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GABRIELLE SOARES MUNIZ PACHECO

BIODIVERSIDADE SUBTERRÂNEA EM CAVERNAS DA GUATEMALA: INFLUÊNCIAS DO HABITAT FÍSICO E IMPACTOS CAUSADOS PELA ATIVIDADE TURÍSTICA

LAVRAS - MG

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

Prof. Dr. Rodrigo Lopes Ferreira

Orientador

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SUBTERRANEAN BIODIVERSITY IN GUATEMALA CAVES: INFLUENCES OF THE PHYSICAL HABITAT AND IMPACTS CAUSED BY TOURISTIC ACTIVITY

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“There is more in us than we know. If we can be made to see it, perhaps for the rest of our lives we will be unwilling to settle for less.”

“Há mais em nós do que sabemos. Se conseguirmos perceber isso, talvez pelo resto de nossas vidas, não estaremos dispostos a nos contentar com menos.”

Kurt Hahn

RESUMO

Essa dissertação desenvolve-se acerca de assuntos relacionados à ecologia de cavidades naturais subterrâneas, mais especificamente sobre a influência do substrato e também da atividade turística sobre a composição e riqueza da fauna de invertebrados terrestres em cavernas. Para este trabalho então, invertebrados terrestres foram coletados em dez cavidades nas regiões cársticas de Alta Verapaz e Petén, na Guatemala, num período entre junho e julho de 2017. Conta com dois artigos escritos conforme as regras de periódicos científicos. O primeiro foi escrito de acordo com as normas do periódico "International Journal of Speleology". Esse capítulo teve o objetivo de investigar as similaridades da fauna de invertebrados cavernícolas das dez cavidades coletadas e acessar quais características do substrato possuem maior influência sobre a estrutura da comunidade de invertebrados cavernícolas na Guatemala. O segundo capítulo foi elaborado de acordo com as normas do periódico "Tourism Management" e teve o objetivo de medir possíveis efeitos do turismo sobre a comunidade de invertebrados terrestres na Gruta de Lanquín, município de Lanquín, região de Alta Verapaz, Guatemala. Contribuindo assim para o conhecimento, manejo e conservação do patrimônio bioespeleológico da Guatemala.

Palavras-chave: Caverna; Biodiversidade, Invertebrados; Substrato; Heterogeneidade de habitat; Turismo; Guatemala

ABSTRACT

This dissertation is developed on subjects related to the ecology of subterranean natural cavities, more specifically on the influence of substrate and tourism activity on the species composition and richness of terrestrial invertebrate fauna in caves. For this work, terrestrial invertebrates were collected in ten cavities in the karst regions of Alta Verapaz and Petén, Guatemala, between June and July of 2017. It contains two scientific papers, written in scientific journal format. The first was written according to the norms of the "International Journal of Speleology" journal. The objective of this chapter was to investigate the similarities of the cave invertebrate fauna from the ten caves included in this study and to investigate which substrate features have the greatest influence on the structure of the cave invertebrate community in Guatemala. The second chapter was elaborated according to the norms of the "Tourism Management" journal and had the objective of measuring possible effects of tourism on the community of terrestrial invertebrates in Gruta de Lanquín, Lanquín municipality, Alta Verapaz region, Guatemala. Thus, contributing to the knowledge, management and conservation of the biospeleological patrimony of the Guatemala.

Keywords: Cave; Biodiversity; Invertebrates; Substrate; Habitat heterogeneity; Tourism; Guatemala

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO

Essa dissertação desenvolve-se acerca de assuntos relacionados à ecologia de cavidades naturais subterrâneas, mais especificamente sobre a influência do substrato e também da atividade turística sobre a composição e riqueza da fauna de invertebrados terrestres em cavernas. Para este trabalho então, invertebrados terrestres foram coletados de modo ativo, com o auxílio de pinças e pincéis, em dez cavidades nas regiões cársticas de Alta Verapaz e Petén, na Guatemala, num período entre junho e julho de 2017. Conta, além dos elementos pré-textuais, com dois artigos redigidos conforme as regras de periódicos científicos. Foi acordado ainda que ambos os capítulos seriam redigidos em língua inglesa para que o processo de publicação dos manuscritos pós defesa seja facilitado.

O primeiro artigo foi elaborado de acordo com as normas do periódico "International Journal of Speleology" e discorre acerca dos efeitos dos diferentes tipos substrato sobre as comunidades de invertebrados terrestres em dez cavernas das regiões de Alta Verapaz e Petén, na Guatemala. Utilizando transectos, a fauna de invertebrados foi coletada e as características do substrato foram medidas. Um total de 10.354 espécimes foram registrados, distribuídos em 38 ordens, 78 famílias e 177 espécies, 29 das quais foram consideradas troglóbias. Além disso, os resultados mostraram que, quando considerando a riqueza e composição total de espécies, a estrutura da comunidade respondeu principalmente à presença de matéria orgânica. Porém, quando considerando apenas as espécies troglóbias, a composição e a riqueza responderam à presença de pedra e blocos.

O segundo artigo, por sua vez, foi elaborado de acordo com as normas do periódico "Tourism Management" e discorre acerca dos efeitos do turismo sobre a comunidade de invertebrados terrestres na Gruta de Lanquín, município de Lanquín, região de Alta Verapaz, Guatemala. Nesse artigo, grupos de seis quadrantes foram posicionados tanto na parte turística quanto na parte não turística na caverna, onde os invertebrados foram coletados e as características do substrato foram medidas. Os resultados mostraram que a composição da fauna diferiu entre as duas áreas. A partição da diversidade beta indicou que as espécies troglóbias podem estar estruturadas diferentemente dentro da caverna quando comparadas ao restante das espécies da comunidade nessa caverna. Por último, foi detectado que os caminhos designados aos turistas possuem um subtrato diferente daquele encontrados nas áreas adjacentes. Foi recomendado que as visitas à essa caverna sejam sempre guiadas, a fim de que os turistas não acessem lugares não permitidos e que o tempo da visita seja controlado para que o menor impacto possível seja gerado na comunidade de invertebrados da caverna. Os resultados desses estudos consistem numa base biológica e ecológica que pode subsidiar a criação de novos parâmetros para o manejo e conservação de cavernas na Guatemala.

SEGUNDA PARTE - ARTIGOS

Artigo 1 – Biodiversidade subterrânea em um carste na América Central: o papel dos micro-habitats da caverna na estruturação de comunidades de invertebrados

Este capítulo foi escrito em formato de artigo (versão preliminar), redigido conforme as normas para publicação da revista “International Journal of Speleology” E-ISSN: 1827-806X, disponível em: https://scholarcommons.usf.edu/ijs/submission_guidelines.pdf

SUBTERRANEAN BIODIVERSITY IN A KARST IN CENTRAL AMERICA: THE ROLE OF CAVE MICROHABITATS IN STRUCTURING INVERTEBRATE COMMUNITIES

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ABSTRACT

Several studies have tried to elucidate which are the main substrate features that drive the invertebrate community in cave environments. Some of them have found that the main drivers of species richness are the biotic features such as guano, organic debris and roots, while others found that the invertebrate communities are influenced mostly by the heterogeneity of physical habitats available in the cave. Therefore, the objective of this study was to investigate the similarities in the cave invertebrate fauna from 10 caves located in three different regions of Guatemala and to assess which substrate features determine the invertebrate community structure. Using transects, the invertebrate fauna was collected and the substrate features were measured. A total of 10,354 specimens were registered, distributed in 38 orders, at least 78 families and 177 species, 29 of which were considered troglobites. Furthermore, results showed that, when considering the total species richness and composition, the community structure responded mainly to the presence of organic matter. However, when considering only the troglobitic species, they responded to the presence of physical microhabitats such as cobbles and boulders. The findings of this study provide a biological background for the creation of new parameters for management and conservation of caves in Guatemala.

KEYWORDS

Cave; Biodiversity; Invertebrates; Substrate; Habitat heterogeneity; Guatemala

INTRODUCTION

Patterns of species distribution and factors that act towards the structuring of communities have always been significant drivers for ecological studies (Gibert & Deharveng 2002). For caves, understanding these patterns and factors is paramount for conservation purposes, since the organisms that inhabit these environments are known to be relatively sensitive to many kinds of stressors, both natural and anthropic (Howarth 1983).

Few studies have been trying to elucidate the main environmental factors structuring invertebrate communities inside cave environments. Among the main factors encountered, some stand out, for example seasonality (Mammola et al. 2015, Bento et al. 2016), lithology (Souza-Silva et al. 2011b), landscape structure (Christman et al. 2016, Pellegrini et al. 2016, Cardoso 2017, Mammola & Leroy 2017), distance from cave entrance (Prous et al. 2004, Prous et al. 2015, Cerqueira 2018), linear projection of the cave (Simões et al. 2015, Pellegrini & Ferreira 2016), presence of water (Simões et al. 2015), food availability (Ferreira & Martins 1998, Gnaspini & Trajano 2000, Gnaspini 2012), microclimate (Mammola et al. 2015), speleogenesis (Jiménez-Valverde et al. 2017) and habitat structure (Cardoso 2017, Cerqueira 2018).

Other studies have tried to elucidate which are the main substrate features that drive the community structure (species richness and composition) inside the cave environment. Some of them have found that the main drivers of species richness (on ferruginous tropical caves) are the biotic features such as guano, organic debris and roots (Jaffé et al. 2016), while others found that the invertebrate communities are influenced mostly by the heterogeneity of physical habitats available in the cave (Prous 2005, Cordeiro 2008, Oliveira 2014, Pellegrini et al. 2016, Gomes 2017, Zepon & Bichuette 2017).

Currently, it is accepted that invertebrates have preferential microhabitats inside the cave environment (Culver & Pipan 2009, Moseley 2009, Souza-Silva & Ferreira 2009, Mammola et al. 2016). Such preferences for specific types of substrates are due to a variety of reasons, including behavioral, physiological and morphological adaptations (Howarth 1983, Gomes 2017, Zepon e Bichuette 2018). These microhabitats encompass different abiotic (lakes, water bodies, puddles, types of substrates and rocks of different textures and sizes) and biotic (roots, guano, vegetal debris and carcasses) features (Ferreira 2004, Ferreira et al. 2007, Culver & Pipan 2009, Souza-Silva et al. 2011a, Simões et al. 2015, Gomes, 2017). Thus, the habitat heterogeneity acts on the invertebrate communities by increasing the niche and microhabitat availability for the fauna (Zagmajster et al. 2018).

Although progress has been made trying to elucidate the influence of habitat structure on species richness and composition of cave communities in different regions of the world, other places like Central America are still understudied, especially Guatemala.

