Biologia
https://doi.org/10.1007/s11756-024-01692-8

ORIGINAL ARTICLE

Ants (Hymenoptera: Formicidae) in subterranean natural cavities of Minas Gerais, Brazil

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Received: 3 October 2023 / Accepted: 17 April 2024

Abstract
A list of ant species collected in caves at different localities of Minas Gerais state, Brazil is presented, based on specimens deposited in the Entomological Collection Padre Jesus Santiago Moure (DZUP). Of the 51 species/morphospecies found, two are new records for the state. We encourage an increase in ant collection efforts in Brazilian caves using different sampling techniques and comparative approaches in order to improve the current knowledge of ant diversity in these environments.

Keywords Formicidae · Karstic areas · Survey · Biodiversity · Southwestern Brazil

Introduction

Subterranean natural cavities in karst landscapes are intimately connected to soil and surface systems, offer shelter and feeding resources to several faunal groups (Ferreira and Martins 1999; Boyles et al. 2011; Sakoui et al. 2020), and play a critical role in the regulation and provision of ecosystem services, such as organic matter decomposition or contaminant filtering (Christensen et al. 2001; Lovley 2001; Röling and van Verseveld 2002). They may occur in a variety of carbonate rocks and non-carbonate rocks. Karstic systems are under continuous threat as a consequence of climate change and anthropogenic activities (Culver and Pipan 2019; Wynne et al. 2019).

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In Brazil, caves, grottos, furnas and similar areas formed by natural processes are legally defined as "subterranean natural cavities" including the biotic communities sheltered there, as well as its hydric and mineral content (Brazil, Decree No. 6.640 of November 07, 2008). Most of Brazilian caves are located in limestone (Auler and Farrant 1996; Jansen et al. 2012; ICMBio/CECAV 2023), and with a total of 23,378 caves currently registered in the *Cadastro Nacional de Informações Espeleológicas* (CANIE), the country is home to a valuable and diverse speleological patrimony to research and preserve. Some estimates indicate the existence of more than 300 thousand caves across the country (Oliveira et al. 2023; Auler et al. 2019) (Fig. 1).

The relevance of Brazilian subterranean natural cavities (hereinafter caves) as reservoirs of specialized biota has been recognized by several authors for almost five decades (Dessen et al. 1980; Trajano 1987; Trajano and Gnaspini-Netto 1991; da Rocha R 1994; Trajano 2000; Ferreira and Horta 2001; Trajano and Bichuette 2010; Simões et al. 2015; de Fraga et al. 2023; Howarth 2023). However, these environments are not at the forefront of global conservation issues (Mammola et al. 2019) nor frequently prioritized for biodiversity surveys. Several considerations could explain our last affirmation, most of them correlated: (i) *Sampling logistics:* collecting organisms in caves can be highly time-consuming. Most caves are located in difficult-to-reach areas and their interior is dark and confined, defying the logistics that standardized biodiversity surveys require (e.g. collection

