



Available online at scholarcommons.usf.edu/ijis

International Journal of Speleology

Official Journal of Union Internationale de Spéléologie



Recreational caving impacts of visitors in a high-altitude cave in Bolivian Andes: main effects on microhabitat structure and faunal distribution

Laís Furtado Oliveira ^{1*}, Rodrigo Lopes Ferreira ¹, Jaime Iván Rodríguez Fernández ², and Marconi Souza Silva ¹

¹Universidade Federal de Lavras, Instituto de Ciências Naturais, Departamento de Ecologia e Conservação, Centro de Estudos em Biologia Subterrânea, Caixa Postal 3037, CEP 37200-900, Lavras, MG, Brasil

²Laboratorio Boliviano de Biota y Desarrollo, Calle Montevideo 188 esquina capitán Ravelo, La Paz, Bolivia

Abstract: The cave's physical environment can be affected by tourism activities but only a few studies evaluated how recreational use may affect the cave fauna, mainly in caves with a low number of visitors per year. To test the hypothesis that recreational use led to changes in habitat structure and invertebrate diversity, distinct scales along a cave were analyzed. Distinct areas with and without human visitation were analyzed and transects (10 x 3 m) and quadrats (1 x 1 m) were used to access the invertebrate communities and environmental traits. Thirty-two invertebrate species were recorded, among which six are troglobitic. The similarity of non-troglobitic species differed between the visited and non-visited areas. Substrate composition inside transects differed between the two areas and the differences were higher in the percentage of matrix rock and fine sediments. The distance from the entrance influenced the similarity of non-troglobitic species while troglobitic fauna responded to the proportion of sandy sediment. Inside quadrats, both matrix rock and fine sediments influenced the similarity of non-troglobitic species. Similarity of non-troglobitic species in the visited area was explained by the proportion of matrix rock in transects and quadrats. The proportion of cobbles influenced the similarity of non-troglobitic species in quadrats in the non-visited area. The non-troglobitic species richness inside quadrants was positively related to the amount of guano, wood, fine sediment, boulders, cobbles, matrix rock, sand sediment, and plant debris. Differentiation in habitat structure and faunal composition between the two areas seems to be an effect of distance from the entrance and spatial heterogeneity, but not recreational activities.

Keywords: cave management, impacts, cave conservation, Andes

Received 8 March 2022; Revised 30 June 2022; Accepted 10 July 2022

Citation: Furtado Oliveira, L., Lopes Ferreira, R., Rodríguez Fernández, J.I., Souza Silva, M., 2022. Recreational caving impacts of visitors in a high-altitude cave in Bolivian Andes: Main effects on microhabitat structure and faunal distribution. *International Journal of Speleology*, 51(2), 93-103. <https://doi.org/10.5038/1827-806X.51.2.2418>

INTRODUCTION

Among the several human activities carried out in caves, recreational and religious tourism has been recurrent all over the world. Such activities, however, vary on the types of use, the number of visitors, accessed areas, and the type of pathways to accessing the caves (Var, 2004; Romero, 2009; Wilson, 2019; Pellegrini & Ferreira, 2016).

However, the tourist use of caves can promote changes in both their physical and environmental conditions due to the installation of structures that allow or facilitate the access of visitors (walkways, lighting, stairs, elevators, trails), as well as due to the traffic

of people (Slaney & Weinstein, 1997; Bočić et al., 2006; Osborne, 2019). Among the real and potential impacts arising from these activities, there is the deposition of garbage, fauna trampling, changes in temperature and humidity conditions, changes in the availability of food resources, introduction of exotic species, contamination, and changes in physical-chemical characteristics of the floor in both terrestrial and aquatic environments (Bunting & Balks, 2001; Eberhard, 2001; Pacheco et al., 2020). Thus, the practice of cave tourism, is among the main concerns of cave conservationists, who seek to understand how tourist use is affecting subterranean ecosystems (Culver & Sket, 2002; Pellegrini & Ferreira, 2016; Mammola et al., 2020).

*laisfurtado2@gmail.com.br

Most of the touristic caves are altered not only due to the excessive number of visitors but also due to the lack of prior planning regarding the installation of infrastructure, the definition of visiting routes, and the ascertainment of the carrying capacity of the cave (Hamilton-Smith, 2004; Bočić et al., 2006; Romero, 2009; Pellegrini & Ferreira, 2016). However, although some impacts on the cave floor cannot be avoided, due to the need for access adjustments for visitors, adequate management practices, such as route marking, and definition of pathway limits can prevent the impacts to become diffuse in many areas of the cave essential for cave fauna conservation (Pellegrini & Ferreira, 2012, 2016; Pacheco et al., 2020), thus reducing damage not only to the physical habitat but also to the fauna (Bunting & Balks, 2001; Bočić et al., 2006; Faille et al., 2015; Pellegrini & Ferreira, 2016).

Studies on the effects of impacts resulting from tourism use on cave fauna are scarce, and most still require detailed comparative assessments and experimental approaches (Eberhard, 2001; Culver & Sket, 2002; Pellegrini & Ferreira, 2012, 2016; Pacheco et al., 2020). In addition, most of these studies are carried out in caves that receive a high number of visitors per year, and the impact of this activity in caves with light tourism is unknown. Even though, such studies are of paramount importance, as they can help in minimizing the effects of human alterations, by providing useful information for ecological zoning and definition of routes and visitation limits, thus avoiding more severe impacts on the cave communities (Hamilton-Smith, 2004; Pellegrini & Ferreira, 2012, 2016; Pacheco et al., 2020).

Accordingly, variables describing the physical, trophic and microclimatic components in the cave substrates were used, along with the composition and richness of invertebrates communities to test two hypotheses: i) human visitation, even if low, promotes changes in the structure of the habitat on the floor, affecting the composition and richness of troglobitic and non-troglobitic species., and ii) the distribution of troglobitic species would be restricted to the area not visited by humans, due to the lower intensity of disturbances.

MATERIAL AND METHODS

Study area

Umajalanta Cave comprises the biggest known cave in Bolivia, having 4,600 m of linear projection. It is developed in limestone rocks and its entrance is located at 2,830 m above sea level, in the Torotoro National Park (18,1145S/65,8116W), a conservation unit of integral protection in the north of the department of Potosí, in the province of Charcas (Guyot et al., 1997) (Fig. 1A–C). The average annual rainfall is 850 mm, with a very dry climate during half of the year (November to March). The average annual temperature is 16.3°C (Garreaud, 2009). Photos and maps of the cave can be seen in Guyot et al. (1997) (<https://cuevasdelperu.org/bolivia-potosi-charcas/caverna-umajalanta/>).

The cave has a wide conduit that develops in the first 300 meters from the entrance, with a floor covered with rock blocks of varying sizes (Guyot et al.,

1997). Subsequently, this conduit presents a significant reduction in both its height and width, is also connected to an upper conduit, which develops in parallel to the main chamber where the drainage flows (Figs 1D–F and 2A). Both conduits connect again around 700 meters from the entrance in a chamber known as “Lago de la Cachuela” (Cachuela Lake). Visitors (approximately 1,500 people/year) usually make a “ring” path along the visited area of the cave, initially accessing the upper gallery located to the right of the cave's main conduit, until reaching the “Cachuela Lake” and then returning towards the entrance through the main conduit (Fig. 2A). Visits to the cave are usually guided, on a route that does not include stretches with water. The paths have few adaptations to assist visitors there's no artificial lighting, no walkways, just one point with stairs and other with ropes ([Supplementary Fig. S1](#)) (Guyot et al., 1997; Zúñiga & Pouilly, 2009). The approximate visitation time is two hours. Umajalanta Cave has only two formally described cave restricted species, the fish *Trichomycterus chaberti* Durand, 1968 and the carabid beetle *Escolatrechus bolivianus* Mateu, 2002, although there are many discussions on the real status of the fish.