There is a reasonable amount of scientific work on the taxonomy of cave invertebrates in Guatemala (see Reddell 1981, Strinati 1994 and Reddell et al. 1996), but there is a noticeable gap when it comes to ecological work. This study, therefore, comes with the objective of testing two main objectives and hypothesis: (i) check if there are similarities in the invertebrate fauna from different karstic regions of the country (Caves present in the same karstic region have similar faunas, while caves present in different regions have dissimilar faunas); (ii) assess which substrate features determine the invertebrate community structure in a set of Guatemalan caves (strictly cavernicole species respond differently to the habitat attributes because they are more specialized to live in the subterranean habitat).

MATERIALS AND METHODS

Study area

With an Equatorial Monsoon climate (Kottek et al., 2006), Guatemala is a tropical country that features several environmental conditions within a relatively small geographic area (Strinati 1994). Furthermore, the country presents a set of limestone karstic landscapes that cover about one third of the country’s area.

The karstic landscapes from Guatemala are divided into four main domains: Huehuetenango, Alta Verapaz, Izabal and Petén (Strinati, 1994). Reddel (1981) described the karst in these areas as remarkable, highlighting the presence of abundant karst dissolution features.

This study was conducted in ten limestone caves from the regions of Alta Verapaz and Petén (Table 1 and Figure 1). Three of those caves are located in the municipality of San Augustin de Lanquín (Alta Verapaz); six are located in Raxruhá (Alta Verapaz) and one in Flores (Petén).

Field procedures

All data was collected in 30 m² (10 m x 3 m) transects along the caves. All transects were placed at least 50 m from each other. The number of transects per cave ranged from 1 to 8 within the ten caves (Table 1), with a total of 25 transects. In this study, it was best suited to use the transects as sampling units instead of caves.

The invertebrate fauna was collected manually with the aid of brushes and tweezers and placed in a solution of 70% ethanol for further examination and identification in the laboratory. When the abundance of invertebrates was considerably high, a few specimens were collected and the remaining individuals were accounted for in the field notebook.

Afterwards, the substrate was characterized according to a field protocol adapted from the ones proposed by Peck and collaborators (2006) and Hughes and Peck (2008). This protocol consists in dividing each transect into 10 sections of one meter each and estimating the percentage of each substrate features: guano, roots, leaves, twigs, trunks, water body, water puddle, actinomycetes, fine gravel (0.06 – 64 mm), cobbles (64 – 1000 mm), boulders (1000 – 4000 mm), matrix rock (> 4000 mm) and human interventions (bridges, pathways and steps made of concrete). To minimize observer error, some precautions were taken. Firstly, all the transects were characterized by the same researcher. Secondly, the arithmetic mean values of the substrate percentages observed at the 10 sections were obtained. Lastly, the Braun-Blanquet (1927) phytosociology density scores table was adapted and then applied to the substrate data. In this adaptation, the percentage ranges were allocated in five categories: <1% = 0; 1 – 5% = 1; 5 – 25% = 2; 25 – 50% = 3; 50 – 75% = 4; 75 – 100% = 5.

Data analysis

Foremost, in order to access whether the communities from the different caves differed from each other, a Multi-Dimensional Scaling (MDS) and Analysis of Similarities (ANOSIM) were performed in Primer 7 Software, both with the caves and municipalities as factors.

Then, to determine which substrate features have the most influences on the invertebrate's species richness, Generalized Linear Mixed Models were made in R Software with species richness as response variable, the substrate features and substrate diversity (Shannon index) as explaining variables and caves as the random factor. Hence, it was possible to compare the invertebrate community on every transect, instead of on every cave.

Lastly, to measure the influence of the substrate types on the species composition, a Distance Based Linear Model (DistLM) was performed in Primer 6 Software. This analysis also had the transects as samples and caves as factors in order to compare the fauna among the transects instead of the caves.

Those analysis were performed for total species and then repeated using only the troglobitic species.

RESULTS

A total of 10,354 specimens were registered in this study. They were distributed in 38 orders, at least 78 families and 177 species, 29 of which were considered troglobites (Table 2). The troglobitic fauna includes one trombiculid Acari, two spiders (Corinnidae and Pholcidae), two campodeid diplurans, four entomobryid and one symphypleona collembolans, one geophilomorpha, three isopoda (Philosciidae, Asellidae, Styloniscidae), two nicoletiid zygentoma, one Samoid opilionid, eight polydesmid diplopods and two chthoniid pseusdoscorpiones.

The analysis of similarities showed that the invertebrate communities differed among the three karstic regions (total $R=0.852$ and $p=0.001$ (Figure 2); troglobitic $R=0.553$ and $p=0.001$ (Figure 3)). They also differed among the ten caves both for the total ($R=0.919$ and $p=0.001$) and troglobitic ($R=0.835$ and $p=0.001$) species.

As for the models, it was observed that guano ($p<0.001$), water bodies ($p=0.0175$), twigs ($p=0.0199$) and roots ($p=0.0660$) were the variables that best explained the total species richness. Troglobitic species richness, on the other hand, was best explained by the null model (intercept p=0.0291). In other words, the troglobitic species richness could not be predicted by any of the substrate features measured in this study.

Total species composition variation was best explained by the presence of guano (prop=0.11503, R^2adj=7.6551E-2, p=0.001), cobbles (prop=6.9715E-2, R^2adj=0,11063, p=0.012) and boulders (prop=6.74E-2, R^2adj=0.14531, p=0.016), explaining 25% of the variation on the total composition. As for the troglobitic species, the variation was best explained in the model by boulders (prop=0.13592, R^2adj=9.8355E-2, p=0.001), cobbles (prop=8.2958E-2, R^2adj=0.14787, p=0.016) and lastly by guano (prop=6.4145E-2, R^2adj=0.1806, p=0,047), totalizing 28% of explanation power on the model.

DISCUSSION

The species richness and composition found in this study is expressive and unprecedented for Guatemala. Previous studies focused mostly on descriptions of new species and unfortunately did not show a broad spectrum of the Guatemalan invertebrate cave fauna (Barr 1973, Christiansen 1973, Gertsch 1973, Muchmore 1973, Conde 1975, Rowland & Reddell 1977, Schultz 1977, Platnick & Pass 1982, Muchmore 1988, Rodriguez and Hobbs Jr 1990, Reddell & Cokendolpher 2001, Espinasa & Zhuang 2009) with rare exceptions (Mitchell & Reddell 1973, Reddell 1981, Reddell & Veni 1996).

It was possible to observe that species composition varied among the three different locations sampled in this study, refuting the first hypothesis. It is generally expected for the cave invertebrate fauna from the same geological unit to be fairly similar, but the findings of this study show that this is not necessarily true for all environments. Here, it was found that the same geological units can have significantly different species composition, which in turn has a direct effect on the conservation of these species and habitats. Furthermore, the fauna from the different caves also showed high level of dissimilarities regardless of the geographic location. It is known that cave invertebrate communities (especially troglobites) show a high level of endemism. The fragmentation of the subterranean habitats fosters evolutionary drift in isolated populations. The long-term persistence and relative stability of subterranean environments compared to epigean ones allow this process to take place (Gibert & Dehraveng 2002).

Studies trying to elucidate the organic and inorganic substrate influence on cave invertebrate community structure are relatively scarce. Still, literature shows that the habitat heterogeneity and diversification increase species richness by allowing a decrease in ecological niche overlap (Poulson & Culver 1969, Ferreira & Souza-Silva 2001, Bento 2011, Simões et al. 2015, Oliveira 2014, Pellegrini et al. 2016, Gomes 2016, Resende & Bichuette 2016, Cardoso 2017, Cerqueira 2018).

The direct and significant relationship between the total species richness and composition with the organic features of the substrate (guano, twigs and roots) and water bodies highlights the importance of food resources, especially guano, for the structuring of the invertebrate cave communities. The presence of water bodies, although is not considered an organic feature itself, often represent an important organic input in the cave environment, especially if such water body has an allochtonous origin (Poulson & Lavoie 2001, Souza-Silva et al. 2011a, Simões et al. 2015).

Since most caves can be characterized as oligotrophic environments, the presence of organic resources often mean that these places have higher concentrations of invertebrate fauna. Several authors have already showed the importance of guano deposits and vegetal debris inside the cave environment. Beyond the habitat availability, they also act as food resource for the lower levels of the food web, allowing a greater species richness, especially in permanent dry caves (Decu 1986, Gnaspini-Neto 1989, Ferreira & Martins 1998, Ferreira & Martins 1999, Gnaspini & Trajano 2000, Ferreira et al. 2000, Ferreira et al 2007, Santana et al. 2010, Schneider et al. 2011, Gnaspini 2012, Pellegrini & Ferreira 2012, Pellegrini & Ferreira 2013, Jaffé et al. 2016).

The presence of guano tends to be of extreme importance in permanently dry caves (Ferreira et al. 2007). In this study, however, even though most of the caves have water bodies present, guano was still a strong structurer for the cave invertebrate community. Here, the presence of guano seems to be more important for the invertebrates than the presence organic matter (mostly vegetal debris) carried by the water. Still, most of the transects were positioned away from the water bodies and that might be the reason why the importance of presence of guano was intensified in our study.

Troglobitic species, on the other hand, seem to be structured differently within the caves, responding to different substrate features. For them, the presence of organic matter of any source does not seem to be one of the main drivers for species distribution in a cave. Instead, they seem to have a stronger response to places with a higher variety of abiotic microhabitats (cobbles and boulders) and a weaker response to the presence of guano. It is expected, therefore, to find a greater species richness and composition at more heterogenic habitats because they provide more space to shelter a larger number of species. According to Mammola et al. (2016) environments formed by the agglomeration of gravel comprise void spaces that can and provide terrestrial invertebrate species with microhabitats, food resources, protection and refuge.

More importantly, the presence of guano in abundance in a cave can eventually attract a huge diversity of invertebrates, most of them non-troglobites, can lead to the emergence and establishment of large populations on it. Perhaps the presence of these communities with significantly large populations and a high level of biological interactions on the guano are repelling some troglobitic species, which are often more sensitive.

The findings of this study highlight the importance of biological surveys for understanding the cave biodiversity and gives insights on how this biodiversity might be distributed on the landscape. Conservation actions have to be careful and well thought through, since caves in the same karstic units can have completely different faunas. Furthermore, it provides scientific biological background for the creation of new parameters for management and conservation of caves in Guatemala. It is highly advised that environmental laws are created in order to protect Guatemala's unique speleological patrimony.

