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International Journal of Speleology
Official Journal of Union Internationale de Spéléologie

Abiotic factors influencing anuran occupation of Neotropical Brazilian caves

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Abstract: Despite increasing research on the Neotropical underground environment, anurans remain poorly understood in this habitat. It was analyzed scientific literature records of anurans in Brazilian natural caves and performed a redundancy analysis (RDA) to identify the environmental, taxonomic, geographic, geological and land-use variables that influence their cave occupancy. It was examined a total of 247 literature records, encompassing 83 species/morphospecies, which revealed distinct cave-dwelling tendencies. Some anuran species occupy caves at altitudes between 5 to 21 meters above sea level (m asl), in areas characterized by rocky outcrops and grassland. Others are associated with caves surrounded by forest, savanna, pasture or mosaic of agriculture and pasture. A third group is linked to caves with varying lithologies. These findings highlight specific ecological scenarios for anuran occurrence in Neotropical caves. Conserving cave-dwelling anurans in the Neotropical region depends on understanding the factors influencing their subterranean occupancy. Preserving native vegetation and maintaining undisturbed landscapes are essential. This will safeguard these sensitive species and reinforce their role as bioindicators of ecological impacts in cave environments.

Keywords: Altitude, amphibians, land use, lithology

Received 6 May 2024; Revised 18 August 2025; Accepted 21 August 2025

Citation: Sperandei, V.F., Vaz-Silva, W., Tejerina-Garro, F.L., 2025. Abiotic factors influencing anuran occupation of Neotropical Brazilian caves. International Journal of Speleology, 54(2), ijs25132. https://doi.org/10.5038/1827-806X.ijs2513

INTRODUCTION

Natural subsurface environments exhibit distinct physical and functional structural characteristics (Ortuño et al., 2013; Culver & Pipan, 2019) that govern biotic and abiotic interactions. These environments encompass human-accessible caves, rock fissures, groundwater systems, subterranean habitats, and other geological formations (Culver & Pipan, 2019).

Caves harbor simplified biological communities compared to surface environments (Peck, 1976; Badino, 2010; Tobin et al., 2013). They share distinct ecological characteristics, including stable average temperature and relative humidity, permanent absence of natural light, and limited nutritional resources (Culver & Pipan, 2019; Mammola, 2019; Mammola et al., 2020). These characteristics act as an environmental filter, increasing mortality for organisms lacking subterranean adaptation (whether through habits or physiological conditions) or prompting their return to the surface (Zerba & Collins, 1992; Culver & Pipan, 2019; Simões et al., 2015). Cave energy dynamics are entirely allochthonous and oligotrophic due to negligible primary production. Nutrients primarily particulate organic matter of animal and plant origin, enter caves through recharge water, wind action, or via animal vectors migrating between surface and subsurface environments (Souza-Silva et al., 2021; Souza-Silva & Ferreira, 2022).

The presence and density of caves are influenced by local lithology (Jansen & Pereira, 2015). Carbonate rock outcrops (karst) have specific physicochemical characteristics, including solubility and porosity (Lepsch, 2010; Rubioli et al., 2019), which facilitate the formation of numerous and extensive caves systems (Culver & Pipan, 2019). Similarly, ferruginous lithologies exhibit high speleological density, with formations typically occurring below

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the soil surface layer (Dutra, 2015). Both lithological types are frequently targeted by mining activities, posing significant threats to cave ecosystems, which rank among the most endangered habitats in the Neotropical region (Ferreira et al., 2018; Mammola et al., 2019; Ferreira et al., 2022a).

Caves exhibit microclimatic variations and distinct niches from the entrance zone to deeper areas, creating gradients of abiotic conditions and resource availability (Tobin et al., 2013; Prous et al., 2015; Mammola & Isaia, 2018). Natural light distribution establishes three distinct zones: i) a photic zone near entrances with direct light exposure, ii) a disphotic zone with indirect light incidence, and iii) an aphotic zone completely devoid of light. This zonation promotes habitat heterogeneity and influences community structure (Lunghi & Manenti, 2020; Souza-Silva et al., 2021). Deeper cave zones show greater environmental stability, typically maintaining saturated humidity, reduced food input, and simplified trophic networks with fewer energy transfer levels (Culver & Pipan, 2019).