Sampling design

Once the main impacts in recreational cave are observed in the floor (Bunting & Balks, 2001); to assess the habitat traits and the richness and composition of the invertebrate communities, eleven transects (3 x 10 m) herein are considered as “mesoscale” and 33 quadrats (1 x 1 m) herein considered as “microscale” were distributed along the cave floor (Fig. 1G). The non-visited and visited areas were considered “macroscales”. Quadrats and transects were arranged on the cave floor starting from 200 meters from the entrance to deeper regions, six located in the visited area and five in non-visited area (Fig. 2A, B). The distances of the quadrats and transects concerning the cave entrance were measured with a laser measuring tape (as well as the distances between them). Three quadrats were placed inside each transect, two at the extremities and one in the median portion (Fig. 2B). Each quadrant presents 10 x 10 cm subunits, which enable the substrate structure assessment (Souza-Silva et al., 2021). The collection of biotic and abiotic data was performed in a single sampling event, in November 2017.

Invertebrate sampling

The invertebrate sampling was carried out in the transects and quadrats separately using the direct intuitive search - DIS (Wynne et al., 2019; Souza-Silva et al., 2021), and active collection with the aid of forceps and brushes moistened with 70% alcohol. Sampling was conducted, in both transects and quadrats, by a team of two biologists with experience in caving and manual collection of invertebrates. The time spent in quadrats and transects was variable. All invertebrate specimens were collected and kept in vials containing 70% alcohol for later identification and separation into morphotypes (Oliver & Beattie, 1996). Experts reviewed species from the orders Coleoptera, Isopoda, and Acari.

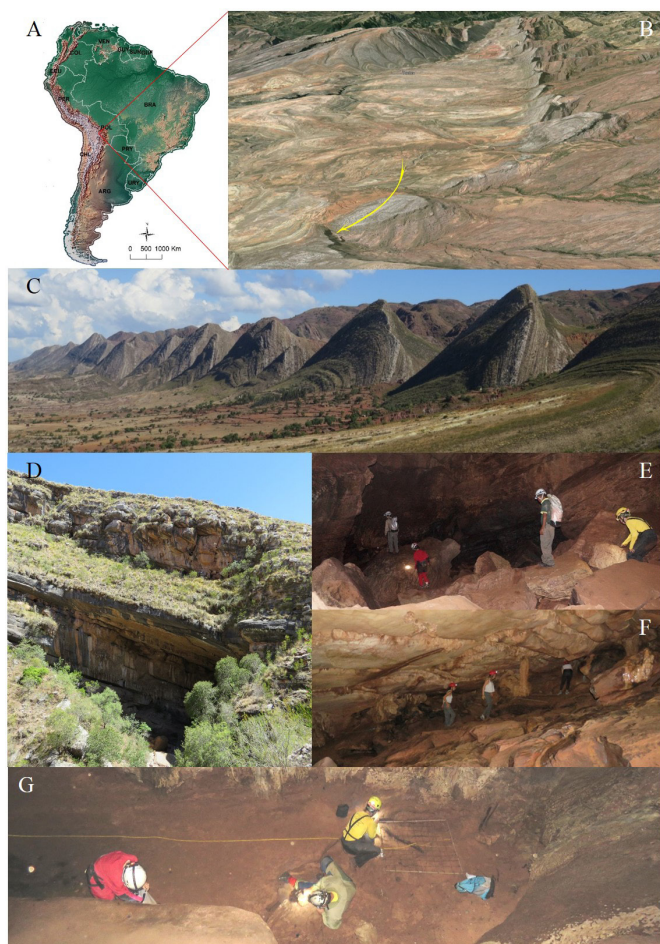


Fig. 1. Umajalanta Cave location at Cochabamba region (A), National Park of Torotoro, Bolivia (B and C). Umajalanta Cave entrance (D). Non-visited area (E) and visited area (F) and Sampling methods (G). The yellow arrow in B indicates the cave entrance position.

Potentially troglobitic species were determined through the identification of troglomorphic traits, which comprise morphological changes usually associated with the evolution in subterranean environments. The troglomorphisms frequently observed were the reduction or absence of ocular structures and pigmentation, as well as the elongation of sensory and locomotor appendages (Culver & Pipan, 2009). The invertebrates collected are deposited in the Lavras Subterranean Invertebrate Collection (ISLA), linked to the Center of Studies on Subterranean Biology at the Federal University of Lavras, Minas Gerais, Brazil (biologiaubterranea.com.br).

Habitat structure survey at different scales

The habitat structure was determined by visual inspection and quantification of the surface area occupied by each organic and inorganic substrate within the transects and quadrats (Wentworth, 1922, Souza-Silva et al., 2021). For doing such, transects were lengthwise divided into ten perpendicular sections of one meter by three meters. In each of the ten sections, the percentages of the area occupied by different types of substrates, both organic and inorganic, were measured (Pacheco et al., 2020; Souza-Silva et al., 2021) (Fig. 2, [Supplementary Table S1](#)). Subsequently, to obtain a single value for each substrate in the whole transect, the values for each section were summed and divided by 100. In the quadrats, substrate types

were evaluated using photographs ([Supplementary Table S2](#)). Digital photographs (4000 x 3000 pixels) were taken in the field in a vertical position (camera positioned at 90° relative to the cave floor) using the Canon Powershot SX50, HS. Subsequently, the images were analyzed in the laboratory using the ImageJ software (Rasband, 1997), in which the substrates were measured according to the area they occupied (Pacheco et al., 2020). Temperature and humidity measurements were taken in each transect, with the aid of a digital thermohygrometer (accuracy $\pm 1^\circ\text{C}$ for temperature and $\pm 5\%$ for relative humidity), placed on the floor for at least fifteen minutes.

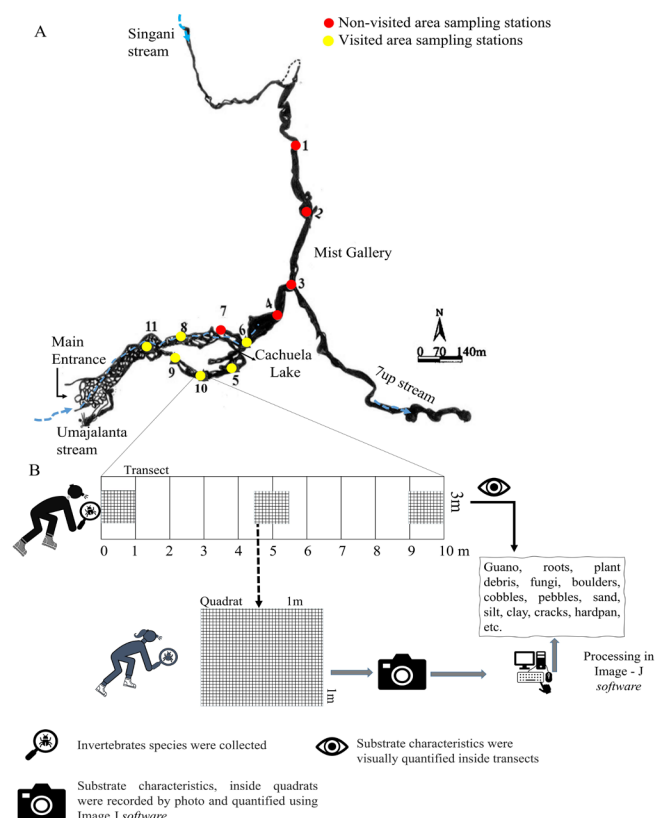


Fig. 2. An infographic showing the sampling stations (A) in visited (06 to 11, except 7) and non-visited areas (1 to 4 and 7) inside Umajalanta Cave. Schematic diagram of biotic and abiotic data sampling (B) at the cave floor using transects as standardized areas.

