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Trophic Dynamics in a Neotropical Limestone Cave

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ABSTRACT
The temporal budgets of the input, retainment and use by invertebrates of detritus and root tufts were evaluated in a short tropical limestone cave (337 m long). Detritus penetrate only through the stream in lower quantities in the dry season, contrary to what happens in the rainy season. However, water transport energies in the rainy season prevent detritus retainment. Roots tufts that emerge from the bottom of the stream provide shelter and food for several species. The abundance (log_{10}) ($R^2 = 0.63$; $P < 0.02$) and richness (log_{10}) ($R^2 = 0.63$; $P < 0.01$) related positively with the root tuft biomass (log_{10}). In the terrestrial environment (ground), guano is the main secondary resource available for the invertebrates; the constant production of this resource has shown to influence the structure and distribution of invertebrates. Unfavorable temperature conditions and, especially low soil moisture, promote low plant detritus consumption rates. Historically, different authors assumed that organic resources imported by water are more available in caves in rainy seasons. It is clear that the importation of organic detritus in the rainy season is higher than in the dry season, but as shown in this work, the stochastic pulse flows continually disturb and remove the previously accumulated resource. So, the food that is truly used by the cave communities is that transported at the end of the rainy season (and during all the dry season) that becomes available for the cave fauna. The cave functionality depends, so, directly of the epigean food resources.

Key words: cave, invertebrates, organic matter, resource availability, trophic budgets

INTRODUCTION

Caves are underground environments in which the absence of light impedes the presence of photoautotrophic organisms and determines a dependence on different allochthonous organic matter transfer processes for the biota maintenance (Simon et al. 2007). The primary autochthonous production rarely occurs, mainly through chemoautotrophic bacteria (Sarbu et al. 1996, Chivian et al. 2008).

The allochthonous organic matter penetrates in the caves carried by rivers, runoffs and water that percolates from the roof or wall, through openings or fractures (Simon et al. 2003). The biological transport is made mainly through root growth, animals that transit at the caves or even by the animals that randomly enter there (Howarth 1983, Jasinska et al. 1996, Ferreira and Martins 1998).

Underground ecosystems with streams connected to the surface, receive organic matter from upstream, which is transformed, retained and exported downstream. The water that serves as means of transportation, acts on the movement of large amounts of organic matter (Gibert et al. 1994, Webster et al. 1999, Simon and Bienfield 2001).

The most appropriate method for the study of the flow of organic matter in the underground environments is that which includes food resources relevant to the biota maintenance and in which the balance between the input and output of energy can be quantified (Simon et al. 2007). However, studies that relate the balance between the availability and processing of food resources in caves are still scarce (Gibert 1986, Jasinska et al. 1996, Graening and Brown 2003, Simon and Benfield 2002 and 2003, Simon et al. 2007, Souza-Silva et al. 2007). Such studies, however, are crucial for the understanding of the trophic dynamics and their influence on the maintenance of the underground diversity. The movement of resources among habitats can increase the productivity in locals poor in resources and influence the structure and stability of food networks (Huxel and McCann 1998).

Most works concerning the trophic dynamics in caves have focused on Chemoautotrophically based cave ecosystems (Sarbu et al. 1996, Chivian et al. 2008). Furthermore, recent studies are using stable isotopes to determine different energy fluxes in cave environments (Simon et al. 2003). However, it is important to understand the coarse particulate organic matter dynamics in a cave, since these dynamics determine all its systemic functionality.

With the intention of contributing to a better understanding of the trophic dynamics in underground envi-

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ronments, the present study had as a general objective, to understand the balance among the import, consumption and retainment rates of food resources in a limestone cave, based on the following questions: (1) what are the coarse particulate organic matter importation, retainment and consumption and root primary production rates in a short subterranean stream, (2) what are the secondary production rates in a short cave system, (3) What are the ecological relationships of the root biomass and the structure of the associated aquatic macrofauna (4) What are the associated mesofauna in terrestrial and aquatic detritus in a short cave system?