Published online: 13 May 2024

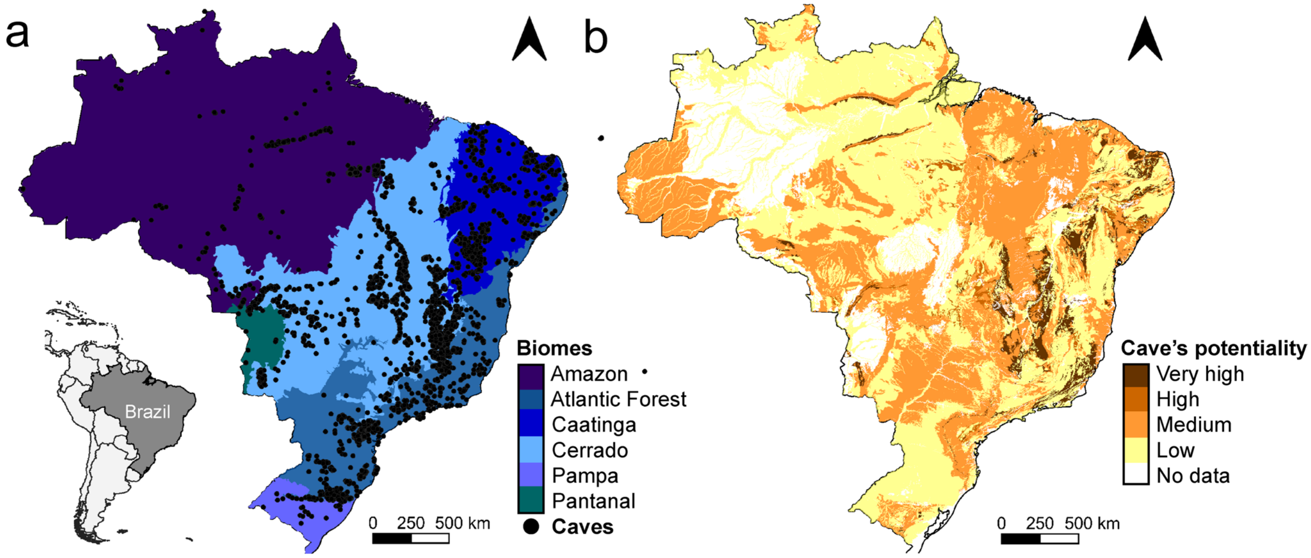


Fig. 1 Caves in Brazil by **a** biome and **b** potential degree of cave occurrence. Source: *Cadastro Nacional de Informações Espeleológicas* (Modified from CANIE 2021)

techniques, robust sampling design, trained personnel); (ii) *Ethical considerations*: caves and subterranean species, especially troglobites are highly sensitive to disturbances, which may limit the extent and frequency of the studies made there, especially considering the need for special permits usually obtained after long and bureaucratic processes; (iii) *Funding*: depending on the taxa, conducting biodiversity studies in these environments can be resource-intensive and require specialized equipment that are not easily affordable by researchers (Wynne et al. 2019).

Nevertheless, the fauna that lives in caves and the immediate surroundings have been the object of numerous studies and different forms of classification have already been proposed (Schiner 1854; Racovitza 1907; Christiansen 1962; Barr 1968; Thinès and Tercafs 1972; Holsinger and Culver 1988; Trajano and de Carvalho 2017). The classification of Schiner-Racovitza is the most frequently used in the literature (but see Trajano and de Carvalho (2017)), and organize cave animals in the following classes: (1) *troglobites* (var. troglobionts) referring to organisms restricted to the underground which present morphological and ecological specializations (ex. blindness, loss of body pigment); (2) *trogloxenes* for those species that live in underground environments, but need the resources of surface environments to complete their life cycle; (3) *troglophiles* if they can complete their life cycle both in the underground or the surface; or (4) *accidentals*, when their presence in subterranean cavities is unexpected. Bats, fishes, crustaceans, beetles and arachnids are among the most frequently studied organisms in cavities that fill these classes in Brazil (Gnaspini 1996; Mattox et al. 2008; Brescovit et al. 2012; Bichuette et al. 2015), but other taxonomic groups present in these environments may be difficult to assign to any category (Trajano 2000, 2001; Trajano and de Carvalho 2017).

From forest canopies to arid lands, urban buildings and the underground, ants (Formicidae) have made their way to colonize the most different environments, constituting one of the most ubiquitous, abundant, dominant and diverse insects in the tropics (Kass et al. 2022). In comparison to above-ground efforts to survey ants, caves represent one of the frontiers for documenting their diversity (Wilkie et al. 2007). Studies carried out in Brazil suggest that the presence of ants in caves is highly frequent, being either trogloxene (Kempf 1961; Pape 2016) or accidental since most specimens are collected in surrounding areas or the entrance (Wilson 1962; Tinaut and Lopez 2001; Dáttilo et al. 2010; Dáttilo 2012; Prous et al. 2015). In any case, the ant species listed from cavities is not short, and mostly belong to the subfamilies Formicinae, Ponerinae and Myrmicinae (Trajano 1987; Trajano and Gnaspini-Netto 1991; da Rocha R 1994; Tinaut and Lopez 2001; da Silva 2006; Dáttilo et al. 2010; Dáttilo 2012; Santana et al. 2010; Ferreira et al. 2016).