Data analysis

Invertebrates abundance and richness were obtained by counting individuals and morphotypes of each sample unit (11 transects and 33 quadrats, however, 5 of the 33 did not present fauna).

Differences in richness between visited and non-visited areas (macro-scale) were assessed using a one-way ANOVA non-parametric test (Kruskal-Wallis) (Gallucci, 2019). To assess the differences in the community composition between the visited and non-visited areas, a permutational analysis of variance (PERMANOVA) with 999 permutations was performed using the Bray-Curtis Similarity index (Anderson et al., 2008). A distance-based test for similarity homogeneity of multivariate dispersions from a centroid (PERMDISP) was used to obtain measures of the dispersion between visited and non-visited areas (Anderson et al., 2008).

The total community β -diversity was obtained with the beta function from the BAT package in R software

(R Core Team, 2019) (Cardoso et al., 2015). We also partitionate the β -diversity (β_{total}) in replacement (β_{repl}) and richness difference (β_{rich}) inside visited and non-visited areas. The β_{repl} is related to species replacement, while β_{rich} is related to the species loss or gain between sample stations (Legendre, 2014).

The number of undetected species (the extrapolated richness for the transects dataset) was calculated using a non-parametric richness estimator (Jackknife 1). The level of 'completeness' of the sampling effort was achieved by dividing the observed number of taxa by the projected values calculated by Jackknife 1 estimator (Ávila et al., 2019).

Finally, we presented a representation of the troglobitic species according to the spatial distribution along the cave, in a shaded plot. The species composition has been re-ordered in cluster analysis using Whittaker's Index of Association (Clarke et al., 2014). The sample units were grouped with a cluster analysis utilizing the Bray-Curtis similarity index, by clustering of average similarity.

The influence of substrate traits and human visitation on the composition (Bray-Curtis similarity) of the invertebrate communities along the cave was evaluated using a linear distance-based model (DistLM), using the *Forward step-wise* method and the Akaike model selection criterion corrected for small samples (AICc) (Anderson et al. 2008). The distance-based redundancy analysis (dbRDA) was subsequently used to assess the percentage of data that fit the model together with the proportion of explanation of the data variation (Clarke & Gorley, 2006). These analyzes were carried out independently for transects and quadrats and non-troglobitic and troglobitic fauna. The variables included were species composition and richness as response variables and tourism, elements of the substrate, temperature, humidity, and distance from the entrance as predictive variables. The temperature and humidity variables were not used in the analysis of the quadrats. A Similarity Profile (SIMPROF) cluster analysis was performed to objectively define the groups within the dbRDA graphic plot.

Linear models (GLM e GLMM) were performed to predict the influence of abiotic variables on the species richness using transects (GLM) and quadrats (GLMM) as sample units. The correlation between predictor variables guano (GUA), wood (WOO), fine sediment (SEF: 0.002 to 0.05 mm), Sand (SAND: 0.05 to 2 mm), boulders (CB: 64 to 250 mm), cobbles (SB: 250 to 500 mm), matrix rock (RCM >4000 mm), plant debris (DBR), distance from the entrance (DTE), temperature (TEM), humidity (UMI) and tourism (T), were tested using Spearman's correlation, from the Performance Analytics package in R software (R Core Team 2019). Variables with high correlation values ($\rho > \pm 0.60$) (Zuur et al., 2010), were excluded from the model. The model used was with lesser Residual Deviance. After selection, species richness was used as the response variable, and wood, matrix rock, sand, plant debris, humidity, and tourism as fixed variables. In GLM, a quasipoisson distribution with logistic link function was applied to the response variable, derived from

count data, since these data showed high dispersion for the Poisson error distribution. For the GLMM, a negative binomial error distribution was applied with a logistic link function for the response variable.

A permutational analysis of variance (PERMANOVA) with 999 permutations based on Euclidean distance was used to identify differences in the substrate composition between visited and non-visited areas (macro-scale) using transects (mesoscale) and quadrats (micro-scale) as sample units (Anderson et al., 2008). The differences in the amount of floor substrates composition, both for transects and quadrats in the visited and non-visited areas were evaluated using a one-way ANOVA non-parametric test (Kruskal-Wallis) (Gallucci, 2019). Kruskal-Wallis test and histogram density plots were built using the *Jamovi* free statistics program (2020). All the significance was evaluated at $p < 0.05$.

RESULTS

Microhabitat structure on the cave floor

The substrates occurring on the cave were guano, woods, plant debris, fine clay sediment (SEF), sand sediment, boulders, cobbles, and matrix rock. The substrate components measured for the transects and quadrats from the visited and non-visited areas are shown in [Supplementary Tables S1 and S2](#). SEF was the predominant component of the non-visited area floor and RCM in the visited area. Substrate composition inside transects differed between the visited and non-visited areas of the cave ($F_{PERMANOVA} = 2.89$, $P = 0.006$). Significant differences were also observed in the amount of RCM (KW-H (1; 11) = 7.53, $p = 0.006$) and SEF (KW-H (1; 11) = 6.533, $p = 0.011$) inside transects among visited and non-visited areas (Fig. 3A, B).

Substrate composition inside quadrats differed ($F_{PERMANOVA} = 4.54$, $P = 0.001$) between the visited and non-visited areas of the cave. For the quadrats, only the amount of RCM (KW-H (1; 28) = 9.032, $p = 0.003$) differed significantly between visited and non-visited areas.

Composition and richness of invertebrate communities

A total of 510 invertebrate specimens were found, distributed in at least 23 families and 32 species (Fig. 4A; [Supplementary Tables S3-S6](#)). In the transects, 32 species were observed, while in the quadrats 21 species were found. The richest orders in the transects were Coleoptera (7 spp.), Diptera (6 spp.), and Araneae (5 spp.), while in the quadrats the richest were Coleoptera (5 spp.), Araneae, Diptera, and Collembola (3 spp. each) ([Supplementary Table S3](#)).

Six species with troglomorphic traits belonging to Coleoptera (3 spp.), Acari (1 sp.), Collembola (1 sp.), and Dubioniscidae (1 sp.) were found. Some of these species are shown in Figure 5 along with the troglomorphic Siluriformes *Trichomycterus chaberti*. Such species were observed in both the visited and non-visited areas of the cave (Figs 4B and 5). However, only seven quadrats had troglobitic species and only Dubioniscidae was not collected inside the quadrats.