METHODS

Study area

This study was carried out in a limestone cave, "Lapa do Córrego dos Porcos" (LCP) located in Damianópolis, Goiás, Brazil (14º33"S 46º10"W) from August, 2001 to July, 2002. The vegetation surrounding the cave is "*cerrado*" a tropical savannah (Rizzini 1996). The dry season occurs from April to September (up to 50 mm) and the rainy season, from October to March, with up to 100 mm of rain (INMET 2003, Fig. 5).

The cave possesses 337m of horizontal projection and the main conduit has a small stream. There are six openings to the epigean environment: entrances 1 and 2, accessed through the perennial stream; entrances 3 and 4 only receive pluvial water contribution and entrances 5 and 6, situated on the higher slope of the emerging limestone ridge, do not receive any pluvial water contribution (Fig. 1).

The stream water originates from an epigean swamp and continues 100m in a small depression surrounded by riparian vegetation up to the entrance of the cave. At the end of the depression, water flows through limestone blocks and reaches the main cave conduit.

Procedures

The environmental variables in the terrestrial environment (temperature and air humidity) and in the stream (pH, current speed and flow) were measured bimonthly in different parts of the cave.

The primary production in the cave was estimated through the quantification of the of the root growth of the external vegetation in the hypogean stream. The roots were completely sectioned, conditioned in plastic bags, dried (100ºC/48 h) and weighed. Bimonthly, the roots that had grown at each point were collected again, dried and weighed. Such procedure supplied temporal variations in the primary production measure through the root growth. Once the natural growth of the roots is strongly altered by the cutting, which is a totally non-natural process, our data represents an estimate of the root growth capacity (Kuroha and Satoh 2007).

The secondary production was evaluated bimonthly through the collection, drying and weighting of all the bat guano present in the terrestrial environment of the cave (100ºC/48 h). The material was collected in the deposits (in the case of the aggregated bat colonies) or was obtained through sweeping of the cave floor.

To quantify the detritus transported to the cave, three contention nets were installed (PVC, 0.65 cm^2 mesh) covering the whole transverse extension of three stations in the hypogean stream (Fig.1). Net 1 (75cm x 176cm), located 30 meters downstream from the sinkhole, withheld the detritus coming from the entrances 1 and 2 of the cave. Net 2 (79cm x 140cm) was installed 20 me-