The most extensively studied cave-dwelling vertebrates include fishes, chiropterans (flying mammals), and birds that nest near cave entrances (Trajano & Bichuette, 2006). Anurans are also documented in caves, though they are typically classified as accidental visitors, that is, organisms that enter caves incidentally but lack the adaptations to survive underground, often perishing or returning to the surface (Trajano & Bichuette, 2006). This classification system remains debated, as some anuran species exhibit behaviors characteristics of trogloxenes, actively using caves during specific life stages (Luría-Manzano & Ramírez-Bautista 2017; Suwannapoom et al. 2018; Dos Santos et al., 2022a). These amphibians may employ caves as thermal refuges to prevent desiccation, seek protection from predators, and participate in subterranean trophic networks (Sperandei et al., 2023, 2024).

Brazil harbors the world's highest anuran diversity, with 1,114 documented species (Segalla et al., 2021). Among these, 41 species are listed as threatened (ICMBio, 2018). The number of species recorded in Brazilian caves varies from 34 in the Caatinga, Cerrado, and Amazon biomes (Dos Santos et al., 2022a) to 54 when the Atlantic Forest and transition areas are also included (Matavelli et al., 2015; Sperandei et al., 2024). The occurrence of anurans in caves is related to the high humidity levels required for their physiological processes, particularly cutaneous respiration through their permeable integument (Eterovick et al., 2010; Matavelli et al., 2015).

In temperate regions characterized by harsh winters and subzero temperatures, caves serve as natural refuge offering stable thermal conditions and food resources (Miller & Niemiller, 2008; Biswas, 2014). Similarly, in the Neotropical region, caves provide essential shelter for anurans in areas experiencing extreme temperatures and low humidity (Eterovick et al., 2010). This is particularly evident in biomes like the Caatinga (a tropical semi-arid climate; BSh in Köppen-Geiger classification; Trajano & Bichuette, 2006; Alvares, 2013) and Cerrado (with Am, Aw, Cwa and Cwb climate types sharing similar dry seasons; Alvares, 2013). Additionally, caves offer reduced predation pressure compared to surface environments (Pough et al., 2008; Andrade et al., 2021; Dos Santos et al., 2022b). Despite their protected status as national biological, geological, and cultural heritage sites, Brazilian caves face significant anthropogenic threats such as mining operations, urban expansion, and land-use changes (Ferreira et al., 2022b).

This study aimed to assess the influence of environmental (presence of water, photic zone, land use), geographic (biome, altitude), and geological (lithology) variables on the occurrence of anurans in Brazilian caves, based on literature records. It is hypothesized that anuran occurrence in caves is significantly associated with these environmental, geographic, and geological variables. Among the environmental factors, the presence of water in caves is expected to favor anuran occurrence, as it maintains high humidity levels critical for amphibian physiology (Matavelli et al., 2015). The light gradient (photic zone) may also influence anuran presence, as most species are considered accidental cave visitors, entering opportunistically rather than as obligatory inhabitants (Trajano & Bichuette, 2006). Furthermore, cave lithology likely plays a role in anuran occurrence, as different rock types create distinct microhabitat conditions (Lunghi et al., 2018; Vaz-Silva et al., 2020).

MATERIAL AND METHODS

Anuran data

It was compiled records of anurans in Brazilian natural caves though systematic searches of scientific literature using multiple databases: Google Scholar, SCOPUS, Web of Science, and AmphibiaWeb. Google Scholar provides comprehensive coverage of scientific publications across various repositories and languages (Falagas et al., 2008; Delgado & Repiso, 2013; Martín-Martín et al., 2021). While SCOPUS and Web of Science offer robust search engines for scientometric studies (Oliveira & Gracio, 2011; Mongeon & Paul-Hus, 2016), they often lack indexing for many local and regional Brazilian journals. This multi-database approach minimized potential biases in the literature-based data collection (Archambault et al., 2009; Mongeon & Paul-Hus, 2016).

For the systematic literature search, it was used individual and combined keywords (Da Silva et al., 2011; Urbizagástegui-Alvarado, 2022), with a cutoff date of December 2022. The keywords, used separately in Portuguese/English, were: "anuros/anurans", "anfíbios/amphibians", "sapos/frogs", "cavidades subterrâneas/underground cavities", "habitats subterrâneos/underground habitat", "ambientes subterrâneos/underground environment", "grota/grotto", "depressão/gruna", "toca/burrow", "cavernas Brasileiras/Brazilian caves", "cavidades subsolo/subterranean cavities", "habitat subsolo/

subterranean habitat", and "ambiente subsolo/ subterranean environment". For combined keywords searches, it was used the Boolean operator "or" for expressions with the same meaning, and "and" for keywords of different natures. All identified articles were reviewed and analyzed for data extraction, with no time restrictions imposed.