Among the troglomorphic invertebrates, the only described species is *Escolatrechus bolivianus* Mateu, 2002 (Coleoptera: Carabidae: Trechinae).

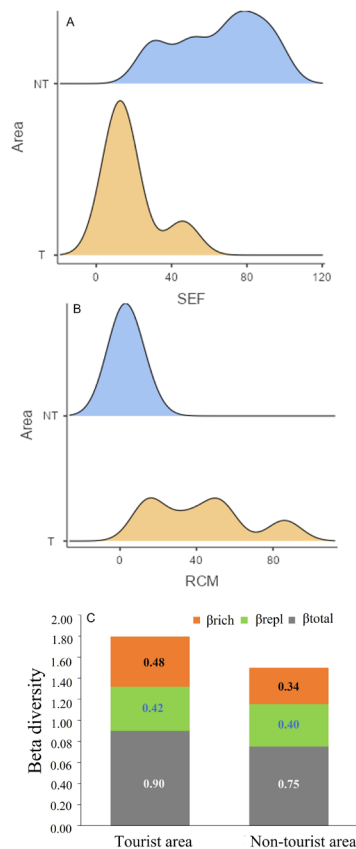


Fig. 3. Histogram density plots (A and B) with the amount of fine sediment - SEF (A) and matrix rock - RCM (B). Beta diversity (C) between visited and non-visited areas in the floor of Umajalanta Cave, National Park of Torotoro, Bolivia. Total beta diversity (Btotal), Beta diversity replacement (Brepl), and beta diversity richness difference (Brich).

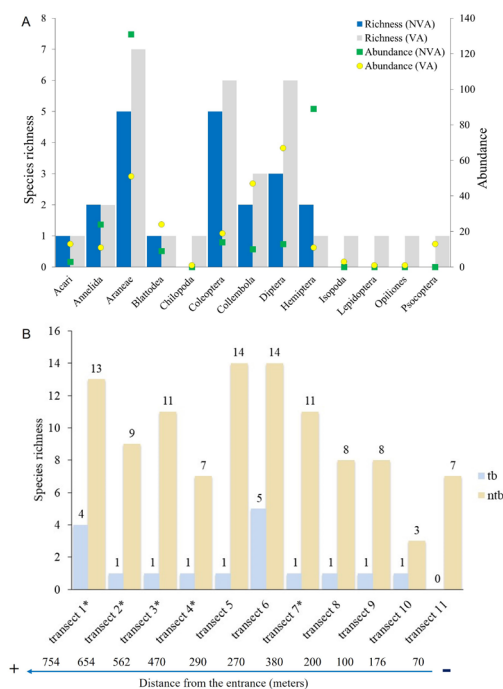


Fig. 4. Total richness and abundance of the invertebrates (A) on the floor of visited area (VA) and non-visited area (NVA) in Umajalanta Cave, Bolivia, and richness of troglobites (tb) and non-troglobites (ntb) fauna between sample stations (B). Non-visited area sampling stations (*).



Fig. 5. The fish (A) and some invertebrates (B, C, D) species with troglomorphic traits were observed in Umajalanta Cave. Four specimens of *Trichomycterus chaberti* (A; scale bar: 1 cm), *Escolatrechus bolivianus* (B), *Dubioniscidae* sp1 (C), and *Hamotus* sp1 (D). For B, C and D the scale bars are 1 mm.

In the visited area, 29 species and 253 individuals were observed, being Coleoptera (6 spp.), Diptera (6 spp.), and Araneae (5 spp.), the richest taxa. All the species six with troglomorphic traits were recorded in the visited area. In the non-visited area, 21 species and 257 individuals were found, with the richest orders being Araneae (5 spp.), Coleoptera (5 spp.), and Diptera (3 spp.). Four species with troglomorphic traits were recorded on the non-visited area (*Hamotus* sp1, Carabidae sp1, Rhagidiidae sp1, and Entomobryomorpha sp2).

Species composition inside transects ($F_{\text{PERMANOVA}} = 3.08$, $P = 0.001$) and quadrats ($F_{\text{PERMANOVA}} = 3.13$, $P = 0.002$) differed only for non-troglobitic species between the visited and non-visited areas of the cave. Furthermore, it was observed a greater dispersion in the fauna similarity on the visited area - T (average = 49.575, standard errors = 2.238) in relation to the non-visited area - NT (average = 31.254, standard errors = 3.238) (groups (NT, T); $t = 4.3208$, P (permidisp) = 0.003). The higher turnover ($\beta_{\text{total}} = 0.90$) in the visited area, had a greater contribution of nesting ($\beta_{\text{rich}} = 0.48$) (Fig. 3C).

The average richness inside the transects corresponded to 9 species in the visited area ($sd = 3.9$), and 10 species in the non-visited area ($sd = 1.8$), but no significant differences were observed among such areas. Although the average richness inside quadrats was higher in the non-visited area 3 spp. ($sd = 1.6$) compared to the visited area 2.24 spp. ($sd = 1.2$), also no significant differences were observed. The estimated richness suggests that the sampling effort achieved adequate levels of completeness since the observed richness corresponded to over 74% of the estimated richness.

Influence of habitat traits on fauna composition and richness inside transects

Considering the eleven transects evaluated throughout the cave, the distance from the entrance was the main component that influenced variations in non-troglobitic species composition ($AICc = 89.15$, $R^2 = 0.26$, $p = 0.001$) (Table 1). All variables used in the DistLm model explained 53.2% of the total variation

observed in the composition of non-troglobitic fauna inside the transects (Fig. 6A). On the other hand, the composition of the troglobitic fauna responded to the amount of SAND (AICc = 91.855, R² = 0.26, p = 0.01). All variables used in the DistLm model explained 69.8% of the total variation in the composition of the troglobitic fauna. The amount of RCM was the component that best explained the variation in the

non-troglobitic species composition in those six transects located in the visited area (AICc = 51.429, R² = 0.42, p = 0.04) (Table 1).

On the other hand, none of the substrate components explain variation on composition and richness of non-troglobitic fauna as well as the composition and richness of troglobitic species inside the non-visited area (Supplementary Table 7).

Table 1. Predictor variables of the species composition of troglobite (tb) and non-troglobite (ntb) fauna in the visited area and non-visited area of Umajalanta Cave, Torotoro, Bolivia. Distance from the entrance (DTE), fine sediment (SEF: 0.002–0.05 mm), Sand sediment (SAND: 0.05–2 mm), cobbles (SB: 250–500 mm), matrix rock (RCM).

Scale	N	Area	Predictor	Response	AICc	R ²	p	Group
Transects	11	both	DTE	Composition	89.15	0.26	0.001	ntb
Transects	11	both	SAND	Composition	91.855	0.26	0.01	tb
Quadrats	28	both	RCM + SEF	Composition	230.76	0.24	0.001	ntb
Quadrats	14	visited area	RCM	Composition	116.72	0.23	0.003	ntb
Quadrats	15	non-visited area	SB	Composition	113.41	0.25	0.006	ntb
Transects	6	visited area	RCM	Composition	51.43	0.42	0.004	ntb

Influence of habitat traits on fauna composition and richness inside quadrats

Considering the 28 quadrats, the amount of RCM and SEF explained variations on non-troglobitic

species composition (AICc = 230.76, R² = 0.24, p = 0.001) along with the cave. Figure 6B shows that all the sampled variables explained 32% of the species composition variation inside quadrats.