According to the latest report of the *Centro Nacional de Pesquisa e Conservação de Cavernas* (CECAV), the state of Minas Gerais accounts for 46.38% (11,029) of the total of caves known in Brazil (ICMBio/CECAV 2023). This study presents the ant diversity found in caves of two municipalities of Minas Gerais state based on specimens deposited in the *Coleção Entomológica Padre Jesus Santiago Moure* (DZUP). We highlight the role of biological collections and interdisciplinary networks to shed light on the diversity of ants in Brazilian caves.

Methods

Study site and specimen acquisition

All studied ants come from a donation to the entomological collection DZUP of the Universidade Federal do Paraná (UFPR), Curitiba, Brazil. It consisted of batches of specimens collected by qualitative samplings in caves of two municipalities in Minas Gerais. Ants from Prudente de Morais were collected in caves of limestone massifs near the plateau of Lagoa Santa in the Cerrado (Brazilian savanna) biome (*Maciço da Escrivânia*, *Maciço dos Ingleses* and *Maciço da Limeira*) at elevations that range from 697–791 m, during 2019. The karst of Lagoa Santa is recognized for its high number of caves, developed in phyllites and carbonates and is a reference for archeology and paleontology in Brazil (Kohler 1989; Holten and Sterll 2011; de Brito et al. 2014). Specimens from Nova Lima were collected between 2015–2019 in ferruginous caves of the *Parque Estadual Serra do Rola Moça* in the *Quadrilátero Ferrífero* region, at elevations that range from 1310–1385 m. The protected area covers 3,942 hectares and it is located in the transition zone between the biomes of Cerrado and the Atlantic Forest (Reis and Machado 2019) (Fig. 2) (Fig. 3, Online Resource 1: Table S1).

Maps showing collection sites in Nova Lima and Prudente de Morais were elaborated in QGIS v.3.16.7 (QGIS 2023).