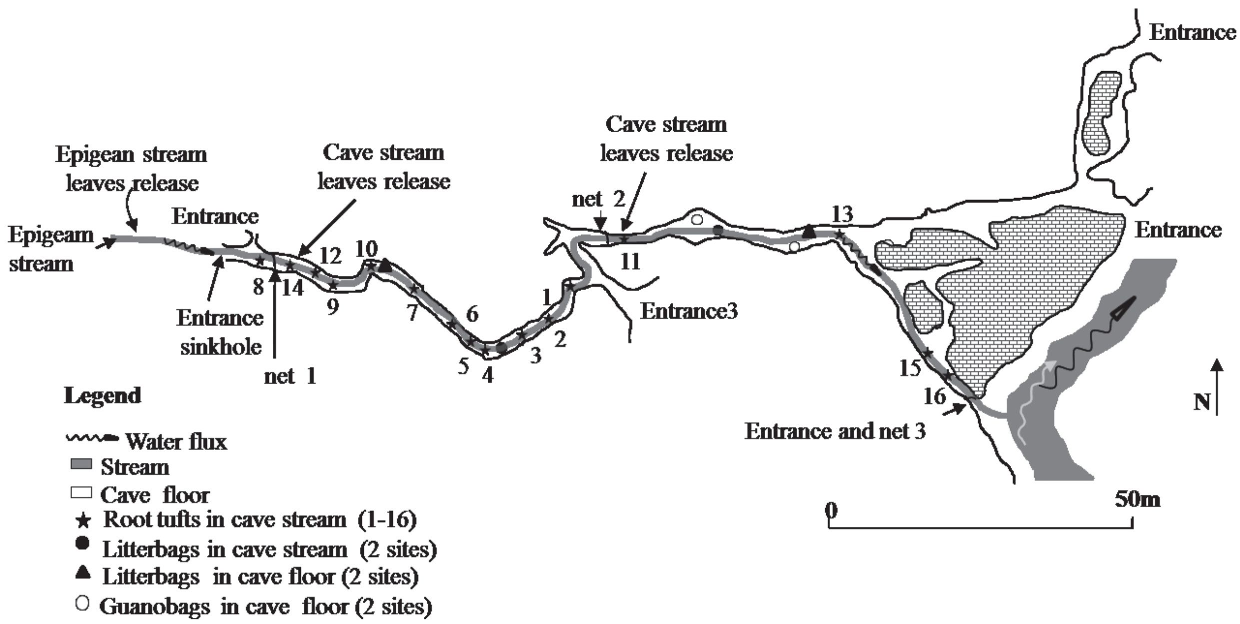

Fig 1 - Schematic map of "Lapa do Córrego dos Porcos" cave (LCP). Topography by Emilio Manoel Calvo, Jóse Augusto O. Motta and Gerson B. Soares from IBAMA-CECAV.

ters downstream from entrance 3. Net 3 (82cm x 180cm) was installed 30 meters upstream from entrance 4 (resurgence), with the purpose of capturing detritus exported from the cavity. All retained detritus was removed bimonthly, dried and weighed (100ºC/48 h). Furthermore, the separation of the material into leaves, seeds, fruits, roots, trunks and animal carcass fragment categories was conducted. Since the detritus retained in the nets was exposed to the leaching action and processed by the fauna, the correction factor was carried out for the value of the retained matter using the daily rate of resource processing in the hypogean stream (litter bag method).

The detritus retainment capacity by the sediment of the stream bottom, in the dry and rainy seasons, was estimated from the liberation, in the water, of plant leaves marked with spray paint (Simon and Benfield 2001). The leaves retained in the bottom sediment were collected along the stream 24 hours after their release at each point. Fifty leaves were released in the epigean stream (in the vicinity of the sinkhole), fifty leaves after net 1 and fifty leaves after net 3 (Fig. 1).

The analysis of the detritus processing was performed by conditioning plant detritus in 216 nylon bags (10x10 cm) and placed in the cave at the same time and divided into four distinct stations. Three types of bag mesh (with 5x7 mm; 1x1 mm and 0.1x 0.1 mm of mesh size) where used to exclude different invertebrate sizes (Gallas et al. 1996). Fifty dry disks (10 from each species) were previously weighed and packed into the litter bags (corresponding to an area of 63.6 mm2 of plant material in each bag). The plant disks were taken from leaves from five tree species present in the adjacent epigean environment: *Ficus calyptroceras* (Moraceae), *Piper* sp. (Piperaceae), *Ilex* sp. (Aquifoliaceae), *Eschweilera* sp. (Lecythidaceae) and *Acalypha* sp. (Euphorbiaceae). The litter bags were placed at two equally distant stations at the stream and in the terrestrial environment (Fig. 1). Triplicates of bags were bimonthly sampled at each mesh size and distinct stations. Only the first sampling was taken after one month.

In order to analyze the processing of animal detritus, feces from the carnivore bat *Chrotopterus auritus* were used. Twenty four bags of bat feces with 1x1 mm mesh size were distributed in two terrestrial stations on the floor of the cave at the same time. Triplicates of bags were bimonthly sampled at distinct stations.

The amount of organic matter remaining after the period of exposure for processing was expressed in percentage of dry weight. Processing of food resources (k-day) at LCP was described by the model $Mt = M_0$ e-Kt. The values for k.day-1 may be slow (0.005 k.day-1) and fast (0.1 k.day-1) in stream and slow (0.009 k.day-1) and fast (0.2 k.day-1) in terrestrial habitats (Oslon 1963, Allan and Castillo 2007, Simon and Benfield 2001).

The invertebrates were extracted bimonthly, from all the organic resources sampled in the cave (root tufts, plant detritus, guano, carcass, etc). The bimonthly extraction of invertebrates, before drying, was made with manual collections of the animals, still alive, using white-bottomed trays and under fluorescent light, with the aid of tweezers, brushes and manual magnifying glasses.

Invertebrates not directly associated to organic resources (especially terrestrial arthropods and zooplankton) as well as vertebrates (bats and fishes) were analyzed in a single quantitative sampling, conducted at the end of the experiment.