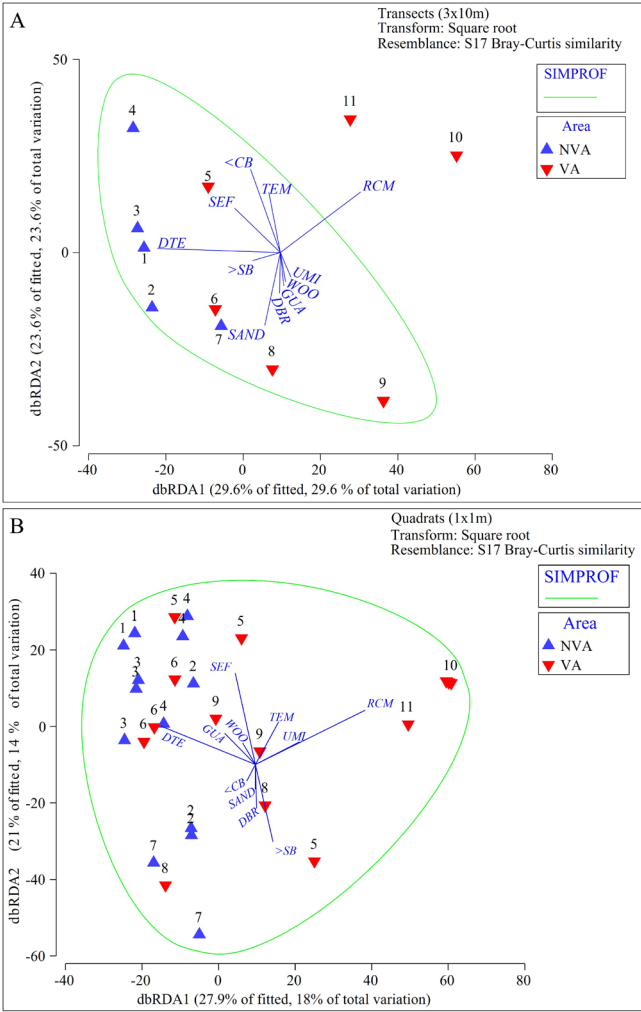


Fig. 6. Distance-based redundancy analysis (dbRDA) showing the influences of the environmental variables on invertebrate cave fauna composition in visited area (VA) and non-visited area (NVA) of Umajalanta Cave, using quadrats (A) and transects (B) as sample units. Numbers from 1 to 11 refer to sample stations. Guano (GUA), woods (WOO), plant debris (DBR), fine sediment (SEF: 0.002–0.05 mm), Sand sediment (SAND: 0.05–2 mm), boulders (CB: 64–250 mm), cobbles (SB: 250–500 mm), matrix rock (RCM), distance from the entrance in meters (DTE), the temperature (TEM) in °C, and the moisture in percentage (UMI).

The quadrats placed at the visited area (sampling stations 5, 6, 8, 9, 10, and 11), revealed that the amount of RCM (AICc = 116.72, $R^2 = 0.23$, $p = 0.003$) explained the variation on non-troglobitic species composition. On the other hand, for the quadrats placed on the non-visited area (sampling stations 1, 2, 3, 4, 7), the amount of SB (AICc = 113.41, $R^2 = 0.25$, $p = 0.006$) explained variation on non-troglobitic species composition.

Table 2. Generalized linear mixed model (GLMM) results showing predictor variables of the non-troglobitic species richness between visited area and non-visited area of quadrats (microscale) of Umajalanta Cave, Torotoro, Bolivia. Abbreviations are identical with those in Figure 6. Significance codes: '****' 0.001, '***' 0.01, '**' 0.05.

Predictor variables	Estimate	Std. error	z value	Pr(> z)
(Intercept)	-1.22E+04	8.54E+02	-14.242	<2e-16 ***
GUA	2.04E+03	8.75E+02	2.333	0.019625*
WOO	2.30E+02	9.25E+01	2.486	0.012902*
SEF	1.16E+02	2.81E+01	4.118	3.82e-05***
CB	1.36E+02	3.23E+01	4.217	2.47e-05***
SB	1.20E+02	3.03E+01	3.942	8.08e-05***
RCM	1.09E+02	2.89E+01	3.778	0.000158***
SAND	1.11E+02	2.69E+01	4.130	3.62e-05***
DBR	1.32E+02	4.68E+01	2.811	0.004946**
DTE	9.65E-01	1.29E+00	0.749	0.453591
TEM	1.32E+02	1.27E+02	1.039	0.298822
UMI	-2.12E+01	4.25E+01	-0.499	0.617644

DISCUSSION

Although the interactions between cave species and habitat components at meso and macro scales are still poorly studied, conservationists need to understand the roles of these environmental factors in determining the structure of communities to help in management actions (Culver & Sket, 2002; Mammola et al., 2019; Mammola et al., 2020; Nicolosi et al., 2021). In caves with human visitation, it should be a constant concern not to alter microhabitats essential for the maintenance of the fauna, especially in caves with endemic and vulnerable species (Elliot, 2004; Pacheco et al., 2020; Nicolosi et al., 2021).

The results revealed that the visited area presented more heterogeneous habitats as well as a more distinct composition of non-troglobitic species when compared to the non-visited area. Despite the influence of the distance from the entrance, the predominance of matrix rock (RCM) in the visited area and of fine clayey sediment (SEF) in the non-visited area determined variations in the fauna composition. On the other hand, the richness of the non-troglobitic fauna responded to the amount of guano, wood, fine sediment, boulders, cobbles, matrix rock, sand sediment e plant debris. Furthermore, unlike our second hypothesis, although the troglobitic species were distributed throughout the entire cave, all species were found in the visited area (Fig. 7), while only 67% were observed in the non-visited area.

The distinction in habitat structure and non-troglobitic fauna composition between the two studied areas seems to be an effect of distance from

The richness of non-troglobitic species responded positively to the amount of GUA, WOO, SEF, CB, SB, RCM, SAND, and DBR inside quadrants (Supplementary Table 8, Table 2). The influence of substrate components on the composition and richness of troglobitic was not performed inside quadrants because the number of samples was very low (only seven quadrats with troglobitic species).

the entrance and habitat differentiation, but not influenced by human visitation. The apparent neutral effect of visitation on non-troglobitic fauna can probably be a consequence of a reduced number of persons and the predominance of primary matrix rock and speleothems on the floor of the visited area.

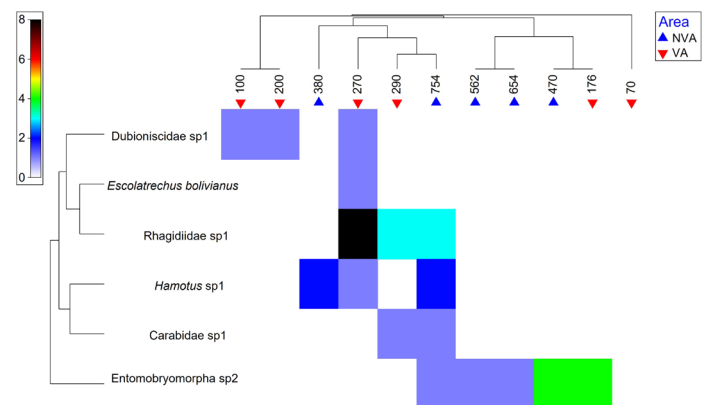


Fig. 7. Distribution and total abundance (0 to 8) of the six arthropods species with troglomorphic traits at the floor of visited area (VA) and non-visited areas (NVA) in Umajalanta Cave, Bolivia. The sample units were grouped with a cluster utilizing the Bray-Curtis average similarity (displayed up). Numbers from 70 to 754 represent the distance from the entrance (m). The species list was grouped with a cluster utilizing Whittaker's Index of Association (displayed left).