Following the initial selection, it was removed duplicates and studies that did not meet the criteria for confirmed anuran presence within caves. From the remaining literature, it was extracted and categorized information into the following variables: "Taxonomic" (family and species/morphotype identification), "Geographic" (municipality, state, biome, altitude, and land use/cover classification), "Environmental" (cave photic zone and water presence) and "Geological" (lithological characteristics; see Table 1).

Table 1. Variable type, categories (with their respective code in parenthesis), and subcategories extracted from anuran literature records in Brazilian caves. m asl = meters above sea level.

Variable	Category	Subcategory
Taxonomic	Family (FA)	Anuran family
	Species (SP)	Anuran species/morphospecies
Geographic	Biome (BI)	Amazon
		Caatinga
		Cerrado
		Ecotone - Cerrado/Atlantic Forest
		Ecotone - Caatinga/Atlantic Forest
		Atlantic Forest
	Altitude (AL) m asl	13, 21, 26, 62, 198, 269, 290, 297, 343, 348, 476, 595, 600, 640, 651, 655, 794, 825, 1437, 1571, 1600, 1602, 1606, 1608, 1614, 1623
Environmental	Water presence (WP)	Absent
		Perennial
		Intermittent
	Photic zone (PZ)	Photic
		Disphotic
		Aphotic
Geological	Lithology (LI)	Sandstone
		Carbonatic
		Conglomerate
		Ferruginous
		Granitic
		Marble
		Quartzite
Land use	MapBiomas classification (MC)	Agriculture and pasture mosaic
		Sugar cane
		Grassland formation
		Forest formation
		Rocky outcrop
		Savanna formation
		Pasture
	Forest formation buffer (FL)	Presence/Absence
	Savanna formation buffer (SA)	Presence/Absence
	Grassland formation buffer (RU)	Presence/Absence
	Rocky outcrop buffer (RO)	Presence/Absence
	Flooded field buffer (FF)	Presence/Absence
	Water buffer (WA)	Presence/Absence
	Ocean buffer (OC)	Presence/Absence
	Pasture buffer (PA)	Presence/Absence
	Agriculture buffer (AG)	Presence/Absence
	Sugar cane buffer (SC)	Presence/Absence
	Coffee buffer (CO)	Presence/Absence
	Forestry - Eucalyptus buffer (FO)	Presence/Absence
	Agriculture and pasture mosaic buffer (APM)	Presence/Absence
	Urban buffer (UA)	Presence/Absence

It was also collected cave registration data (name, official code, and geographic coordinates) for geographic positioning and subsequent land-use characterization, though these were not included as categories for statistical analysis. The nomenclature of all species was verified and updated when necessary, using the Amphibian Species of the World 6.1 database (Frost, 2023).

Geographic, environmental, geological, and land use/cover data

The environmental quality and land use/cover characteristics (Table 1) surrounding each cave were assessed using the MapBiomas platform (Annual land use and land cover mapping project of Brazil; Souza et al., 2020). Geographic coordinates for each cave were obtained from either scientific literature or the National Registry of Speleological Information (CANIE), maintained by the National Center for Cave Research and Conservation (ICMBio/CECAV) (CECAV, 2023). All coordinates were standardized to latitude and longitude in decimal degrees (Datum: SIRGAS2000). From the CANIE registry data, the altitude (meters above sea level; m asl) was also extracted and classified as a geographic variable category.

Using geographic coordinates as reference points, a 500 m radius buffer was created around each cave location. Within these buffers, it was calculated the percentage of each land use/land cover category following the MapBiomas classification system: forest formation, savanna formation, grassland formation, rocky outcrop, pasture, agriculture, forestry, mosaic of uses (agriculture + pasture), and urbanized areas. This spatial analysis was performed by plotting each cave coordinate in MapBiomas and its corresponding 500 m buffer. Afterwards, it was used the ImageJ software (Rasband, 2018) to quantify the presence/absence of each category within these buffers based on the MapBiomas database.