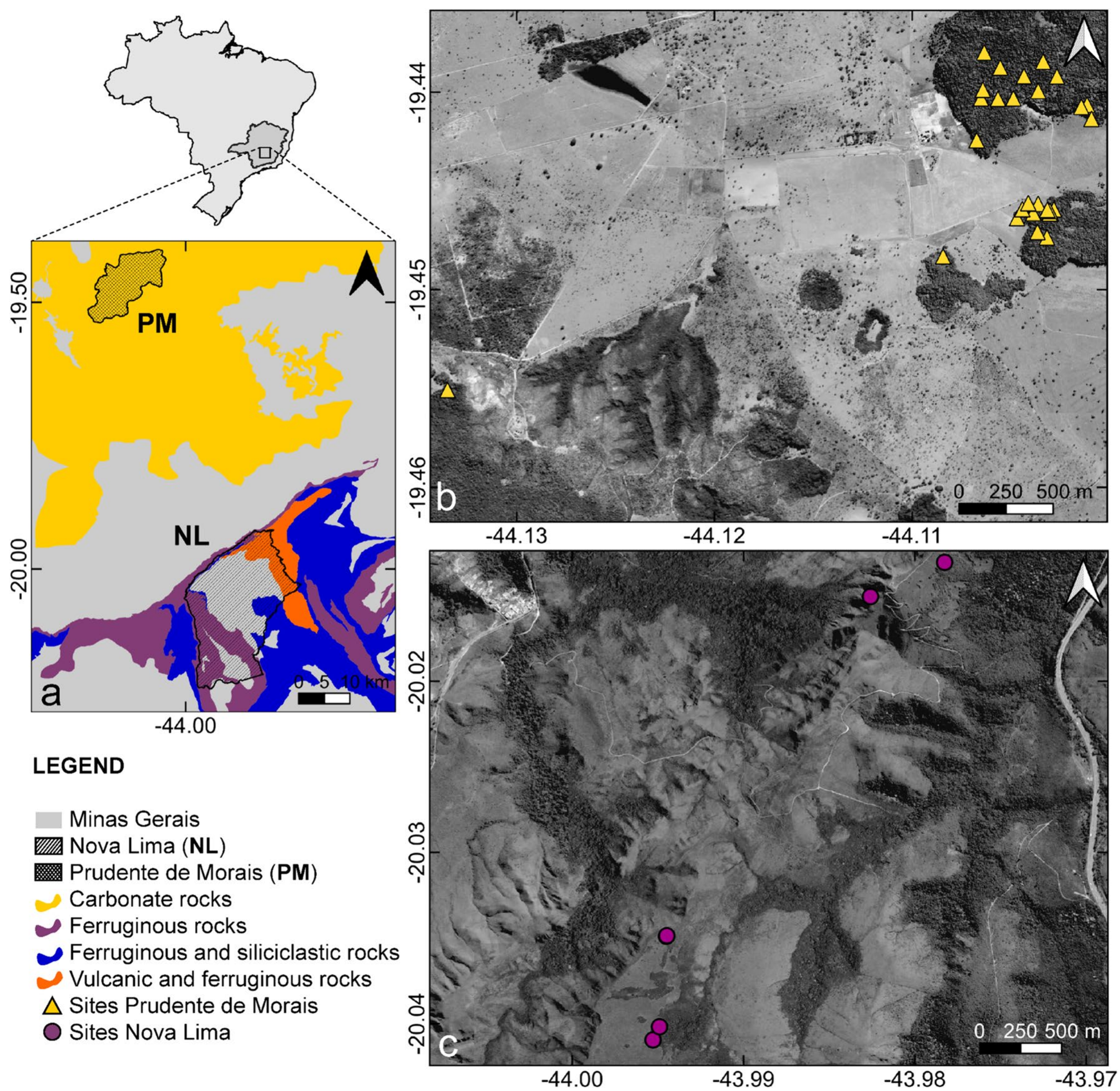


Fig. 2 Map showing the caves sampled in this study, with **a** rock formations at Nova Lima and Prudente de Morais. Modified from CECAV/ICMBio—*Anuário Estatístico* 2019, **b** caves sampled in Prudente de Morais, Minas Gerais, **c** caves sampled in Nova Lima, Minas Gerais

Fig. 3 Study areas. **a** Carbonate outcrops in Prudente de Morais, **b** Serra do Rola Moça, Nova Lima, **c**-**e** Carbonate cave (40L) sampled in Prudente de Morais, **d**-**f** Cave inserted in the iron formation of the *Parque Estadual da Serra do Rola Moça*. Photos: Robson de Almeida Zampaulo

Ant identification

Species were identified using taxonomic literature (Gonçalves 1961; Watkins 1976; Longino 2003; Wild 2007; Ortíz-Sepúlveda et al. 2019). Dr. Amanda Dias and Dr. Otávio Morais confirmed or provided names for the genus *Hypoponera* and *Solenopsis,* respectively. Taxa for which we could not give a name appear as morphospecies at the Online Resource 1: Table S1 and S2. Vouchers are housed in DZUP. High resolution images of the ant genera recorded were made in the Laboratório de Sistemática e Biologia de Formigas at UFPR, using a Zeiss Axiocam camera 305 coupled to a Zeiss Stereo Discovery V20 stereomicroscope. The images were stacked with the software CombineZP, enhanced in Adobe Photoshop CC2014 and plates were made with Adobe Illustrator 2020 (Adobe Systems 2014, 2020).

Data treatment

The sampling effort was non-standardized for both municipalities, which prevented us from conducting any robust or reliable statistical analysis comparing the ant diversity of Nova Lima with that of Prudente de Morais. Therefore, each dataset corresponding to a municipality (set of caves) was analyzed separately through its richness.

We treated the 30 cavities explored in Prudente de Morais and the parcels from the six caves of Nova Lima as sampling units (Online Resource 1: Table S2). For both datasets, we followed the category associated to luminosity zone informed by the collectors (i.e. *entrance*, *penumbra*, *aphotic*). Although our list includes the species records from the original material regardless of instances of missing information in labels, the matrix used for the analysis only includes species records adequately paired with the established sampling units per dataset.