A low number of visitors can produce few damages on the hard substrate, especially when it is more consolidated, being more resistant to erosive alterations. On the other hand, such poor substrates regarding the diversity of microhabitats, prevent (or reduce) the faunal colonization when compared to

clastic and organic sediments. A similar situation of neutral impacts of tourist use on invertebrates was found by Faile et al. (2015) and Nicolosi et al. (2021). Faile et al. (2015) showed that a chamber with huge size at La Verna cave (in France) can prevent changes in microclimate conditions, because of the movement of visitors, and the presence of very large boulders and cracks can offer plenty of protected spaces, allowing 18 troglobitic invertebrates species to escape of direct human disturbance and illumination. Nicolosi et al. (2021) argued that the number of visitors in the Monello Cave (Italy) did not affect the abundance and distribution of *Armadillidium lagrecai* (Isopoda) because they prefer areas more climatically stable inside the cave with the warm temperature and high humidity.

Furthermore, the presence of all observed troglobitic species in the visited area can eventually indicate a neutral effect of tourism on the fauna, as this activity can be low in this cave. However, this situation must be considered with caution, since visitors can deposit organic resources, cause physical changes in the substrate and trample on fauna, among other impacts (Pellegrini & Ferreira, 2012; Pacheco et al., 2020). Pellegrini and Ferreira (2012) evaluated on a mesoscale (3 x 15 m transects), the effect of mass religious tourism (50 thousand people in three days) in Lapa Nova Cave (Brazil), and detected that invertebrates migrate to distant locations from the visited areas as a result of the intense tourism. These authors emphasized that non-visited areas could act as refuges for fauna due to the tourist changes in the cave (agglomeration of people and trampling). Due to the low number of visitors, this situation, however, was not observed in Umajalanta Cave.

Within the quadrants, the greater richness of non-troglobitic species associated with the amount of guano, wood, fine sediment, boulders, cobbles, matrix rock, sand sediment, and plant debris, may result from habitat heterogeneity related to the trophic and physical components on the cave floor. For instance, Pacheco et al. (2020a) showed, for caves in Guatemala, that non-troglobitic invertebrate species responded to the presence of guano, cobbles, boulders, and substrate heterogeneity. In that case, a variety of trophic and physical substrates provided suitable habitats for the invertebrates, thus causing an important increase in both species richness and composition. Usually, a high richness of non-troglobitic invertebrate species in tropical caves can be attributed to the presence of guano piles, plant debris, and habitat diversity (Schneider et al., 2011; Souza-Silva et al., 2011; Ladle et al., 2012; Ferreira, 2019; Pacheco et al., 2020, 2020a).

Specific environmental conditions and resources occur, within the caves, in patches that can vary in space and time (Eberhard, 2001; Mammola et al., 2015; Pacheco et al., 2020). Such “patches” usually limit the distribution of cave species to mosaics of distinct habitats (Novak et al., 2012; Kozel et al., 2019; Souza-Silva et al., 2021). The positive, negative, or neutral influence of these “patches of conditions and resources” on biological communities may

depend on the interaction of different elements, which in turn, can also act individually as “key” elements in the provision of resources and/or shelters for species persistence (Tews et al., 2004; Stein et al., 2014; Pacheco et al., 2020a).

The distance from the cave entrance has been considered an important limiting factor for species distribution, especially for non-troglobitic taxa, since there is a reduction in the food resources available and habitat heterogeneity from the entrance to deeper areas (Souza-Silva et al., 2021). Thus, a lower richness of non-troglobitic species in deeper and non-visited area in Umajalanta Cave may also be related to the food scarcity and reduced microhabitat diversity. On the other hand, since troglobitic species are highly specialized, they can survive in oligotrophic and more stable areas, usually located in deeper cave zones (Novak et al., 2012; Tobin et al., 2013; Souza-Silva et al., 2021). In addition, Pellegrini & Ferreira (2016) showed that non-troglobitic invertebrates associated with tourist areas may migrate during high visitation periods for places far from the visited areas. Thus, non-tourists regions can function as a refuge for troglobitic and non-troglobitic communities as well as a source of individuals for the colonization of tourist areas. However, we must carefully consider this possibility, since the use of different areas by the fauna may be dependent on the dispersal capacity and microhabitat requirements of different species (Faile et al., 2015; Nicolosi et al., 2021).

Different from other studies that used microscale sampling (Pacheco et al., 2020, 2020a; Souza-Silva et al., 2021) the reduced number of troglobitic specimens sampled in the 1 m² quadrants did not allow responses of such organisms to the habitat structure in Umajalanta Cave at this sample size. Pacheco et al. (2020) studying the effects of tourism on the invertebrate fauna of the Lanquin cave (Guatemala), detected, on a microscale, that the sixteen troglobitic species responded to the presence of tourism, fine sediment, matrix rock, cobble, and water puddle. Hence, the response of the troglobitic fauna can be variable between caves and probably dependent on the sampling scale.

Several studies highlighted that if the sampling scale is not defined according to the organism's perspective, environmental parameters determining the species distribution may remain underlying, and preferences for microhabitats will not be easily detected (Rahbek & Graves, 2001; Kováč et al., 2003; Rahbek, 2005; González-Megías et al., 2007; Mehrabi et al., 2014; Pellegrini & Ferreira, 2016a). However, in Umajalanta Cave, only mesoscale analyzes were effective in detecting troglobitic fauna habitat requirements. It is important to note that, in addition to issues related to the low density of troglobites in Umajalanta Cave, variables that are considered a determinant in the distribution of troglobitic fauna, such as temperature and humidity, were not accessed on a microscale in our study. Troglobitic species tend to prefer cave sites that are oligotrophic and have an atmosphere with high humidity and constant temperature (Kozel et al., 2019).

CONCLUSION

In conclusion, the reduced number of visitors and the predominance of consolidated substrates in the visited area of the cave apparently “buffer” the possible influence of human alterations on the habitat structure and the invertebrate communities. Despite this, it is important to implement management and monitoring actions, aiming to prevent the expansion of visitation routes within the cave and defining more restricted routes in the area already visited, avoiding trampling on important substrates for fauna (BirdLife/FFI/IUCN/WWF 2014; Pellegrini & Ferreira, 2012; Pacheco et al., 2020). Thus, management programs associated with monitoring the fauna and the different caves substrates are of paramount importance. In addition, information and environmental education strategies are essential in good practices for the use of tourist caves.

ACKNOWLEDGMENTS

Laís Furtado Oliveira was sponsored by Capes Foundation (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) with 24 months of grants. RLF is grateful to the National Council of Technological and Scientific Development (CNPq) for the research grant No 308334/2018-3. The organization of Torotoro National Park for the reception (SERPAN). Roberta Cerqueira and Félix for help in field samples. Angélico Asenjo (Staphylinidae), Rafaela Bastos Pereira and Giovanna Monticelli Cardoso (Isopods) and Leopoldo Bernardi (Acari) for help in fauna identification. VALE/SA for financial support.