Data analysis

Using data collected from scientific publications (geographic, environmental, and geological variables) and land use/cover classifications for each cave, the first data matrix was created, hereafter referred to as environmental variables. In this matrix, each row represented an independent anuran record. It included the categories and subcategories by variable as listed in Table 1. A second data matrix, hereafter referred to as biological variables, included the taxonomic family and species/morphospecies categories, as detailed in Supplementary Table S1. Categories present in both matrices were converted to a code number. For the environmental data, it was determined the variance inflation factor (VIF) to detect multicollinearity among variables (cut-off threshold VIF ≤ 10.0; Hair et al., 2019). Afterwards, the data were submitted to a redundancy analysis (RDA), a multivariate statistical method suitable for relating matrices of environmental variables and biological responses (Legendre & Legendre, 2012). All analyses were performed using PAST software (version 4.16c; Hammer et al., 2001) and the *Rcmdr* package (Fox, 2005) in R software (R Core Team, 2025).

Table 2. Results of the RDA ordination between environmental variables and anuran species recorded in the scientific literature for Brazilian caves. (A) Eigenvalues, explained variance (%), and correlation (r) by axis. (B) Scores and variance inflation factors (VIF) of environmental variables. (C) Statistical summary of the RDA model (environmental variables and anuran occurrence data).

		Axis 1	Axis 2	VIF
A	Eigenvalue	7.1	0.7	-
	Axis %	21.1	2.0	-
	Cumulative %	21.1	23.1	-
	r	0.5	0.3	
B	MC	**-0.5**	-0.2	6.2
	AL	**0.5**	0.2	4.6
	LI	-0.1	**0.8**	1.4
	PZ	-0.2	0.1	1.1
	BI	0.3	0.3	1.3
	WP	-0.2	0.2	2.3
	FL	0.1	-0.3	2.4
	AS	0.0	0.1	2.8
	RU	**0.7**	-0.1	3.5
	RO	**0.9**	0.0	8.1
	FF	0.0	-0.1	1.6
	WA	-0.1	-0.1	1.8
	OC	-0.1	0.2	1.9
	PA	-0.3	-0.4	3.9
	AG	-0.2	0.1	1.7
	SC	0.0	-0.2	2.2
	CO	-0.1	-0.3	1.9
	FO	0.1	0.2	1.6
	APM	0.2	-0.3	2.7
	UA	-0.1	-0.3	5.6
C	R^2	0.231		
	F	3.394		
	p	**0.001**		

RESULTS

This study compiled 247 independent literature records of anurans in Brazilian caves, encompassing 83 taxa (species and morphospecies) from 12 families within the order Anura (see Sperandei et al., 2024). Of these, 54 were identified to species level (specific epithet), while 29 were classified at genus level (morphospecies; Supplementary Table S1).

The environmental variables showed no multicollinearity (all VIF values <10.0; Table 2). The first two RDA axes explained 23.1% of the total data variability and the species occurrence-environment relationship model was statistically significant (p=0.001; Table 2). The ordination revealed that Axis 1 was primarily influenced by Mapbiomas land use classification (MC), altitude (AL), grassland formation buffer (RU), and rocky outcrop buffer (RO). Axis 2 was associated with lithology (LI). These variables structured the recorded occurrence of Brazilian anurans in caves (Fig. 1).