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FIGURES

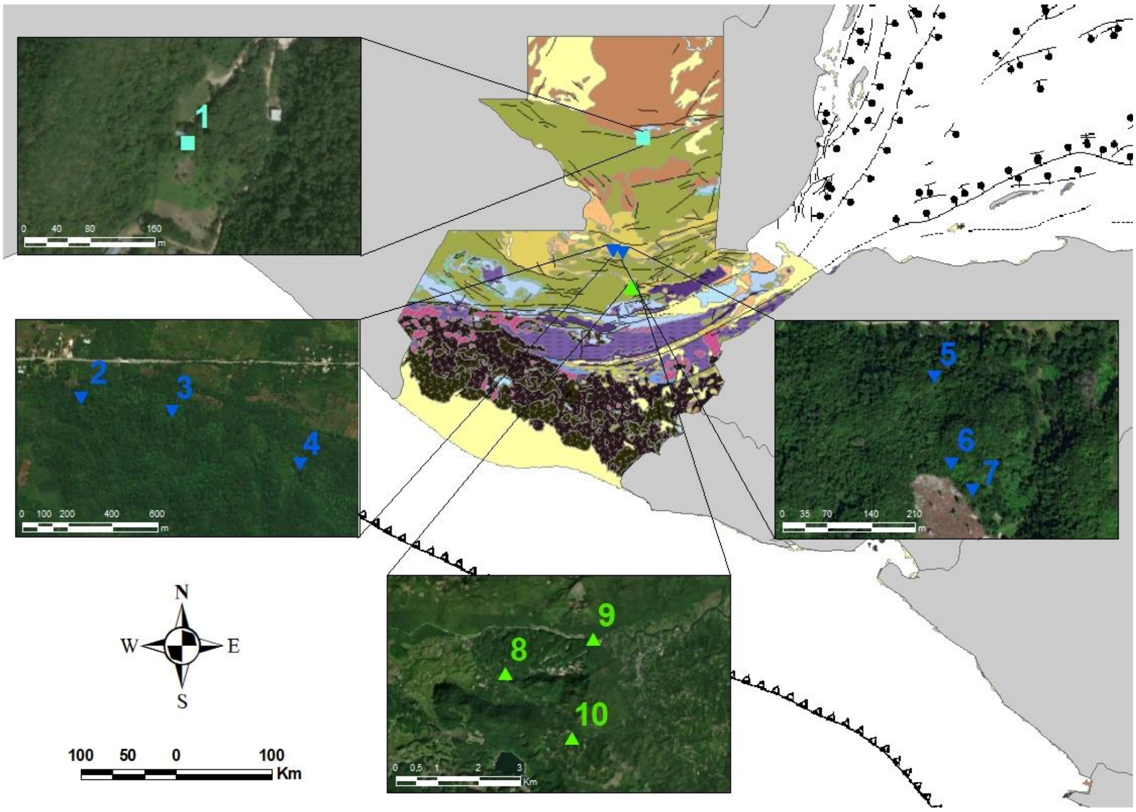

Figure 1 - Map of Guatemala, showing the location of the ten caves included in this study: (1) Cueva Aktun Kan; (2) Cúpula de los Murcielagos; (3) Cueva del Venado; (4) Ventanas de La Seguridád; (5) Cueva Blanca; (6) Cueva El Rostro; (7) Cueva de Arsilla; (8) Cueva Coral; (9) Gruta de Lanquín and (10) Cueva Chipix.

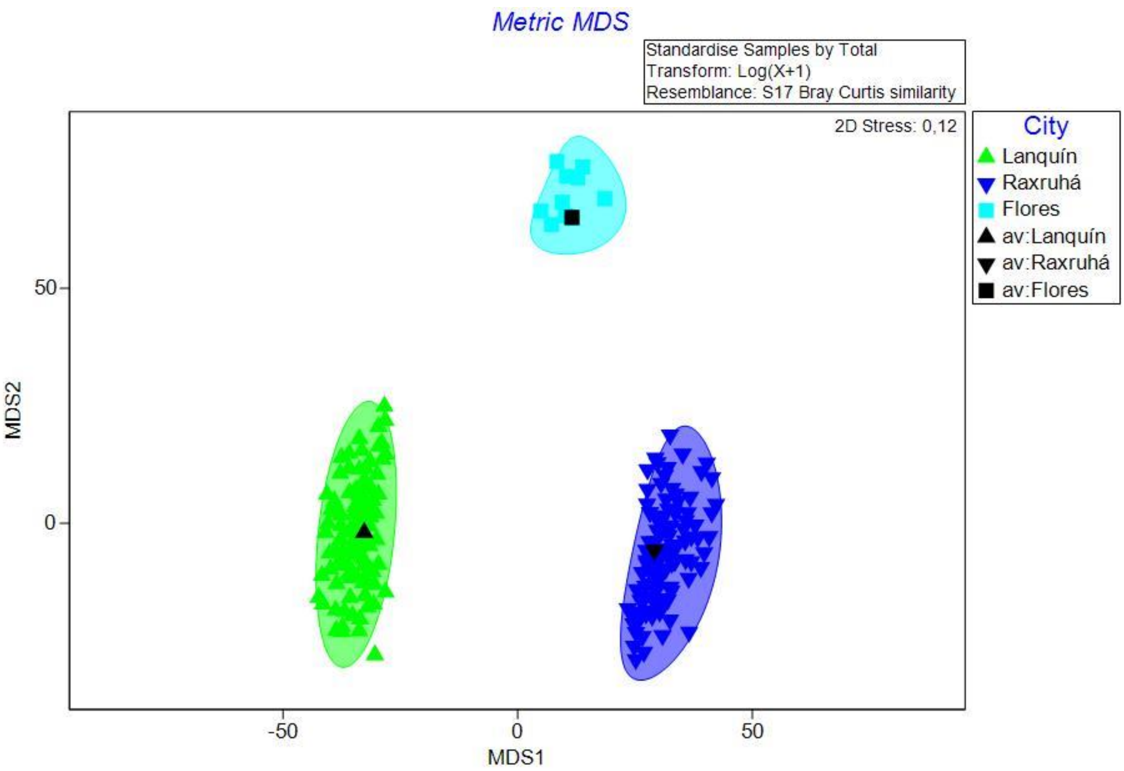

Figure 2 - MDS plot for total species composition

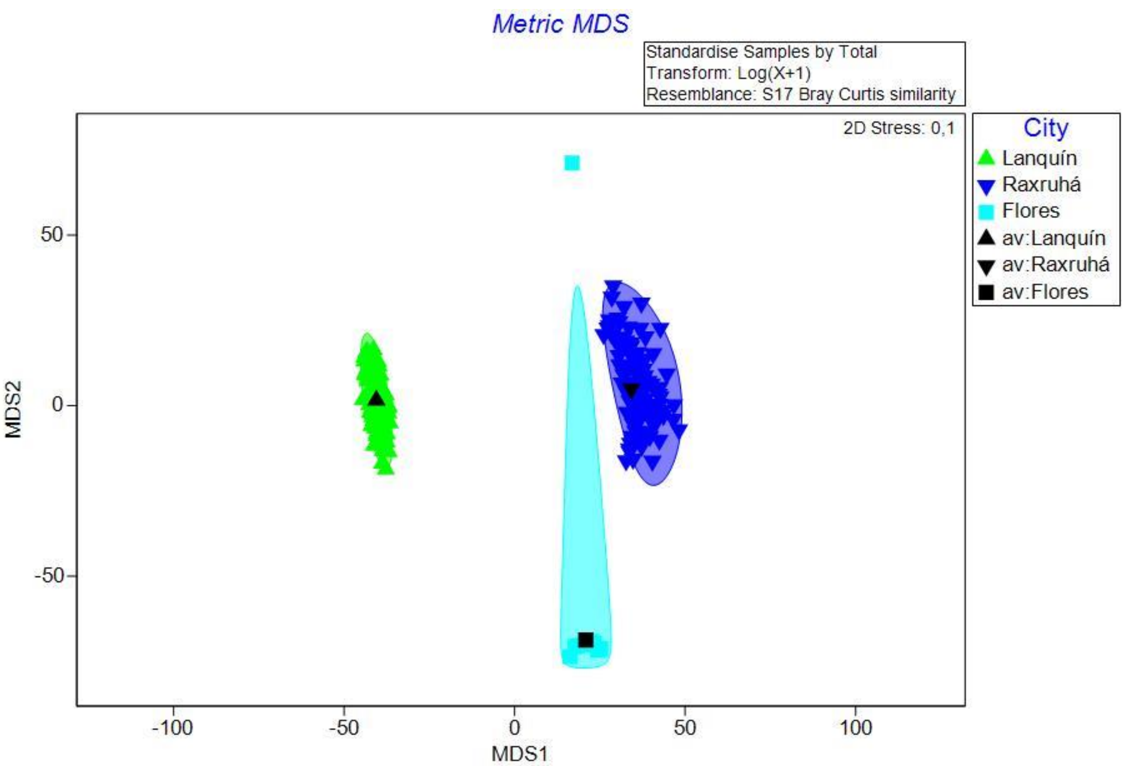

Figure 3 - MDS plot for troglobitic species composition

TABLES

Table 1 - Details of the caves included in this study. N=number of transects.

Cave	Department	Municipality	Coordinates	Altitude	N
Cueva Aktun Kan	Petén	Flores	16Q 191539/1871065	174	3
Cúpula de los Murcielagos	Alta Verapaz	Raxruhá	15P 801025/1758019	215	3
Cueva del Venado	Alta Verapaz	Raxruhá	15P 801412/1757969	218	3
Ventanas de Seguridád	Alta Verapaz	Raxruhá	15P 801964/1757753	220	2
Cueva Blanca	Alta Verapaz	Raxruhá	15P 811098/1756305	180	2
Cueva El Rostro	Alta Verapaz	Raxruhá	15P 811125/1756173	208	1
Cueva de Arsilla	Alta Verapaz	Raxruhá	15P 811159/1756134	187	1
Cueva Coral	Alta Verapaz	Lanquín	15P 820737/1723971	482	1
Gruta de Lanquín	Alta Verapaz	Lanquín	16P 179249/1724774	299	8
Cueva Chipix	Alta Verapaz	Lanquín	16P 178710/1722477	642	1

Table 2 – List of species found in the caves. Asterisks indicate troglobitic species. The letter c stands for caves and the letter t for transects (c1=Gruta de Lanquín; c2=Cueva Coral; c3=Cueva Chipix; c4=Cueva del Venado; c5=Cueva de Arsilla; c6=Cueva el Rostro; c7=Cueva Blanca; c8=Cueva Ventanas de Seguridad; c9=Cueva Cúpula de los Murciélagos; c10=Cueva Aktun Kan).