Authorship statement: RLF formulated the idea and contributed to the literature review. RLF, MSS, LFO built the sample design collected the data and identified invertebrates. LFO and MSS performed the statistical analysis. LFO and MSS wrote the manuscript with collaboration from all co-authors. RLF and JIRF reviewed the manuscript and contributed to the discussion of the results.

REFERENCES

- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. Massey University, Albany Campus, Auckland: New Zealand.
- Ávila, A.C., Pires, M.M., Rodrigues, E.N., Costi, J.A., Stenert, C., Maltchik L., 2019. Drivers of the beta diversity of spider assemblages in southern Brazilian temporary wetlands. *Ecological Entomology*, 45(3), 466-475. <https://doi.org/10.1111/een.12816>
- BirdLife/FFI/IUCN/WWF, 2014. “Extraction and biodiversity in limestone areas”. Joint briefing paper.
- Bočić, N., Lukić, A., Opačić, V.T., 2006. Management models and development of show caves as tourist destinations in Croatia. *Acta Carsologica*, 2(35), 13–21. <https://doi.org/10.3986/ac.v35i2-3.224>
- Bunting, B., Balks, M., 2001. A quantitative method for assessing the impacts of recreational cave use on the physical environment of wild caves. *Australasian Cave and Karst Management Association Journal*, 44, 10-18.
- Cardoso, P., Rigal, F., Carvalho, J.C., 2015. BAT–Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, 6, 232–236. <https://doi.org/10.1111/2041-210X.12310>
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User manual/tutorial: Plymouth. Plymouth, UK: Primer-E.
- Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014. Change in marine communities: an approach to statistical analysis and interpretation. Primer-E.
- Cuff, J.P., Aharon, S., Armiach Steinpress, I., Seifan, M., Lubin, Y., Gavish-Regev, E., 2021. It’s all about the zone: Spider assemblages in different ecological zones of Levantine caves. *Diversity*, 13(11), 576. <https://doi.org/10.3390/d13110576>
- Culver, D.C., Sket B., 2002. Biological monitoring in caves. *Acta Carsologica*, 31(1), 55-64. <https://doi.org/10.3986/ac.v31i1.403>
- Culver, D.C., Pipan, T., 2009. The biology of caves and other subterranean habitats. Oxford University Press, 273 p.
- Durand, J.P., 1968. Etude des poissons recoltés dans la grotte de Umayalanta (Bolivie), *Trichomycterus chaberti* sp. n. *Annales de Spéléologie*, 23, 343–353.
- Eberhard, S., 2001. Cave fauna monitoring and management at Ida Bay, Tasmania. Records of the Western Australia Museum Supplement, 64, 97-104. <https://doi.org/10.18195/issn.0313-122x.64.2001.097-104>
- Elliott, W.R., 2004. Protecting caves and cave life. In: Culver, D.C., White, W.B. (Eds.), *Encyclopedia of caves*. Elsevier Academic Press, Amsterdam, p. 428-467.
- Faillie, A., Bourdeau, C., Deharveng, L., 2015. Weak impact of tourism activities on biodiversity in a subterranean hotspot of endemism and its implications for the conservation of cave fauna. *Insect Conservation and Diversity*, 8(3), 205-215. <https://doi.org/10.1111/icad.12097>
- Ferreira R.L., 2019. Guano communities. In: White, W.B., Culver, D.C., Pipan, T. (Eds.), *Encyclopedia of caves*, 3rd ed. Academic Press, London, p. 474-484.
- Ferreira, R.L., Martins, R.P., 2001. Cavernas em risco de ‘extinção’. *Ciência Hoje*, 29, 20-28
- Gallucci, M., 2019. GAMLj: General analyses for linear models. [jamovi module]. Retrieved from <https://gamlj.github.io/>
- Garreaud, R. D., 2009. The Andes climate and weather. *Advances in Geosciences*, 22, 3-11. <https://doi.org/10.5194/adgeo-22-3-2009>
- González-Megías, A., Gómez, J.M., Sánchez-Piñero, F., 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography*, 30, 31-41. <https://doi.org/10.1111/j.0906-7590.2007.04867.x>
- Guyot, J.L., Soares de Melo Filho, L., 1997. Estudio de los recursos espeleológicos de la Reserva Nacional torotoro (RNT). Formulación de una propuesta de conservación, protección y valorización. Publication CONICOM, Cochabamba, 46 p.
- Hamilton-Smith, E., 2004. Tourist caves. In: Gunn, J. (Ed.), *Encyclopedia of caves and karst science*. Taylor and Francis Group, New York, p. 1554-1561.
- Jamovi, 2020. The jamovi project (Version 1.2) [Computer Software]. Retrieved from <https://www.jamovi.org>
- Kováč, L., Mock, A.J., Luptáčík, P., Košel, V., Fena, P., Svatoň, J., Mašán, P., 2005. Terrestrial arthropods of the Dómica Cave system and the Ardoinská Cave (Slovak Karst)–principal microhabitats and diversity. Contributions to soil zoology in Central Europe I.