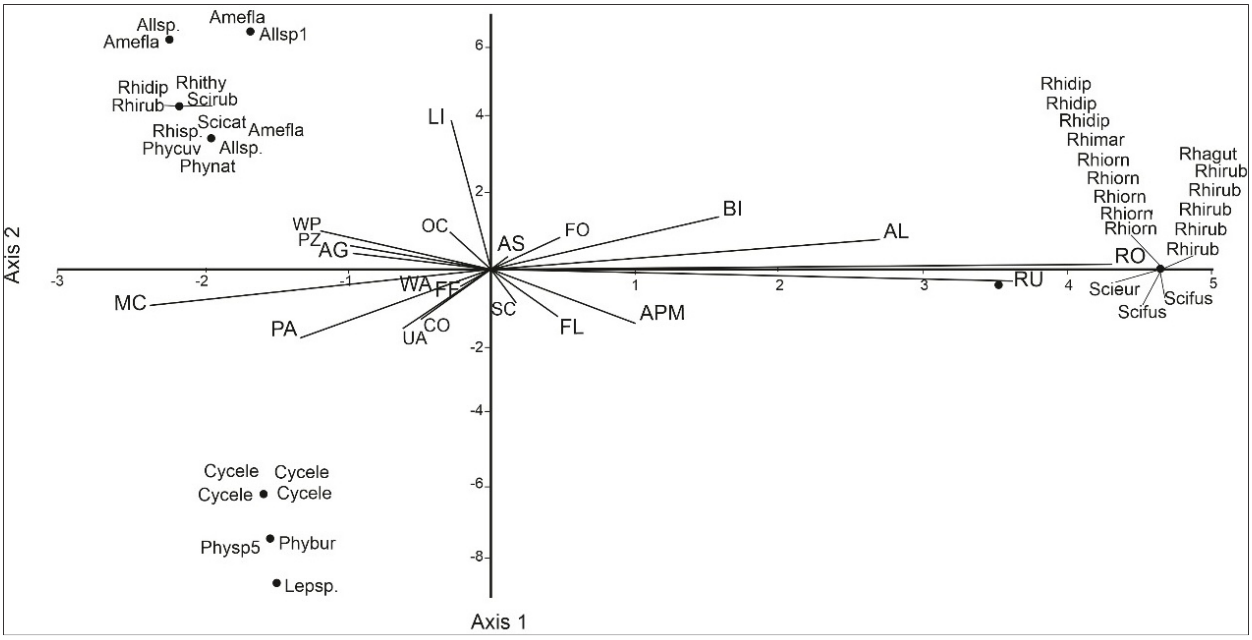

Fig. 1. RDA ordination of environmental variables and anuran occurrence records in Brazilian caves from scientific literature. Only species with extreme scores on each axis are displayed. Codes correspond to those listed in Table 1 (environmental variables) and Supplementary Table S1 (recorded species).

The anurans *Rhaebo guttatus*, *Rhinella marina*, *Rhinella ornata*, *Scinax eurydice*, and *Scinax fuscovarius* were associated with caves in low-altitude areas (5-21 m asl) characterized by rocky outcrops and grassland. In contrast, *Allobates* sp., *Ameerega flavopicta*, *Rhinella thyphonius*, *Rhinella* sp., *Physalaemus cuvieri*, *Physalaemus nattereri*, *Scinax catharinae*, and *Scinax ruber* were found in caves exhibiting distinct environmental characteristics, namely, surrounded by forest, savanna, pasture, or a mosaic of agriculture and pasture areas. *Rhinella diptycha* and *Rhinella rubescens* occurred in caves with both types of environmental characteristics (Fig. 1). Additionally, *Allobates* sp., *Ameerega flavopicta*, *Allobates* sp. 1, *Leptodactylus* sp., *Cycloramphus eleutherodactylus*, *Physalaemus* sp. 5, and *Phyllomedusa burmeisteri* were associated with caves in various lithologies, including ferruginous, sandstone, marble, carbonatic, and conglomerate formations (Fig. 1).

DISCUSSION

The results of this study indicate that variables such as land-use classification, altitude, and the presence of grassland formations and rocky outcrops influence the occurrence of anurans in Neotropical Brazilian caves. This highlights the relevance of the landscape surrounding cavities in structuring anuran communities in subterranean environments. Elements like open vegetation and terrain directly affect species' use of these underground habitats. For instance, *Rhaebo guttatus*, *Rhinella marina*, and *Scinax fuscovarius*, frequently associated with open and anthropized environments (Pinheiro et al., 2012; Entiauspe-Neto et al., 2016; Toledo et al., 2017), were recorded in low-altitude areas (5–21 m asl) dominated by pastures and rocky outcrops. This trend suggests their tolerance to drier, unstable environmental conditions with anthropogenic disturbances.

Additional results indicate that local geology, specifically lithology, also influences the composition of anuran species inhabiting these cavities. Species like *Allobates* sp., *Ameerega flavopicta*, *Allobates* sp. 1, *Leptodactylus* sp., *Cycloramphus eleutherodactylus*, *Physalaemus* sp. 5, and *Phyllomedusa burmeisteri* were associated with caves featuring specific lithologies, including ferruginous formations, sandstones, marbles, carbonatic, and conglomerate formations. This suggests that the type of cave lithology, particularly those that allow water infiltration (such as sandstones, carbonatic, conglomerate, and ferruginous in this case), influences the formation of more humid and thermally stable microclimates (Ford & Williams, 2007). These conditions favor occupation by the aforementioned species, which display more restrictive environmental requirements, such as a narrow range of supported temperature and relative humidity tending towards saturation. This is the case for *Allobates* sp. and *Cycloramphus eleutherodactylus*, which prefer caves with availability of crevices, internal humidity, or thermal stability (Sperandei et al., 2023).