	c1t1	**c1t2**	**c1t3**	**c1t4**	**c1t5**	**c1t6**	**c1t7**	**c1t8**	**c2t1**	**c3t1**	**c4t1**	**c4t2**	**c4t3**	**c5t1**	**c6t1**	**c7t1**	**c7t2**	**c8t1**	**c8t2**	**c9t1**	**c9t2**	**c9t3**	**c10t1**	**c10t2**	**c10t3**
Arachnida																									
Amblypygi																									
Phrynidae																									
Paraphrynus emaciatus									3																
Paraphrynus williamsii	1	1		3		1	2	1		6		1		1	6		2			1			1		
Aranae																									
Actinopodidae																									
Actinopodidae sp1											0											2			
Corinnidae																									
Corinnidae sp1*																	1								
Ctenidae																									
Isoctenus sp1									3																
Ctenizidae																									
Ctenizidae sp1														3							2				
Ochyroceratidae																									
Ochyroceratidae sp1													2		11				10		5				
Ochyroceratidae sp2																2	14								
Oonopidae																									
Oonopidae sp1																		2							
Oonopidae sp2	2							4	1																
Oonopidae sp3									1	7	1	1	2						2				1		

Pholcidae																							
Pholcidae sp1	15								1			2	1			5	6	1	3	2	1		
Pholcidae sp2									3														
Pholcidae sp3																							2
Pholcidae sp4	2																						
Scicariidae																							
Loxosceles sp1	2								3														
Scytodidae																							
Scytodidae sp1	1																						
Symphytognatidae																							
Symphytognatidae sp1				6				1															
Tetragnathidae																							
Tetragnathidae sp1																		8					
Theridiidae																							
Theridiidae sp1		1	3	32	2	8	5			5													5
Theridiidae sp2																		4					
Ixodida																							
Argasidae																							
Argas (Ornithodoros) sp1																						2	
Mesostigmata																							
Mesostigmata sp1	6																						
Oplitidae																							
Oplitidae sp1	2		1	2																			
Opiliones																							
Opiliones sp1									1		2												
Gonyleptidae																							

Tricomatinae																								
Tricomatinae sp1					1																			
Samoidae																								
Samoidae sp1*											3									8		7		
Stygnopsidae																								
Stygnopsidae sp1																			10					
Oribatida																								
Oribatida sp1	1									1														
Palpigradi																								
Eukoenenidae																								
Eukoenenia sp1														1										
Parasitengona																								
Parasitengona sp1				2							2													
Pseudoscorpiones																								
Pseudoscorpiones sp1									2															
Pseudoscorpiones sp2											16													
Bochicidae																								
Mexobisium guatemalense	2				1	2		4	1															
Chernetidae																								
Chernetidae sp1							281																	
Cthoniidae																								
Cthoniidae sp1																			2					
Cthoniidae sp2*																				1	8	1		
Cthoniidae sp3*																								2
Cthoniidae sp4*								1																
Cthoniidae sp5											4		2	2										

Cthoniidae sp6														2										
Garipidae																								
Garipidae sp1									1															
Ricinulei																								
Ricinoididae																								
Pseudocellus cookei																							14	1
Sarcoptiformes																								
Acaridae																								
Acaridae sp1																							3	
Acaridae sp2																							1	
Acaridae sp3	1																							
Histiostomatidae																								
Histiostomatidae sp1																							2	
Lohmanidae																								
Lohmanidae sp1																							1	
Schizomida																								
Hubbardidae																								
Stenochrus portoricensis	1		2	3		1	10	10		7	4			2	8	3	3		10		1	2	65	
Trombidiformes																								
Erithracaridae																								
Erithracarus sp1																		2	1					
Rhagidiidae																								
Rhagidiidae sp1														3									1	
Trombiculidae																								
Trombiculidae sp1														2										
Uropodina																								

Uropodina sp1																						146				
Chilopoda																										
Geophilomorpha																										
Geophilomorpha sp1*	2																									
Geophilomorpha sp2										5			2	1	3			11	1		7					
Scutigenomorpha																										
Scutigenomorpha sp1				1			3		5																	
Crustacea																										
Decapoda																										
Pseudothelphusidae																										
Pseudothelphusa sp1									4																	
Isopoda																										
Armadillidae																										
Armadillidae sp1	86																									
Philosciidae																										
Philosciidae sp1*				1		1																				
Littorophiloscea denticulata																					5					
Platyarthridae																										
Trichorhina sp1	96		5	16	1	8	6	62	1		25			12					9			61				
Trichorhina sp2																						1010				
Styloniscidae																										
Styloniscidae sp1*										4																
Diplopoda																										
Polydesmida																										
Polydesmida sp1																			1							
Polydesmida sp2*																										2

Polydesmida sp3*																								4	3
Polydesmida sp4*											3	3										2			
Cryptodesmidae																									
Cryptodesmidae sp1																							15		
Paradoxosomatidae																									
Paradoxosomatidae sp1																							14		
Pyrgodesmidae																									
Pyrgodesmidae sp1*					2		1	3																	
Pyrgodesmidae sp2																							4		11
Pyrgodesmidae sp3													6												
Pyrgodesmidae sp4																				27		52			
Sphaeriodesmidae																									
Sphaeriodesmidae sp1											3	1													
Polyxenida																									
Hypogexenidae																									
Hypogexenidae sp1	3																								
Siphonophorida																									
Siphonophorida sp1																		1							
Spirobolida																									
Spirobolida sp1																							11		
Spirostreptida																									
Spirostreptida sp1	2				6		74																		
Spirostreptida sp2																							33		
Entognatha																									
Entomobryomorpha																									
Cyphoderidae																									

Cyphoderidae sp1																					5					
Entomobryidae																										
Entomobryidae sp1																			42	59	58	10				
Entomobryidae sp2*	1	1		1		46		317		36																
Entomobryidae sp3															7	4	8									
Entomobryidae sp4*																							336	16		7
Entomobryidae sp5*	81	91	152	1652	8	2	1642	467	3	17																
Entomobryidae sp6	22								56	2																
Entomobryidae sp7											18	5	6	21												
Entomobryidae sp8*															34		11									
Poduromorpha																										
Poduromorpha sp1	24		1																							
Poduromorpha sp2										1																
Poduromorpha sp3													1	1												
Symphipleona																										
Symphipleona sp1*																							800	2		1
Gastropoda																										
Pulmonata																										
Pulmonata sp1	2	13	4		1	1																				
Pulmonata sp2	1	5	6	2	3	2	12	3		1							5			6						
Pulmonata sp3																	7									
Pulmonata sp4																				11						
Insecta																										
Blattodea																										
Blattaria																										
Blattaria sp1										8																

Blaberidae																							
Blaberidae sp1							219																
Coleoptera																							
Larvae sp1							1																
Larvae sp2			1																				
Larvae sp3													1										
Larvae sp4															3						1		
Larvae sp5	1			2			1	3	2														
Adephaga																							
Carabidae																							
Carabidae sp1												2		2									
Carabidae sp2		2					2	1															
Carabidae sp3																				1			3
Carabidae sp4																							3
Carabidae sp5																							13
Polyphaga																							
Histeridae																							
Histeridae sp1	2																						
Histeridae sp2							2	2															
Leiodidae																							
Leiodidae sp1																			6				7
Leiodidae sp2		5	12	10		1	5	26															
Limnichidae																							
Limnichidae sp1										1													
Ptilidae																							
Ptilidae sp1										1													

Scarabeidae																										
Scarabeidae sp1										2																
Staphylinidae																										
Staphylinidae sp1	2	48	27	62			2	7	5	1					19					2						
Staphylinidae sp2			1							1											1					
Staphylinidae sp3															2											
Pselaphinae																										
Pselaphinae sp1										4																
Pselaphinae sp2														19					3		1					
Scydmaeninae																										
Scydmaeninae sp1							8		2	1																
Tenebrionidae																										
Tenebrionidae sp1*																							9			
Diplura																										
Campodeidae																										
Juxtlacampa sp1*						16		19	4	5																
Juxtlacampa sp2*													3		3	6	6	2								
Juxtlacampa sp3																							3			3
Diptera																										
Brachycera																										
Anthomyiidae																										
Anthomyiidae sp1			2	1	1	1		1																		
Calliphoridae																										
Calliphoridae sp1																						2				
Drosophillidae																										
Drosophillidae sp1															1											

Drosophillidae sp2	2																					
Drosophillidae sp3					22	9	8	2		2												
Milichiidae																						
Milichiidae sp1																						1
Phoridae																						
Phoridae sp1				1				2														
Phoridae sp2			1	1		1	3								1							
Nematocera																						
Cecidomyiidae																						
Cecidomyiidae sp1					1																	
Culicidae																						
Culicidae sp1													2									
Keroplatidae																						
Keroplatidae sp1											2				9							
Psychodidae																						
Phlebotominae																						
Phlebotominae sp1					1		1															
Phlebotominae sp2				2				1														
Sciaridae																						
Sciaridae sp1		6	6	4					1													
Sciaridae sp2		1	1										1									
Sciaridae sp3																2						
Tipulidae																						
Tipulidae sp1											1											
Hemiptera																						
Auchenorrhyncha																						

Auchenorrhyncha sp1											3												
Heteroptera																							
Cydnidae																							
Cydnidae sp1	2	4	2					1	3	1													201
Cydnidae sp2	1								1	1													21
Hebridae																							
Hebridae sp1											3												
Mesovellidae																							
Mesovellidae sp1										24													
Vellidae																							
Vellidae sp1										1													
Hymenoptera																							
Apocrita																							
Braconidae																							
Microgastrinae																							
Microgastrinae sp1	2		3		2	1	16	12															
Drynidae																							
Aphelopinae																							
Drynidae sp1																					5		
Eucoilidae																							
Eucoilidae sp1	1																						
Formicidae																							
Ectatomminae																							
Gnamptogenis sp1										11													
Formicinae																							
Brachymyrmex sp1																	50	18					

Myrmicinae																							
Crematogaster sp1														1									
Megaloyrmex sp1																				9			
Monomorium sp1				3																			
Octostruma sp1															2								
Ponerinae																							
Hypoponera sp1	11	3								1													62
Pachycondyla sp1				5																			
Scelionidae																							
Scelionidae sp1								1															
Lepidoptera																							
Noctuidae																							
Noctuidae sp1																							3
Tineidae																							
Tineidae sp1	13		7	5	1	7	4	3															
Tineidae sp2																			2				
Odonata																							
Coenagrionidae																							
Coenagrionidae sp1										4													
Orthoptera																							
Orthoptera sp1										1													
Phalangopsidae																							
Arachnopsita cavicola								4		17													
Arachnopsita sp. nov.											1	1	2		22	1	2				3		
Mayagryllus sp1		4	2	1	1		6		3														
Noctivox sp1																				1			

Psocoptera																									
Psocoptera sp1																					1				
Thysanoptera																									
Thysanoptera sp1														1											
Zygentoma																									
Nicoletiidae																									
Nicoletiidae sp1*					4		16																		
Nicoletiidae sp2*															1		2								
Nicoletiidae sp3																							1	2	
Oligochaeta																									
Clitelatta																									
Clitelatta sp1		3	1	4		1	6	1		1															
Clitelatta sp2			2					3																	
Clitelatta sp3														1											
Total Richness	33	15	22	23	19	17	26	29	22	32	18	8	12	17	16	8	13	8	13	14	13	13	31	5	7
Total Abundance	393	188	242	1820	60	108	2334	965	128	180	100	16	29	85	130	26	117	38	111	130	92	154	2791	26	91

Artigo 2 – O turismo influencia a estruturação das comunidades de invertebrados cavernícolas em uma caverna da América Central?