- Institute of Soil Biology AS CR, České Budějovice, 61-70. Kozel, P., Pipan, T., Mammola, S., Culver, D.C., Novak, T., 2019. Distributional dynamics of a specialized subterranean community oppose the classical understanding of the preferred subterranean habitats. *Invertebrate Biology*, 138(3), e12254. <https://doi.org/10.1111/ivb.12254>
- Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23(11), 1324-1334. <https://doi.org/10.1111/geb.12207>
- Ladle, R.J., Firmino, J.V., Malhado, A.C., Rodriguez-Duran, A., 2012. Unexplored diversity and conservation potential of Neotropical hot caves. *Conservation Biology*, 26(6), 978-982. <https://doi.org/10.1111/j.1523-1739.2012.01936.x>
- Mammola, S., Piano, E., Giachino, P.M., Isaia, M., 2015. Seasonal dynamics and micro-climatic preference of two Alpine endemic hypogean beetles. *International Journal of Speleology*, 44(3), 239-249. <https://doi.org/10.5038/1827-806X.44.3.3>
- Mammola, S., Piano, E., Malard, F., Vernon, P., Isaia, M., 2019. Extending Janzen's hypothesis to temperate regions: A test using subterranean ecosystems. *Functional Ecology*, 33, 1638-1650. <https://doi.org/10.1111/1365-2435.13382>
- Mammola, S., Arnedo, M. A., Fišer, C., Cardoso, P., Dejanaz, A. J., Isaia, M., 2020. Environmental filtering and convergent evolution determine the ecological specialization of subterranean spiders. *Functional Ecology*, 34, 1064-1077. <https://doi.org/10.1111/1365-2435.13527>
- Mammola, S., Amorim, I.R., Bichuette, M.E., Borges, P.A., Cheeptham, N., Cooper, S.J., et al., 2020a. Fundamental research questions in subterranean biology. *Biological Reviews*, 95(6), 1855-1872. <https://doi.org/10.1111/brv.12642>
- Mateu, J., 2002. *Escolatrechus bolivianus* gen. n., sp. n. de Trechinae de l'Haut Plateau Bolivien (Coleoptera: Carabidae: Trechinae). https://www.researchgate.net/publication/324757922_Nouvelle_Monographie_des_Trechinae_V5
- Mehrabi, Z., Slade, E.M., Solis, A., Mann, D.J., 2014. The importance of microhabitat for biodiversity sampling. *PloS ONE*, 9(12): e114015. <https://doi.org/10.1371/journal.pone.0114015>
- Nicolosi, G., Mammola, S., Costanzo, S., Sabella, G., Cirrincione, R., Signorello, G., Isaia M., 2021. Microhabitat selection of a Sicilian subterranean woodlouse and its implications for cave management. *International Journal of Speleology*, 50(1), 53-63. <https://doi.org/10.5038/1827-806X.50.1.2370>
- Novak, T., Perc, M., Lipovšek, S., Janžekovič, F., 2012. Duality of terrestrial subterranean fauna. *International Journal of Speleology*, 41(2), 181-88. <https://doi.org/10.5038/1827-806X.41.2.5>
- Oliver, I., Beattie, A.J., 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology*, 10(1), 99-109. <https://doi.org/10.1046/j.1523-1739.1996.10010099.x>
- Osborne, R.A.L., 2019. Saving and conserving the caves: reflections on 37 years of listings, disputes, submissions, and court cases. *Australian Journal of Earth Sciences*, 66(6), 767-778. <https://doi.org/10.1080/08120099.2018.1489895>
- Pacheco, G.S.M., Souza Silva, M., Cano, E., Ferreira R.L., 2020a. The role of microhabitats in structuring cave invertebrate communities in Guatemala. *International Journal of Speleology*, 49(2), 161-169. <https://doi.org/10.5038/1827-806X.49.2.2333>
- Pacheco, G.S.M., de Oliveira, M.P.A., Cano, E., Souza Silva, M., Ferreira, R.L., 2020. Tourism effects on the subterranean fauna in a Central American cave. *Insect Conservation and Diversity*, 14(3), 294-306. <https://doi.org/10.1111/icad.12451>
- Peck, S.B., 1975. A population study of the cave beetle *Ptomaphagus loedingi* (Coleoptera; Leiodidae; Catopinae). *International Journal of Speleology*, 7(1), 19-32. <https://doi.org/10.5038/1827-806X.7.1.3>
- Pellegrini, T.G., Ferreira, R.L., 2012. Management in a neotropical show cave: planning for invertebrates conservation. *International Journal of Speleology*, 41(2), 359-366. <https://doi.org/10.5038/1827-806X.41.2.19>
- Pellegrini, T.G., Ferreira, R.L., 2016. Are inner cave communities more stable than entrance communities in Lapa Nova show cave? *Subterranean Biology*, 20, 15-37. <https://doi.org/10.3897/subtbiol.20.9334>
- Pellegrini, T.G., Sales, L.P., Aguiar, P., Ferreira, R.L., 2016a. Linking spatial scale dependence of land-use descriptors and invertebrate cave community composition. *Subterranean Biology*, 18, 17-38. <https://doi.org/10.3897/subtbiol.18.8335>
- Prous, X., Ferreira R. L., Jacobi, C.M., 2015. The entrance as a complex ecotone in a Neotropical cave. *International Journal of Speleology*, 44(2), 177-189. <https://doi.org/10.5038/1827-806X.44.2.7>
- Prous, X., Ferreira, R.L., Martins, R.P., 2004. Ecotone delimitation: Epigean-hypogean transition in cave ecosystems. *Austral Ecology*, 29(4), 374-382. <https://doi.org/10.1111/j.1442-9993.2004.01373.x>
- Rasband, W.S., 1997. Image, J., US National Institutes of Health. "ImageJ64," US National Institutes of Health, Bethesda, MD.
- Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8(2), 224-239. <https://doi.org/10.1111/j.1461-0248.2004.00701.x>
- Rahbek, C., Graves, G.R., 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, 98(8), 4534-4539. <https://doi.org/10.1073/pnas.071034898>
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Romero, A. (Ed.), 2009. Cave conservation and management. In: *Cave biology: Life in darkness*. Ecology, biodiversity and conservation, Cambridge University Press, Cambridge, p. 182-208. <https://doi.org/10.1017/CBO9780511596841.006>
- Schneider, K., Christman, M.C., Fagan, W.F., 2011. The influence of resource subsidies on cave invertebrates: results from an ecosystem-level manipulation experiment. *Ecology*, 92, 765-776. <https://doi.org/10.1890/10-0157.1>
- Slaney, D.P., Weinstein, P., 1997. Conservation of cave fauna: more than just bats. *Memoirs Museum Victoria*, 56(2), 591-596. <https://doi.org/10.24199/j.mmv.1997.56.55>
- Souza-Silva, M., Martins, R.P., Ferreira, R.L., 2011. Trophic dynamics in a neotropical limestone cave. *Subterranean Biology*, 9, 127-138. <https://doi.org/10.3897/subtbiol.9.2515>
- Souza-Silva, M., Cerqueira, R.F.V., Pellegrini, T.G., Ferreira, R.L., 2021. Habitat selection of cave-restricted fauna in a new hotspot of subterranean biodiversity in Neotropics. *Biodiversity and Conservation*, 1-28.

- <https://doi.org/10.1007/s10531-021-02302-8>
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes, and spatial scales. *Ecology Letters*, 17, 866-880.
<https://doi.org/10.1111/ele.12277>
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), 79-92.
<https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Tobin, B.W., Hutchins, B.T., Schwartz, B.F., 2013. Spatial and temporal changes in invertebrate assemblage structure from the entrance to the deep-cave zone of a temperate marble cave. *International Journal of Speleology*, 42(3), 203-214.
<https://doi.org/10.5038/1827-806X.42.3.4>
- Trontelj, P., Blejec, A., Fišer, C., 2012. Ecomorphological convergence of cave communities. *Evolution* 66, 3852-3865.
<https://doi.org/10.1111/j.1558-5646.2012.01734.x>
- Var, T., 2004. Caving. In: Cross, G.S. (Ed.), *Encyclopedia of recreation and leisure in America*. Charles Scribner's Sons, Detroit, p. 149-151.
- Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology*, 30(5), 377-392. <https://doi.org/10.1086/622910>
- Wilson, J.M., 2019. Recreational caving. In: White, W.B., Culver, D.C. (Eds.), *Encyclopedia of caves*, Academic Press/Elsevier, London, p. 861-870.
<https://doi.org/10.1016/B978-0-12-814124-3.00103-5>
- Wynne, J.J., Howarth, F.G., Sommer, S., Dickson, B.G., 2019. Fifty years of cave arthropod sampling: techniques and best practices. *International Journal of Speleology*, 48(1), 33-48.
<https://doi.org/10.5038/1827-806X.48.1.2231>
- Yao, Z., Dong, T., Zheng, G., Fu, J., Li, S., 2016. High endemism at cave entrances: a case study of spiders of the genus *Uthina*. *Scientific Reports*, 6, 35757.
<https://doi.org/10.1038/srep35757>
- Zúñiga, Z.L., Pouilly M., 2009. Estado del conocimiento y propuesta para la elaboración del plan de manejo del Parque Nacional de Torotoro. Publication SERNAMP, Cochabamba, 31 p.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3-14.
<https://doi.org/10.1111/j.2041-210X.2009.00001.x>