Terrestrial invertebrates species found in the cave had some of their specimens collected using manual collections with the aid of tweezers, brushes and entomological nets. The other invertebrates observed during the collections were counted (Hunter and Millar 2001). In the stream the zooplankton were collected with a 160 µm mesh net (Merle and Schneider 2000, Hunter and Millar 2001). Fish were collected with hand nets (Reis et al. 2006). Chiroptera fauna were collected during the summer with mist nets suspended near bat colonies (Weller and Lee 2007).

All organisms were identified to the highest accessible taxonomic level and grouped into morpho-species or species (Oliver and Beattie 1996). Species composition allowed categorization of fauna into functional groups (Triplehorn and Jonhson 2005, Allan and Castillo 2007).

Data analysis

The term *trophic dynamic*, used here, refers to the relationships among the import, retainment, production and processing processes of the coarse particulate organic matter. In the aquatic environment larger detritus than 0.6 cm were analyzed and in the terrestrial environment those larger than 0.1cm. For such, the following measures were used: (1) importation (daily percentage of coarse particulate organic matter imported to the cavity via stream and terrestrial means), (2) retainment or accumulation (daily percentage of coarse particulate organic matter retained in the cave), (3) exportation (daily percentage of coarse particulate organic matter retained in the retainment net located near the resurgence of the stream), (4) processing (daily percentage of the plant material and bat feces breakdown), (5) primary productivity (daily percentage of organic matter produced through the growth of roots in the cave), (6) secondary productivity (daily percentage of bat feces deposited in the cave).

The qualitative similarity of the fauna for only eight root tufts was obtained using the Bray-Curtis; the dominance through the Berger-Parker index and the diversity and evenness were estimated through the Shannon-Wiener index (Magurran 2004). The program used for the analyses was PAST (Hammer et al. 2001). In order to verify relationships between the richness, abundance, diversity and dominance of the macro invertebrates with the biomass and the distance of the roots in relation to upstream entrance, linear regressions were used (Zar 1984). The linear regression analyses were also used in the evaluation of the eventual relationships between the root biomass and the distance from the upstream entrance.

RESULTS

In the terrestrial environment, air humidity did not change substantially (70-77 %), and the temperature was constant (24-25ºC). Water pH was alkaline (8-9) and water temperature (24-25ºC), current speed (4-5 $m.s^{-1}$) and discharge (0.003 – 0.1 $m^3.s^{-1}$) varied during the year. The most intense discharge occurred in February. However, other rainy periods caused intense punctual flood flows that were discovered especially because of the marks left on the lateral walls of the cave and the damage caused to the collecting nets.

Initially eight root tufts that reached the hypogean stream sediment were found. During the study, eight new root tufts appeared, due to the erosion of the sediment or root tuft growth, totaling 16 points (Table 1). A total of 16 root growth points were observed in the hypogean stream. The biomass initially collected of the 8 root tufts corresponded to 1.138 kg and the average primary productivity along the sample period corresponded to 1.470 g/day (Table 1).

The incorporation in the biomass measured through the dry weight was of 1.482 g/day in October, 1.937 g/day in December, 0.502 g/day in February, 1.470 g/day in April and 0.591 g/day in June (Table 1).

The carnivorous and insectivorous bats were the main agents of the secondary production in the cave. These were responsible for depositing of 97 percent of the detritus present in the terrestrial environment of the cave (guano and prey carcasses). Owl regurgitation (rodent bones and skin) contributed to 3 percent of the detritus produced. The guano of carnivorous bats was deposited in a larger amount than the produced by insectivorous bats (Fig. 2). The highest guano deposition in the cave occurred in February, coinciding with the rainy period (Fig. 3).

Leaves were the most intensely imported resources (70.5%), followed by trunks (27.4%), dry fruits (1.5%), seeds (0.5%) and died roots (0.5%). The capture of detritus was 53.4 percent in net 1 and 46.6 percent in net 2. Comparatively, the capture of detritus in net 3 (export) corresponded to 89 percent of the material retained in nets 1 and 2 (Fig. 4).

The highest import of detritus (nets 1 and 2) happened at the end of October (45.4%), coinciding with the beginning of the rainy season. In February the highest detritus export rate (57.3%) occurred, coinciding with the highest rainfall index (Fig. 5).