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Are there any impacts of tourism on the structure of cave invertebrate communities in a Central American cave?

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Abstract

Human beings inhabit caves since the prehistory for the most diverse reasons. In Central America, due to the Mayan culture, caves have always had a large role in religion and rituals, which persists to the present day. Currently, aside the religious use of the caves, there is a prominent and ever-growing tourism. Tourists are attracted to caves mostly for their scenic beauty and are often unaware of the impacts their presence may have on these sensitive ecosystems. It is known that tourism affects the cave’s physical environment in several ways, but it is yet uncertain how the presence of tourists affects the cave fauna. Therefore, this study comes with the objective to investigate the effects of the tourism activities on the cave invertebrate fauna from the Gruta de Lanquín (Alta Verapaz, Guatemala), and thus contribute for the management and conservation of the biospeleological patrimony of the country. Groups of six quadrats were placed at both the touristic and non-touristic areas of the cave, where invertebrates were collected and the substrate features were measured. Results showed that the fauna composition differed among the two areas. The beta partitioning and the substrate features indicated that the troglobitic species might be structured differently than the rest of the invertebrate community in this cave. Lastly, it was detected that the pathways designated for touristic use have different substrate features than their adjacent areas. It was recommended for the tour in this cave to always be guided so that the tourists do not wander around the designated pathways in order to maintain the conservation of the invertebrate species.

Keywords

cave, conservation, invertebrate, troglobitic, Guatemala

1. Introduction

Human presence in natural caves dates back from prehistory and continues to this day (Stone & Brady 2005). The motivation for this presence, however, have changed throughout the history. Shelters, rituals, burial, religion and tourism are among the human activities that have always had caves as scenery in many regions (Cigna 2012). Currently in central America, the prevailing uses in caves are religious and touristic.

Tourists are attracted to caves especially by their scenic beauty and are often oblivious to the kind of impact that their presence may represent in such ecosystems. Caves usually are environments with little or no contact with the surface, and can have its integrity easily changed when there is additional energy (e.g. extra organic supply) in the system (Poulson & White 1989, Cigna 2012). Therefore, such impacts range from physicochemical (i.e. blackening of the cave formations and changes in the environment conditions) to biological (i.e. stepping on invertebrates, introduction of exotic species). These characteristics, along with the fact that caves are confined spaces, makes them especially susceptible to anthropogenic impacts that will last longer than they would in a surface environment, some of them can even become permanent (Lobo 2006, Lobo et al 2013).

Studies regarding the impacts of tourism on cave invertebrates are quite rare all over the world (Gunn et al. 2000, Eberhard 2001, Moldovan et al. 2003, Ferreira et al. 2009, Souza-Silva & Ferreira 2009a, Whitten 2009, Bernardi et al. 2010, Pellegrini & Ferreira 2012, Faille et al. 2015). Rare exceptions occur in New Zealand, where many articles were published regarding the biology of glowworms (*Arachnocampa* spp.) for their tourism depend on the presence of those invertebrates (Pugsley 1984, Pavlovich 2001, Hall 2013, Merritt & Patterson 2018). Furthermore, studies about the effects of tourism in caves are mainly focused in the impacts on speleothems, microclimate, microbiota and tourist carrying capacity (Pulido-Bosch et al. 1997, Baker & Genty 1998, Song et al. 2000, de Freitas & Schmekal 2003, Cevernik 2006, Russel & MacLean 2008, Lobo & Moretti 2009, de Freitas 2010, Lobo & Zago 2010, Cigna 2012, Lobo et al. 2013). The importance of this study lies in its uniqueness, since this subject has been little explored worldwide and never in Guatemala.

Although caves are considered sacred by the Mayan culture, and thus, the population is quite familiar with caves, knowledge about the cave fauna of Guatemala is minimal when compared to other parts of the world. It is known that several caves in the country are highly exploited for uncontrolled tourism and that the legislation that regulates tourism (CONAP 2018) do not present any specific law about the tourism inside caves and/or about their protection (Decree 4-89 and Government Agreement No. 759-90).

Therefore, in order to investigate the effects of the touristic activity on the cave invertebrate fauna of the Gruta de Lanquín, three objectives were defined: *i)* Compare the total and troglobitic invertebrate community structure (species richness, species composition and beta diversity) in touristic and non-touristic areas of the cave; *ii)* Determine which substrate features dictate the total and troglobitic community structure patterns on both the touristic and non-touristic areas and *iii)* Access whether the path stepping from the tourism activities have influence on the global and troglobitic community structure only of the touristic portion of the cave.

2. Material and Methods

2.1 Study Area

Guatemala is a country that encompasses a high environmental heterogeneity within a relatively small geographic area (Strinati 1994), featuring from desert areas to mountain forests and low land tropical forests. With an Equatorial Monsoon climate (Kottek et al., 2006), the region of Alta Verapaz has an annual average of 3,000 to 4,000 mm of rain, concentrated in the period from May to November (Sapper 1902, Bonis 1967).

Karstic landscapes, specifically limestone, represent a large portion of the country, covering about one third of the national territory. They are divided into four main karstic areas, mostly on the northern and central portions of the country: Huehuetenango, Alta Verapaz, Izabal and Petén (Strinati, 1994). The development of the karst in those areas is remarkable, with abundance of large caves, sinkholes and other karst dissolution features (Reddell, 1981).

This study was conducted at the Grutas de Lanquín National Park, San Agustín de Lanquín, Alta Verapaz, Guatemala (Figure 1). Alta Verapaz represents one of the most important tourist destinations in the country. In 2017, for example, 134,820 foreign tourists were registered there, 45% of those had the intention of visiting caves in the area (INGUAT 2017). Comprising an area of 11 ha, the park was, along with 8 others, one of the first to be stablished in the country in 1955 (CONAP 2018). From the very beginning, the Grutas de Lanquín National Park receives a large number of visitors during the whole year (Dreux 1974, Dudeck 2000).

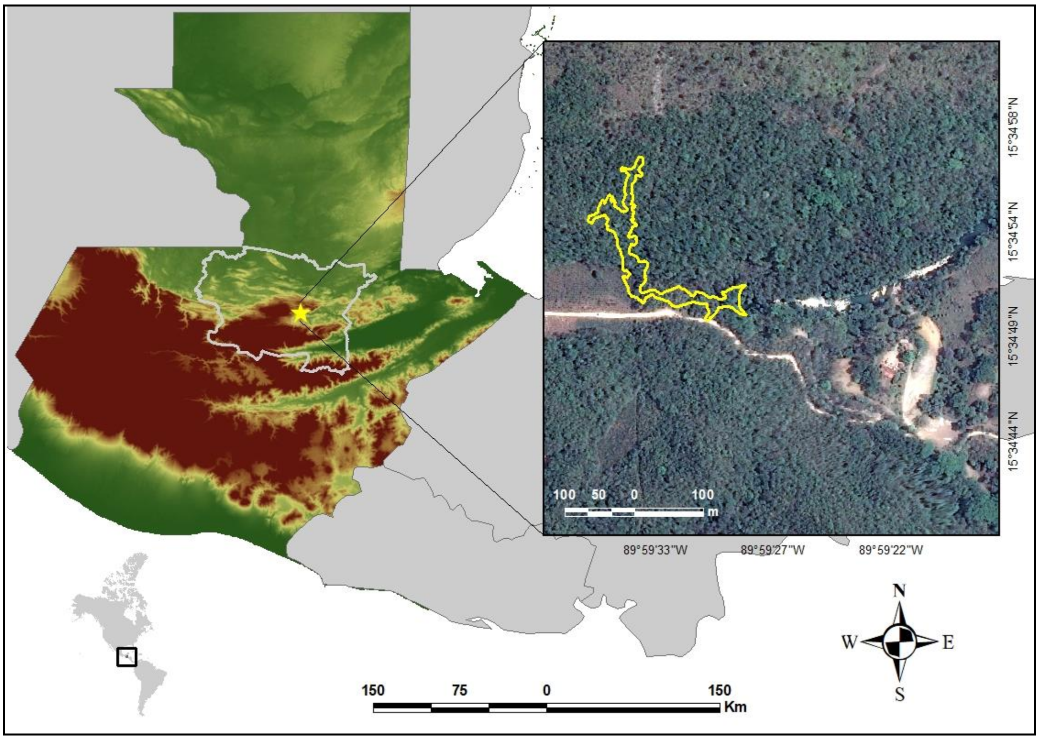

Figure 1 - Map of Guatemala, emphasizing outline of Gruta de Lanquín and the Grutas Lanquín National Park headquarters. The yellow dot shows the location of Gruta de Lanquín.

The cave has a mapped linear projection of approximately 800m (Dreux 1974), being approximately half of those acknowledged for touristic use. The other half of the mapped area, as well as the rest of the cave, estimated to be more than 2km long, receive few to none visitors (Dudeck 2000).

2.2 Data collection

All the data was collected in a single sampling event in June 2017. The invertebrate sampling was made manually, with the aid of tweezers and brushes (Souza-Silva et al 2011). The fauna was collected in quadrats that were placed inside transects, in both the touristic and non-touristic areas. Each area contained four transects and each transects contained six quadrats, totalizing eight transects and 48 quadrats (Figure 2). The transects were placed at least 50m from each other and the quadrats at least three meters from each other. In the touristic area, half of the quadrats were placed directly onto the touristic pathways. All the specimens were then preserved in vials containing 70% alcohol for further screening and identification under a stereomicroscope. The identification went through the highest taxonomic level possible and then, morphospecies were designated in order to obtain data on the communities' richness (Oliver & Beattie, 1996). Troglomorphic traits were identified based on criteria defined in descriptions of closely related species. Although troglomorphisms can be specific to each taxonomic group, some convergences are frequently observed, such as the absence of eyes, elongation of appendages, depigmentation, among others (Christiansen 1962; Barr 1968; Hoch and Ferreira 2012; Novak et al. 2012). For precaution, all species with troglomorphic traits were considered here as potentially troglobitic.