To explore species richness, we elaborated rarefaction curves based on incidence and boxplots to relate it to the luminosity zone at which the specimens were collected. All analyses and graphics were made in the R environment and the interface of R Studio, using the R Base (R Core Team 2020), *vegan* (Oksanen et al. 2022) and *ggplot2* packages (Wickham 2016).

We also compared the list presented here with those from other studies reporting ants for Minas Gerais (Andrade et al. 2007; Costa et al. 2015; Vasconcelos et al. 2018; Vasconcelos et al. 2023a, b).

Results and discussion

Our list includes 51 ant species/morphospecies, belonging to 18 genera and seven subfamilies found in caves of Prudente de Morais and Nova Lima (Table 1; Online Resource 1: Table S1 and S2; Figs. 3, 4, 5 and 6).

Table 1 Number of genera and species recorded by subfamily at caves of Prudente de Morais and Nova Lima municipalities in Minas Gerais, Brazil

Subfamily	Genera	Species	Municipality
Amblyoponinae	1	1	Nova Lima
Dolichoderinae	1	3	Both
Dorylinae	3	6	Both
Ectatomminae	1	1	Both
Formicinae	3	11	Both
Myrmicinae	5	19	Both
Ponerinae	4	10	Both

The number of species recorded here is relatively low in comparison to other studies conducted in different surface ecosystems in Minas Gerais state (Andrade et al. 2007; Costa et al. 2015; Vasconcelos et al. 2018; Vasconcelos et al. 2023a, b). This was expected, since the sampling effort was not specifically intended for Formicidae and ants in caves represent a subset of the local ant fauna. Compared with other studies that have intentionally collected ants in these environments (Ferreira and Martins 1999; Santana et al. 2010; Dáttilo 2012; Castro-Souza et al. 2019) we report greater ant richness. The high heterogeneity, number of samples and volume of the material could explain these results, since the variety of caves explored during the wet and dry season are located in different rock formations and biomes (Prudente de Morais: carbonate rocks of Cerrado; Nova Lima: ferruginous rocks of the Atlantic Forest) (Figs. 2 and 3).

Studies on ant diversity in the Atlantic Forest and the Cerrado indicate that Myrmicinae accounts for most ant records, with *Pheidole* and *Camponotus* being the most frequent genera (Feitosa et al. 2022). Our results agree with previous studies on ant diversity in Brazilian biomes (See Feitosa et al. 2022).

Only 11 species were shared between the caves in Prudente de Morais and Nova Lima and 20 ant species were exclusive for sampled area. Although most of the species listed here are widespread and mainly nest and forage in the soil (Online Resource 1: Table S1; Fig. 5), some species of *Brachymyrmex*, *Camponotus*, *Crematogaster* and *Linepithema* nest and forage in the arboreal strata, and might have been carried into the cavities by flood waters (Online Resource 1: Table S2). The caves studied in Prudente Morais, especially those located at the base of the Limeira

