and their surrounding areas in these regions. Therefore, the number of shared species can potentially serve as an indicator of the conservation status of the areas surrounding the caves or, possibly, of the caves themselves. However, it is crucial to validate this hypothesis by conducting studies on additional caves in different regions. By aligning conservation efforts with faunal similarity patterns, it is possible to optimize resources and prioritize surface areas with higher conservation value when the goal is to preserve cave ecosystems as a whole.

Furthermore, an imperative aspect emerging from our results is the significant influence of humidity on species similarity across all lithologies. Given the anticipated impacts of climate change on temperature and humidity (Mammola et al., 2019; Marjakangas et al., 2022; Nanni et al., 2023), it becomes paramount to project potential consequences for these interactions. While our primary focus was not on climate change, the relevance of this issue cannot be ignored. Increased temperatures and decreased humidity, particularly if surpassing the breakpoints identified, may potentially alter the balance observed in subterranean ecosystems and disrupt the connection between subterranean and surface environments.

As the scientific community face the challenges posed by climate change, our study reinforces the urgency of considering spatial and temporal dimensions in conservation planning, providing a roadmap for preserving the balance of subterranean ecosystems in the face of environmental change. Future research should involve a more extensive exploration of climate change scenarios, incorporating climate models for the specific study areas. Predicting temperature increases, humidity changes, and their implications for invertebrate communities will enhance the robustness of conservation recommendations. Additionally, expanding the taxonomic resolution of the analysis could provide a more detailed understanding of shared species proportions and their ecological implications.

The findings of our study advance the understanding of ecological interactions between subterranean and surface environments within diverse lithologies, contributing to the broader understanding of ecological interactions between subterranean and surface environments and acting as a stepping-stone for future research. The breakpoints offer quantitative thresholds that can guide conservation efforts and land management practices to preserve the balance of subterranean ecosystems. Furthermore, it reinforces the idea that a cave is connected to the environment in which it is inserted biologically, climatically and geologically, bringing to light the need to incorporate such spatial context into conservation strategies under a biological point of view. The preservation of caves surrounding areas is, therefore, essential to sustain environmental conditions for species to transit between the subterranean and surface environments and maintain the biological connectivity between them, especially under the light of a climate change scenario.

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