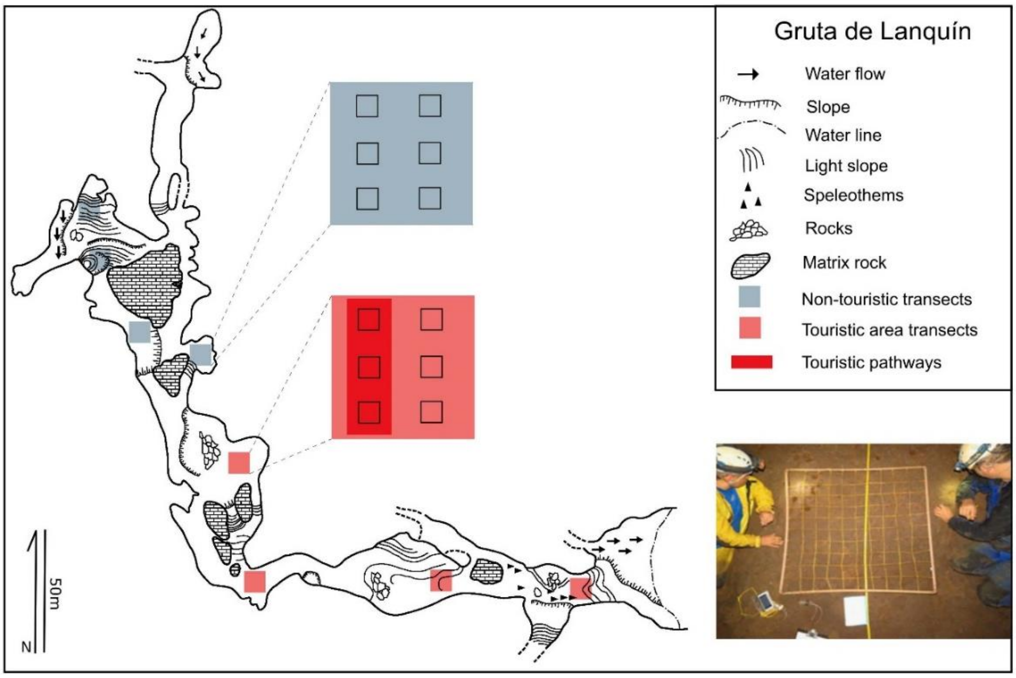

Figure 2 - Sketch of Gruta de Lanquín modified from Dreux (1974) showing the sampling design schematics. Detail: Researchers collecting invertebrates at a quadrat.

To measure the substrate features at the quadrats, a photograph was taken as close as possible to a 90º angle, at the researcher's chest high (Figure 2 - Detail). Afterwards, the substrate areas were measured at Zeiss ZEN 2.3 lite (blue edition) software.

2.3 Statistical analysis

2.3.1 The invertebrate community structure of the touristic and non-touristic areas of the cave

In order to compare the species richness from the touristic and non-touristic areas of the cave, a Generalized Linear Mixed Model (GLMM) was carried out in R software. The model was built with the species richness as the response variable, tourism as fixed predictor variable and transects as the random variable.

To access the differences in the community composition between the touristic and non-touristic areas, a Multidimensional Scaling (MDS) and a Permutational Analysis of Variance (PERMANOVA) were performed in PRIMER 6 & PERMANOVA+ software. After that, in order to find out which species were responsible for the changes observed in the species composition, a Similarity Percentages (SIMPER) analysis was also carried out in PRIMER 6 & PERMANOVA+ software.

Lastly, the Beta Diversity Partitioning (Baselga & Orme 2012) of the community was performed in R software. For this analysis, both the Bray Curtis (abundance) and the Jaccard (presence and absence) similarity indexes were considered.

Because troglobitic species may respond differently to availability of organic resources and habitat, this process was made for the total species richness and composition and then repeated, only considering the troglobitic species.

2.3.2 Substrate features and the community structure patterns

To access if the substrate features have influence on the invertebrates' species richness, a Generalized Linear Mixed Model (GLMM) was carried out in R software. To build the model, the substrate variables (guano, organic matter, puddle, fine gravel, cobble, boulder and matrix rock) had their areas standardized. The model then had the species richness as response variable, the substrate variables as fixed variables and transects as random factor.

A Distance-Based Linear Model (DistLM) was carried out in Primer 6+ software with the objective of determining which of the substrate variables (guano, organic matter, puddle, fine gravel, cobble, boulder and matrix rock) best explained the species composition on both the touristic and non-touristic areas.

This process was made with the total species richness and composition and then repeated, only considering the troglobitic species.

2.3.3 Soil compaction and its influence on the community structure of the touristic area of the cave.

In order to access the effects of the soil compaction from the intense stepping on the touristic pathways on the species richness, a GLMM was made in R software with the species richness as response variable, the stepping as fixed variable and transects as random variable.

Additionally, GLMMs were also made to test if the stepping had any effects on the environmental variables. For these, seven models were built, testing guano, organic matter, puddle, fine gravel, cobble, boulder and matrix rock as independent variables, stepping as fixed variable and transects as random variables.

A Permutational Analysis of Variances (PERMANOVA) was performed in Primer 6+ software to access if there were any differences in the species composition amongst the touristic pathways and their adjacent areas.

This process was also made with the total species richness and composition and then repeated, only considering the troglobitic species.

3. Results

A total of 5,618 invertebrates were accounted in Gruta de Lanquín. They belong to 28 orders and 42 families, distributed in 66 species (Figure 4 and supplementary material). From this total, eight species were considered troglobitic. The most representative orders were Diptera (nine species), Coleoptera (eight species) and Araneae (seven species). As for the troglobitic fauna, there were two species of Collembola (Entomobryidae), two species of Polydesmida (one unidentified and one Pyrgodesmidae), one Isopoda (Phyloscidae), one Thysanura (Nicoletiidae – *Anelpistina* sp.n, Figure 3A), one Dipluran (Campodeidae – *Juxtlacampa* sp.n, Figure 3C) and one Pseudorscorpion (Ideoroncidae - *Typhloroncus guatemalensis*, Figure 3D).

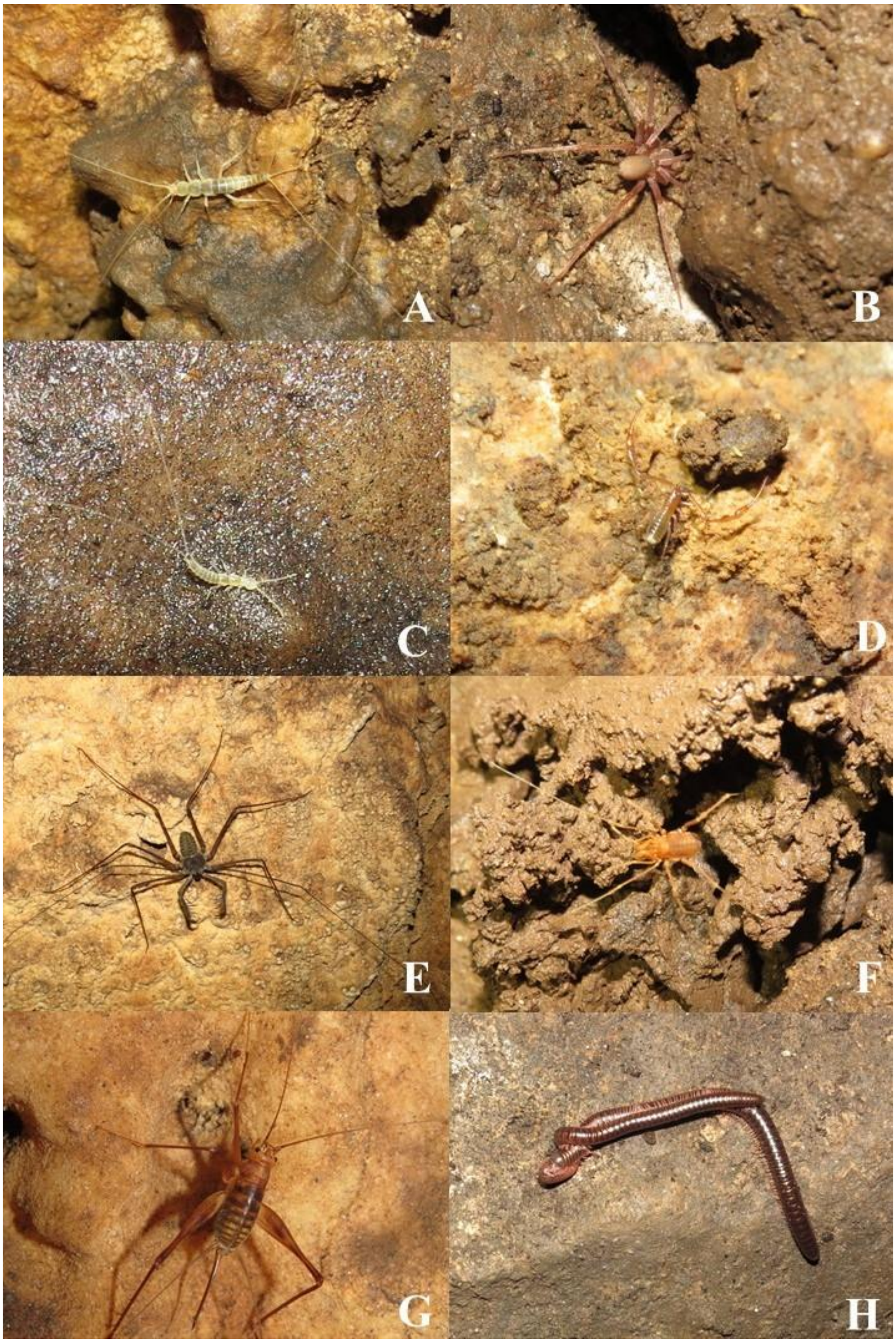

Figure 3 - Specimens of the fauna from Gruta de Lanquín: (A) *Anelpistina* sp. (Zygentoma: Nicoletiidae); (B) Troglobitic spider (not collected); (C) *Juxtlacampa* sp. (Diplura: Campodeidae); (D) *Typhloroncus guatemalensis* (Pseudoscorpiones: Ideoroncidae); (E) *Paraphrynus williamsii* (Amblypygi: Phrynidae); (F) Stygnopsidae sp. (Opiliones – not in the quadrats); (G) *Arachnopsita* sp. (Orthoptera: Phalangopsidae) and (H) Spirostreptida sp (Diplopoda).