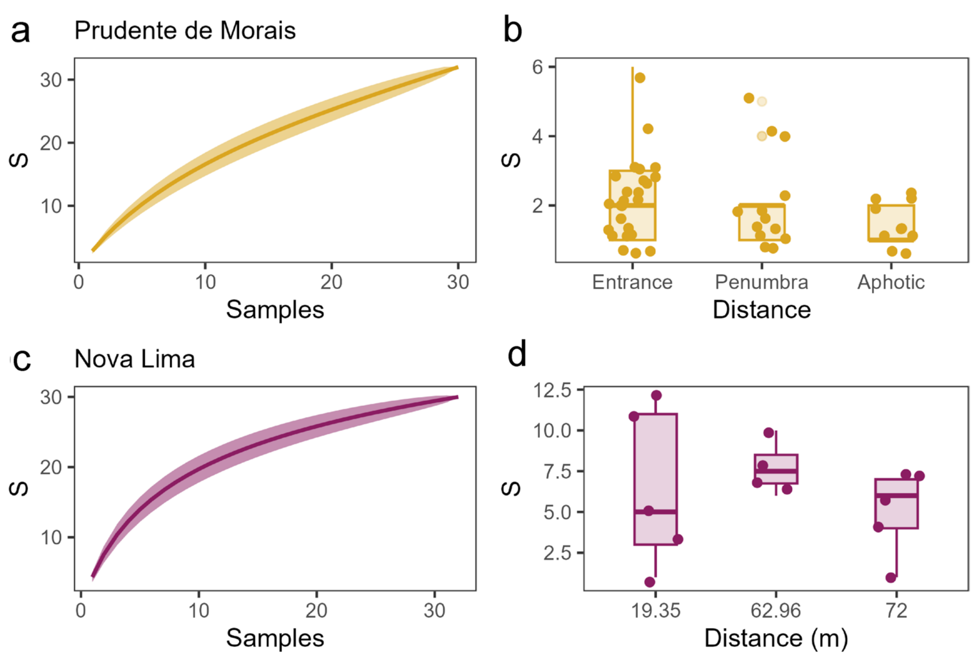
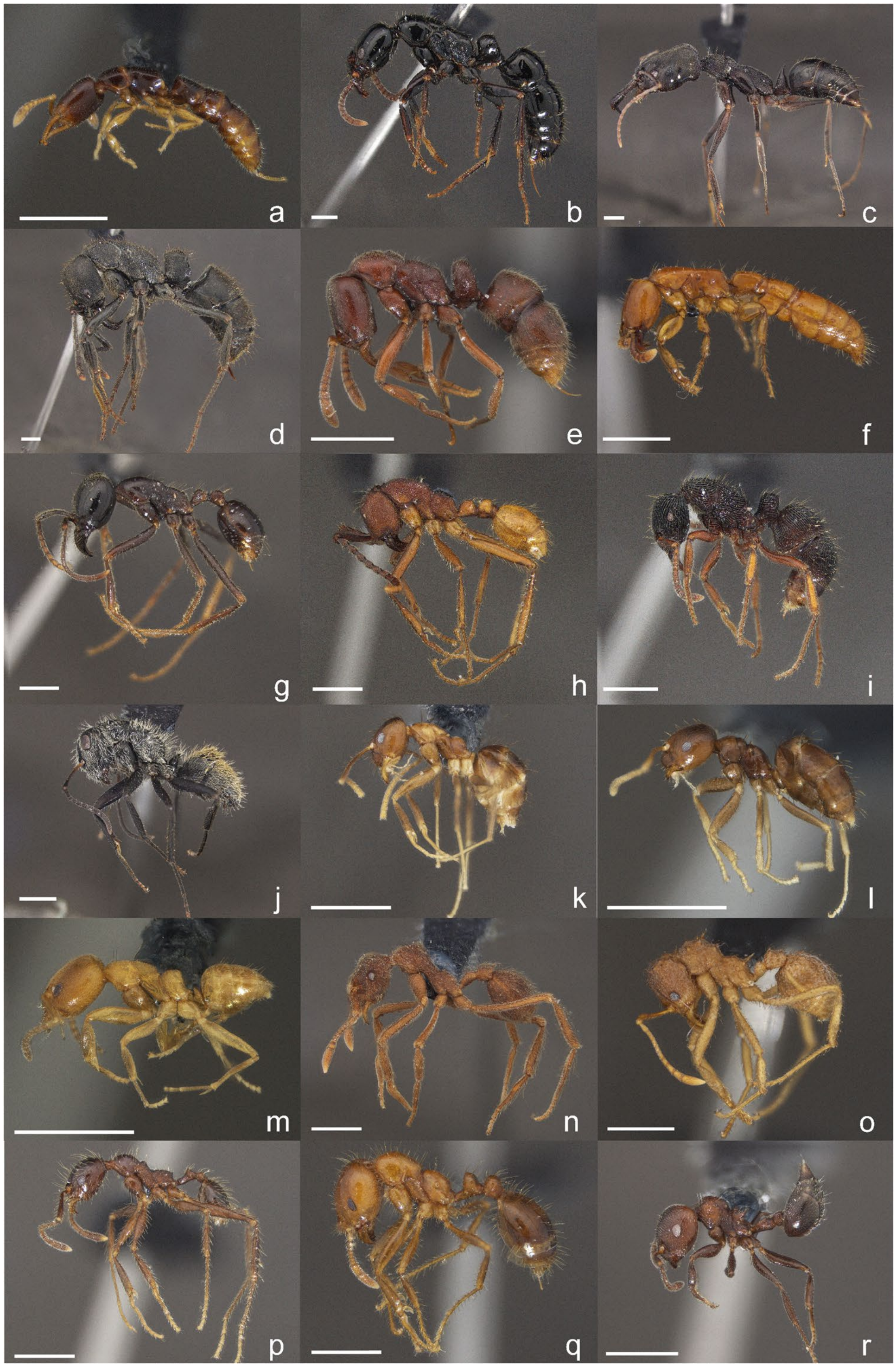