The observed relationships indicate that different anuran groups respond distinctly to environmental gradients, reflecting their specific ecological requirements. These trends reinforce the premise that community composition, particularly in subterranean environments, is shaped by a complex environmental filter (Ernst & Rödel, 2008). This filter is composed of various elements: light (Poulson & White, 1969), organic matter (Mammola, 2019), water and chemical (De Waele & Gutiérrez, 2022), and biological filter (related to colonization and dispersion; Nicolosi et al., 2023). Generalist species, such as *Rhinella diptycha* (Severgnini et al., 2020) and *Rhinella rubescens* (Fraga & Wiederhecker, 2021), were found in caves across two distinct environmental settings: i) low-altitude rocky outcrops and grassland (5–21 m asl), and ii) areas characterized by forest, savanna, pasture or a mosaic of agriculture and pasture. This suggests these species demonstrate greater ecological plasticity, but their distribution appears not be influenced by the environmental variables considered in this study. In contrast, species with more restricted preferences or endemic status, such as *Oreobates antrum* (endemic to the Cerrado biome; Vaz-Silva et al., 2018), showed an association with specific environmental conditions. This suggests higher ecological specialization or dependence on microhabitats (Ernst & Rödel, 2008). Several categorical variables that could explain anuran use of physical space within cavities, such as luminosity zone or the presence of water at the recording point inside the cave, have low reporting frequencies in the scientific literature consulted. Nevertheless, it is possible that most anurans in Neotropical caves are found in the entrance zone, suggesting that the cave serves as shelter or refuge during the animals' resting periods (Bichuette et al., 2022; Dos Santos, 2022a). This observation supports the classification of anurans in Neotropical caves as trogloxenes, given their habits are linked to the subterranean environment, including reproduction, foraging, and use for refuge or shelter.

The results also highlight the influence of anuran literature records in a region located within an ecotone between the Atlantic Forest, Cerrado, and Caatinga biomes. This area is characterized by low elevations and carbonate substrate, representing the typical karst environment found in northeastern Goiás, northern Minas Gerais, southern Tocantins states, and throughout northeastern Brazil. In these regions, human settlements are often established near caves, primarily driven by the exploitation of subterranean water resources (Donato, 2011; Gallão & Bichuette, 2015). Furthermore, this study's results indicate that anthropogenic activities within a 500 m radius of cave have shaped a landscape primarily consisting of pastures and a mosaic of agricultural areas and natural remnants.

The findings suggest that the presence of rupestrian fields and rocky outcrops associated with lithologies is relevant for the occupation of subterranean environments by Neotropical anurans. These locations also show a higher prevalence of cavities. However, it would be expected that geological aspects, particularly the lithological characteristics of cave surroundings, would correlate with cavity abundance, given that rocks with physicochemical properties favorable to speleogenesis (such as carbonates) tend to form more cavities (Frisia & Borsato, 2010).

The results of this study underscore the importance of considering multiple abiotic factors in the management and conservation of Brazilian caves, particularly given increasing land-use intensity and pressures on unique geological formations. These factors address broader questions about biodiversity and biotic conditions for habitat colonization (Mammola, 2019). Effective conservation strategies should encompass not only cave interiors but also their surroundings and local geodiversity, which have proven determinant for anuran occurrence in these subterranean ecosystems (Sperandei et al., 2023, 2024).

Furthermore, significant knowledge gaps persist regarding cave-dwelling anurans that require addressing. This includes a need for population studies and target-species research, along with more precise biospeleological classifications. Proper assessment of these organisms in caves is crucial for both biological research and determining speleological relevance in environmental licensing processes (Brasil, 2008, 2017; Sperandei et al., 2023).

CONCLUSION

This study demonstrated that the documented anuran occupation of Neotropical Brazilian caves is influenced by abiotic factors, including land use, altitude, and lithology across different ecological scenarios. The formation of distinct taxonomic groups associated with specific environmental and geological contexts reveals that subterranean habitat occupation by anurans is not random, but rather a response to a complex environmental filter. These findings highlight two key aspects: i) the need to expand knowledge about distribution patterns of cave-dwelling anurans by identifying priority areas for future research; ii) the requirement for effective conservation strategies that consider not only cave interiors but also their immediate buffer zones and local geodiversity. These are critical elements for maintaining subterranean biodiversity and protecting native vegetation in Neotropical karst areas.

ACKNOWLEDGMENTS

This study was partially funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, Finance Code 001. The first author was supported by a CAPES scholarship. The authors thank the anonymous reviewers for their valuable suggestions on earlier versions of this paper.

Authorship statement: VFS, WVS, and FLTG declare that they participated in the entire preparation of this article, from the conception of the idea to statistical tests and preparation of the text.

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