3.1 Overview of impacts observed in the cave

General impacts observed in the cave during the sampling event include non-functional electrical installations, graffiti, litter and blackening of speleothems due to the former use of carbide lamps and the current use of tallow candles for lighting (Figure 4).

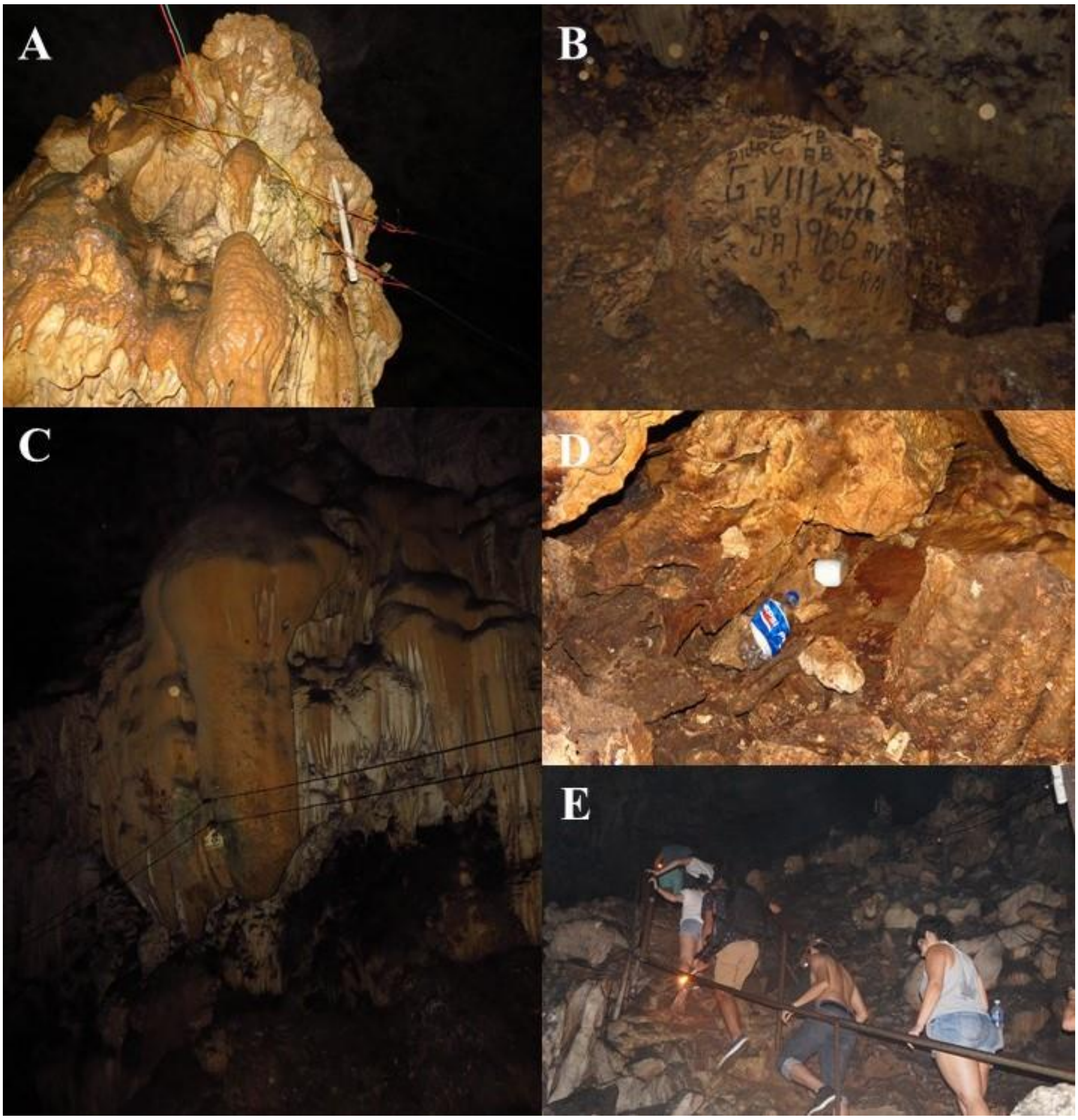

Figure 4 - Visual impacts in Gruta de Lanquín: (A) Electrical installation for artificial lighting; (B) Graffiti from the year of 1966; (C) Electrical installation and blackened speleothems; (D) Litter left by tourists and (E) Tourists in the cave with tallow candles.

3.2 The invertebrate community structure of the touristic and non-touristic areas of the cave

The species richness showed no statistically significant differences between the areas, both when considering the total species richness (p=0.491) and the troglobitic species richness (p=0.13377).

On the other hand, species composition differed both for total species richness (p= 0.002, figure 5A) and troglobitic species richness (p=0.002, figure 5B). Some species contributed more than others for those dissimilarities between the two areas of the cave, specially the two troglobitic species of Entomobryidae springtails, that accounted for 59.7% of the dissimilarities when considering all the species and for 94.07% of the dissimilarities when considering only the troglobitic ones (Table 1).

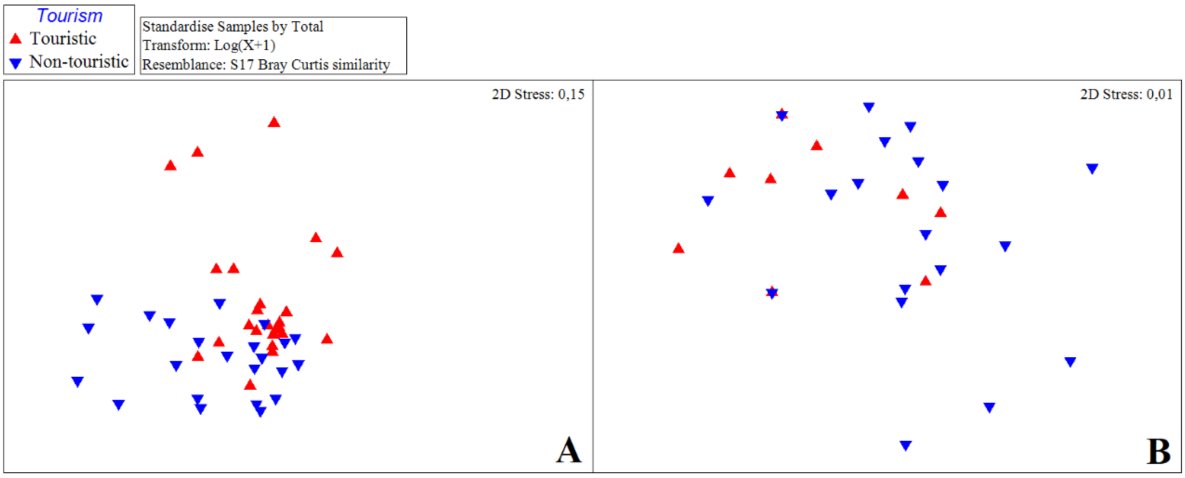

Figure 5 - Differences in species composition between the touristic (red triangles) and non-touristic (blue triangles) areas of the cave. Graph A represents the total species composition and graph B represents the troglobitic species composition.

The Beta Diversity Partitioning analysis showed a predominance of species turnover (94,28%) for total species, while the troglobitic species sustain a value of 100% nestedness.

Table 1 – Results from SIMPER analysis, showing the average abundances of each species that contributed to the model on the touristic and non-touristic areas; the averaged dissimilarities between the areas; dissimilarities standard deviation; species contribution percentage for the model and cumulative percentual contribution for the model.

	Touristic Av.Abund	**Non-touristic Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Total						
Entomobryidae sp2*	48.75	142.75	45.35	1.44	53.21	53.21
Entomobryidae sp1*	0.17	2.67	5.54	0.49	6.49	59.7
Armadillidae sp1	1.83	0	2.94	0.32	3.44	63.15
Staphylinidae sp1	2.67	0.42	2.89	0.44	3.39	66.54
Trichorhina biocellata	2.29	1.08	2.57	0.38	3.02	69.55
Leiodidae sp1	0.71	1.58	2.15	0.57	2.53	72.08
Larvae sp4 (Diptera)	3.42	0	1.9	0.25	2.23	74.31
Microgastrinae sp1	0.08	1.08	1.7	0.54	1.99	76.3
Pulmonata sp2	0.58	0.58	1.45	0.54	1.71	78.01
Juxtlacampa sp1*	0.08	0.46	1.23	0.3	1.44	79.45
Drosophillidae sp1	0	0.54	1.21	0.27	1.42	80.87
Spirostreptida sp1	0.13	1.04	1.08	0.28	1.27	82.14
Entomobryidae sp3	2.54	0	1.02	0.27	1.19	83.33
Pulmonata sp1	0.83	0.04	1.02	0.48	1.19	84.53
Blaberidae sp1	0	2.42	0.89	0.32	1.05	85.57
Tineidae sp1	1.38	0.21	0.83	0.34	0.97	86.55
Uropodina sp1	2.25	0	0.75	0.2	0.88	87.43
Sciaridae sp1	0.54	0	0.74	0.43	0.87	88.3
Poduromorpha sp1	0.88	0	0.72	0.26	0.84	89.14
Pyrgodesmidae sp1*	0	0.38	0.67	0.3	0.79	89.93
Stenochrus portoricensis	0	0.63	0.58	0.37	0.68	90.61
Troglobitic						
Entomobryidae sp2*	55.71	142.75	63.49	2.13	83.07	83.07
Entomobryidae sp1*	0.19	2.67	8.41	0.53	11	94.07

3.2 Substrate features and the community structure patterns

No substrate features had statistically significant influence on the total species richness.The troglobitic species richness, in the other hand, responded mainly to the presence of boulders (p=0.0023).

Total species composition responded (although with low power of explanation) mainly to the presence of fine gravel (prop= 6.6297E-2, R^2adj=4.5999E-2, p=0.002), water puddles (prop=5.4072E-2, R^2adj=8.1273E-2, p=0.011) and boulders (prop=4.3999E-2, R^2adj=0.10739, p= 0.019). Troglobitic species composition responded to the presence of water puddles (prop=0.17187, R^2adj=0.15261, p=0.008) and matrix rock (prop=0.13585, R^2adj=0.27476, p=0.003).

3.3 Soil compaction and its influence on the community structure of the touristic area of the cave.

The tourist stepping activity had no significative effects on the species richness in the touristic area (total p=0.244, troglobitic p=0.161). Although our analysis was not able to detect differences on the species richness due the stepping activity, they showed that this activity affected the cave environment, more specifically the presence of guano ($p<0.001$), fine gravel ($p<0.001$), cobble (p=0.0336) and boulders ($p<0.0001$) in this part of the cave.