Fig. 4 Analyses performed in this study. **a**, **c** Rarefaction curves, **b**, **d** Boxplots relating richness and distance at which ants were collected in subterranean cavities at Prudente de Morais (yellow) and Nova Lima (purple)

Fig. 5 Ant genera recorded in this study. Lateral view of **a** *Fulakora*, **b** *Neoponera*, **c** *Odontomachus*, **d** *Pachycondyla,* **e** *Hypoponera,* **f** *Acanthostichus,* **g** *Labidus*, **h** *Neivamyrmex*, **i** *Holcoponera*, **j** *Camponotus*, **k** *Nylanderia*, **l** *Brachymyrmex*, **m** *Linepithema*, **n** *Apterostigma*, **o** *Acromyrmex*, **p** *Pheidole*, **q** *Solenopsis*, **r** *Crematogaster*. Scales: 1 mm. Photos: Natalia Ladino



and Escrivânia massifs, are subject to flood pulses during the rainy season, which would explain the occurrence of these species. No differences in ant composition related with seasonality were found. While in Prudente de Morais the ant richness was greater at the entrance of caves, followed by the penumbra, in Nova Lima richness slightly increased with the distance – interpreted from the luminosity zone. (Fig. 4b, d).

Even though ants are frequently cited as inhabitants of caves, studies showed this affirmation is fairly imprecise, since ants are mostly found near the entrance of these environments (Dáttilo 2012). Their presence then, can also be interpreted as *accidental* (Wilson 1962; Tinaut and Lopez 2001; Dáttilo et al. 2010; Dáttilo 2012) or as a result of the attractiveness that resources, such as guano (bat feces) can

Fig. 6 Ecological interactions of the sampled species with the cave environment. **a**, **b** *Solenopsis* sp. foraging invertebrate remains, **c**, **d** *Odontomachus* sp. and *Camponotus ager* (Smith, 1858) carrying eggs, **e** Cultivation of fungi by *Apterostigma wasmannii*, **f** *A. wasmannii* litter with associated beetles, **g** Pseudoscorpion (Chernetidae) preying on ant in a ferruginous cave (RM-38); **h** Spider (Pholcidae: *Mesabolivar* sp.) preying on ant in a carbonate cave (42L). Photos: Robson de Almeida Zampaulo

provide (Ferreira and Martins 1999, Ferreira et al. 2010; Dáttilo 2012). It is important to consider the study scope and methods when assigning a term to ant records in caves, in order to avoid misinterpretations of the natural history of the species found. What is an entrance for a human for a particular cave may not be the entrance for an ant, since the surface could very well be much nearer via another route that is impossible for a human to traverse. In the case of caves associated with iron formation, for example, these caves are very superficial, which may favor the occurrence of nests that are in contact with the soil and the matrix rock. In addition, this type of rock, especially the "*canga*" has a high primary porosity, which may favor the colonization and foraging of ants in this environment. Also, if clarification of data treatment and terminology is not provided and ants were not the primary target of a given study, but are being recorded as a product of another- or broader research, the terms *troglobiont*, *troglophile*, *trogloxene* or *accidental* could be imprecise, since the terms assume dynamics of nesting and foraging inside caves that might be unknown.

Many ants nest and forage in the ground strata and may present drastically reduced or absent eyes, depigmented bodies, small and slender forms, reduction in their appendages and spinescence (Wong and Guénard 2017), features that can be confused with *troglomorphisms* (i.e. cave-associated characters, See Romero 2011). Therefore, cavities can be part of the area explored by them. The recognition of ants as cave-inhabitants and their categories, depends on the accumulation of biological, ecological, geographic and population data through time, that indicate a permanent correlation of the occurrence of a given ant species to conditions in underground cavities or with organisms fully adapted to them (Trajano and de Carvalho 2017). Our results may indicate that in most cases, some ants listed for caves could be taking advantage of these environments for foraging but not necessarily for nesting. However, for some species, nests containing individuals of different castes have been observed. Ants of the genus *Apterostigma*, for example, use caves to grow fungi (Dejean et al. 2015) and as "garbage dumps" (Asenjo et al. 2018), places where different species of beetles (Staphylinidade, Scarabaeidae, among others) and associated mites (Staphylinidade, Scarabaeidae, among others) can be observed. Furthermore, ants, whether accidental or not, can serve as food for a wide range of predators found in caves, including spiders and pseudoscorpions (Fig. 6).

The examination of specimens from Nova Lima allowed us to record for the first time *Brachymyrmex cordemoyi* Forel, 1895 and *Apterostigma wasmannii* Forel, 1892 for Minas Gerais state. If *B. cordemoyi* is reported in Espirito Santo, the species distribution will be confirmed in all the states of southeastern Brazil. This is the second report of *A. wasmannii* for southeastern Brazil. Even with the records being incidental, the report of new species or geographic range expansions for ants from cave explorations is not rare. For example, *Carebara urichi* (Wheeler, 1922) has as type locality the Guácharo Cave, Monagas, Venezuela (Wilson 1962), and the first record of *Acromyrmex hystrix* (Latreille, 1802) for the Maranhão state of Brazil (Dáttilo et al. 2010) comes from a unique collection effort in a cave of the municipality of Estreito.

Conclusion

Caves are in continuous change since – as other environments, they are impacted by biotic and abiotic processes and subject to internal and external pressures that may adversely affect the organisms that occur there. However, caves are among the least explored environments on the planet and are comparatively uncommon when it comes to selecting sites for ant inventories in terrestrial environments. Considering the diversified speleological patrimony of Brazil, the potential of cave occurrence in the country (see Fig. 1) and both the ant richness recorded here and in previous studies in karstic areas, the inclusion of subterranean natural cavities for future ant surveys is encouraged. In addition to presenting a list of species that occur in caves in the state of Minas Gerais, this study highlights the need to (i) conduct ant collection efforts in Brazilian caves; (ii) consolidate collaboration networks with colleagues actively collecting in these environments to examine replicates of their samples; and (iii) to access baseline information about these environments, which have proved their relevance in providing valuable information for the documentation of ant diversity.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11756-024-01692-8.

Acknowledgements The authors thank Aline da Silva Reis, which contributed to the collection of the ants in field and Rogério Dell' Antônio, coordinator of the Cadastro Nacional de Cavernas CNC for his collaboration on recovering the type of subterranean cavity of most of the sites explored in this study. Also, we thank Dr. Amanda Dias and Dr. Otávio Morais for the confirmation of *Hypoponera* and *Solenopsis* species. RMF was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq (grant 301495/2019-0). The biological material used in this study was collected in accordance with SISBio authorizations Number: 50702-1 from the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and AMF nº 24.011/2019 from the Secretaria de Estado de Meio-Ambiente e Desenvolvimento Sustentável do Estado de Minas Gerais.

Data availability The data that support the findings of this study are openly available in the Supplementary Information, and includes: (i) Table S1. List of ants from karst areas recorded in this study, (ii) Table S2. Material examined in this study, with vouchers deposited at the Entomological Collection Padre Jesus Santiago Moure (DZUP), Universidade Federal do Paraná (UFPR), Curitiba, Paraná, Brazil. Available in https://doi.org/10.1007/s11756-024-01692-8

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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