Finally, there were no statistically significative differences between the community composition of the touristic pathways and their adjacent areas (global p=0.401, troglobitic p=0.538).

4. Discussion

Results showed that the community structure differed significantly between the touristic and non-touristic areas. Among the species responsible for the differences in the community composition, the two troglobitic Entomobryid species stood out and explained 59.7% of the variation for the total species composition and 94.07% for the troglobitic species composition. That was probably due to their unique high abundances at the non-touristic area (see supplementary material and Table 1).

The Beta Diversity pattern observed for the species composition in this study is noteworthy. When observing the invertebrate community as a whole, turnover stands out explaining 94.28% of the differences in species composition. This high turnover is likely due to the presence of an important bat colony on the non-touristic area of the cave, meaning that large amounts of guano are deposited there every day, changing the environmental conditions and concentrating one of the main sources of the organic inputs of the cave (Souza-Silva 2003, Ferreira 2005, Souza-Silva et al. 2008, Kuns et al. 2011, Gnaspini 2012) in this area. Furthermore, it is known that bat guano in caves tend have a very specific associated fauna (Ferreira & Martins 1998, Ferreira et al. 2000, Gnaspini & Trajano 2000, Ferreira et al. 2007, Gnaspini 2012) which is supported by the large presence of some species in this part of the cave, such as the Entomobryid collembolans, Chernetid pseudoscorpions, Drosophilid flies, *Stenochrus portoricensis* schizomids, Tineid moths, Phalangopsid crickets and Blaberid cockroaches.

The presence of large bat colonies only on the non-touristic area may eventually indicate an indirect influence of tourism, as bats may be being scared away by the presence of tourists in the touristic area, a behavior already registered before in several different contexts (Mann et al. 2012, Cardiff et al. 2012, Paksuz & Özkan 2012, Furey & Racey 2016). However, the touristic area of the cave currently has more hydric activity than the non-touristic area, with countless active speleothems dripping constantly, which might also contribute for the changes in the habitat and therefore for the differences in the fauna observed between these areas.

The 100% nestedness from the troglobitic species shows, in the other hand, that the troglobitic fauna from the touristic part of the cave is a subset of the one from the non-touristic part of the cave (Wright & Reeves 1992, Baselga 2010) (supplementary material). These results indicate that the total richness and troglobitic invertebrate species richness might be structured differently in this cave, which in turn reflects on different possible conservation outcomes.

In this study, areas with the presence of fine gravel, water puddles and boulders showed to be an important predictor for total species richness and composition, while the presence of boulders, water puddles and matrix rock were the important predictors for troglobitic species richness and composition. It is known that the subterranean fauna has preferential microhabitats to live in, like guano and organic matter deposits, areas with high humidity and under rocks (Culver & Pipan 2009, Moseley 2009, Souza-Silva & Ferreira 2009b, Mammola et al. 2016). Therefore, in order to combine the activities of tourism with the preservation of these hypogean environments, when making a management plan, one should be aware of such cave micro-habitats, since those are more prone to shelter the cave invertebrate fauna, including some specific, more specialized types of invertebrates (Ferreira & Martins 1998, Gnaspini & Trajano 2000, Ferreira 2008, Pellegrini & Ferreira 2012, Sánchez-Fernandez et al. 2018).

Although there are several visual impacts in the cave, the tourists seem to respect the designated pathways, which is essential for preserving and maintaining the conditions for the fauna to prosper. This is especially important given that this study showed that the substrate on the touristic pathways (more specifically the presence of guano, fine gravel, cobble and boulders) is significantly different when compared to their adjacent areas. According to Ferreira and collaborators (2009) and Pellegrini and Ferreira (2012), the establishment of well-defined touristic routes and pathways is a priority when setting a management plan for any subterranean habitats that takes into consideration the subterranean fauna.

Following the management plan proposed by Pellegrini and Ferreira (2012), pathways should be stablished in places where there is low incidence of troglobitic and possibly pathogenic organisms. Furthermore, the installation of footbridges in places where the natural substrate of the cave is used as pathways is highly recommended for this cave. These footbridges prevent the direct contact of the tourists with the cave soil, thus minimizing the direct impacts on the invertebrates and on the compaction of the cave substrate.

Since the are no trustworthy studies or records about the fauna of Gruta de Lanquín before the implementation of tourism, we will never know if the conditions currently exhibited in this cave is anywhere close to the pristine conditions of when it was first discovered. Similarly to what was stated by Pellegrini and Ferreira (2012), there is no way to assume how this community have behaved throughout the years and neither the extent of the impacts from the touristic activities. Although touristic activities can be really harmful for terrestrial invertebrate communities inside caves, Faille and collaborators (2015) showed that this is not a rule that apply for every cave.

Notwithstanding, when preserving a cave where biospeleological studies are still not sufficient, the precaution principle should always be used (Lobo et al. 2013). Regarding the invertebrate fauna, this principle would apply to the preservation of the well stablished path for tourists for most part of the touristic area of the cave, with a few dispersion points. This path should, as far as possible, avoid places with the presence of guano deposits and other organic matter patches, as well as places with significantly high humidity. For these reasons, it is recommended for the tour to Gruta de Lanquín to be always supervised by a guide to control where the tourists go and for how long they remain inside the cave. Some authors defend a daily limit in the number of visitors in order to avoid permanent damages to the cave environment (Cigna, 2012), but a deeper and more complete study is still recommended. According to the methodology proposed by Lobo and collaborators (2013), the speleology, geology, archaeology and microclimate features of the cave should also be investigated in order to elucidate the ideal number of tourists to visit the Gruta de Lanquín per day, as well as the number of tourists per group.

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Supplementary Material

Table 2 - List of species collected in Gruta de Lanquín, asterisks show the species that were considered troglobitic. The letter T indicates the transects.

Taxa	Touristic				Non-touristic				Species abundance
	T1	T2	T3	T4	T5	T6	T7	T8	
Arachnida									
Amblypygi									
Phynidae									
Paraprhynus williamsii	1		1	4					6
Aranae									
Dictynidae									
Dictynidae sp1	8								8
Oonopidae									
Oonopidae sp1	4							3	7
Oonopidae sp2				1					1
Pholcidae									
Pholcidae sp1	2				1		1		4
Scytodidae									
Scytodidae sp1	1								1
Symphytognatidae									
Symphytognatidae sp1					1			2	3
Theridiidae									
Theridiidae sp1					3	1		1	5
Mesostigmata									
Mesostigmata sp1	6								6
Oplitidae									

Oplitidae sp1	11	2				9	22
Opiliones							
Gonileptidae							
Tricomatinae							
Tricomatinae sp1			1				1
Oribatida							
Oribatida sp1	1						1
Pseudoscorpiones							
Bochicidae							
Mexobisium guatemalense		1	1		1		3
Chernetidae							
Chernetidae sp1					13		13
Chthoniidae							
Chthoniidae sp1*						1	1
Sarcoptiformes							
Acaridae							
Acaridae sp1	3						3
Schizomida							
Hubbardidae							
Stenochrus portoricensis			2	1	7	5	15
Uropodina							
Uropodina sp1	54						54
Chilopoda							
Geophilomorpha							
Geophilomorpha sp1	1						1
Scutigenomorpha							

Scutigenomorpha sp1			1			1			2
Crustacea									
Isopoda									
Armadillidae									
Armadillidae sp1	44								44
Philoscidae									
Philoscidae sp1*					1				1
Platyarthridae									
Trichorhina biocellata	52		3		1	4	9	12	81
Diplopoda									
Polydesmida									
Polydesmida sp1*			1	2			1		4
Pyrgodesmidae									
Pyrgodesmidae sp1*					4	4	1		9
Polyxenida									
Hypogexenidae									
Hypogexenidae sp1	3								3
Spirostreptida									
Spirostreptida sp1	1		2		1		24		28
Entognatha									
Entomobryomorpha									
Entomobryidae									
Entomobryidae sp1*	1	2	1		3	53		8	68
Entomobryidae sp2*	68	70	288	744	19	2	2742	663	4596
Entomobryidae sp3	61								61
Poduromorpha									

Poduromorpha sp1	21								21
Gastropoda									
Pulmonata									
Pulmonata sp1	3	6	1	10		1			21
Pulmonata sp2	1	1	6	6	3	1	5	5	28
Pulmonata sp3		1	1			1			3
Insecta									
Blattodea									
Blattaria									
Blaberidae									
Blaberidae sp1							58		58
Coleoptera									
Larvae sp1	22						1		23
Larvae sp2							1		1
Larvae sp3	4						1	1	6
Polyphaga									
Histeridae									
Histeridae sp1	1								1
Histeridae sp2								2	2
Leiodidae									
Leiodidae sp1		3	8	6		1	4	33	55
Staphylinidae									
Staphylinidae sp1	1	24		39		1	1	8	74
Scydmaeninae									
Scydmaeninae sp1					1		5		6
Diplura									

Campodeidae									
Juxtlacampa sp1*		1	1			6		5	13
Diptera									
Brachycera									
Anthomyiidae									
Anthomyiidae sp1				1		1		1	3
Drosophillidae									
Larvae sp4	81			1					82
Drosophillidae sp1					10	2		1	13
Phoridae									
Phoridae sp1	1		2	1					4
Streblidae									
Streblidae sp1					1				1
Nematocera									
Cecidomyiidae									
Cecidomyiidae sp1							1		1
Psychodidae									
Phlebotominae									
Larvae sp5		1							1
Sciaridae									
Sciaridae sp1	6	3	2	2					13
Larvae sp6	4	1							5
Hemiptera									
Heteroptera									
Cydnidae									
Cydnidae sp1	5	2	2	1				1	11

Cydnidae sp2	1								1
Hymenoptera									
Apocrita									
Braconidae									
Microgastrinae									
Microgastrinae sp1	1		1		7	1	12	6	28
Eucoilidae									
Eucoilidae sp1	1								1
Formicidae									
Formicinae									
Monomorium sp1				2					2
Ponerinae									
Hypoponera sp1	8	3							11
Scelionidae									
Scelionidae sp1								1	1
Lepidoptera									
Tineidae									
Tineidae sp1	33				1	1	2	1	38
Orthoptera									
Phalangopsidae									
Mayagryllus sp1				1	2	1	1		5
Zygentoma									
Nicoletiidae									
Nicoletiidae sp1*						1	23		24
Oligochaeta									
Clitelatta									

Clitelatta sp1		1		2		1	1	1	6
Clitelatta sp2								2	2
Clitelatta sp3	1								1
Richness by Transect	36	14	16	18	19	20	23	23	66
Abundance by Transect	517	119	321	826	63	85	2915	772	5618