In the dry season, there was retainment of 96 percent of the leaves released in the epigean stream close to the sinkhole. Inside the cave, 66 percent of the leaves liberated after net 1 were retained and 79 percent of the leaves liberated after the net 2 were retained. In the rainy season, there was retainment of 94 percent of the leaves liberated in the epigean stream close to the sinkhole. Inside the cave, 22 percent of the leaves liberated after net 1 were retained and 10 percent after net 2 were retained. Flood events were observed in the hypogean stream during the rainy season.

The plant detritus processing rate in the hypogean stream was fast (Table 2). During the first 31 days a rapid weight loss occurred, represented by the loss

Table 1 – Productivity (dry weight in grams/day) of submerged root tufts in a short subterranean stream.

Root tufts	July-01	October-01	December-01	February-02	April-02	June-02
1	**41.624**	0.159	0.540	0.070	0.036	0.177
2	**426.571**	0.235	0.115	0.013	0.035	0.066
3	**448.294**	0.102	0.095	0.013	0.200	0.037
4	**139.490**	0.251	0.039	0.031	0.061	0.009
5	**14.910**	0.112	0.338	0.029	0.090	0.020
6	**35.798**	0.062	0.002	0.042	0.002	0.012
7	**24.767**	0.067	0.017	0.012	0.062	0.001
8	**7.521**	0.050	0.004	0.034	0.001	0.037
9	-	**0.128**	0008	0.009	0.018	0.005
10	-	**0.316**	0.053	0.008	0.294	0.013
11	-	-	**0.725**	0.045	0.013	0.005
12	-	-	-	**0.195**	0.133	0.068
13	-	-	-	-	**0.004**	0.004
14	-	-	-	-	**0.267**	0.057
15	-	-	-	-	**0.132**	0.000
16	-	-	-	-	**0.124**	0.080
Total	1138.975	1.482	1.937	0.502	1.470	0.591
Mean	142.372	0.148	0.176	0.042	0.092	0.037
SD	186.753	0.091	0.249	0.051	0.094	0.046

Numbers in bold represent the initial weight of each root in the first collection.

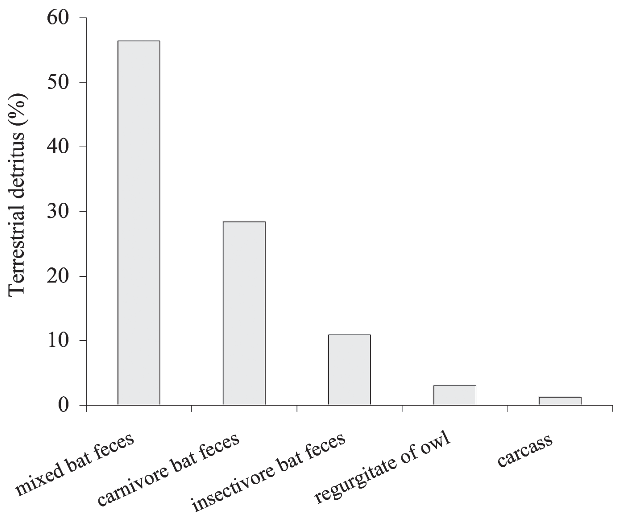

Fig 2 - Type of detritus transported to terrestrial environment in a tropical limestone cave.

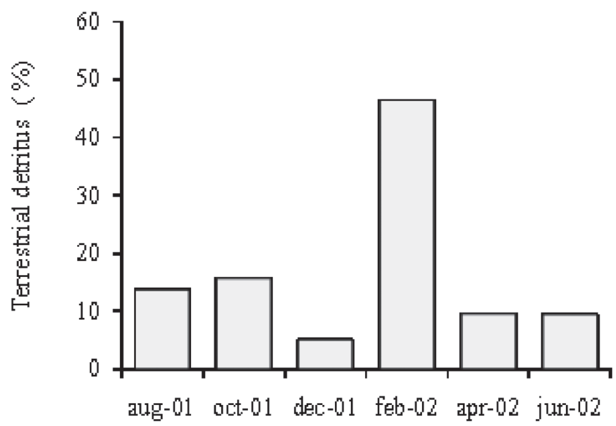

Fig 3 - Variation in detritus input to terrestrial environment in a tropical limestone cave.

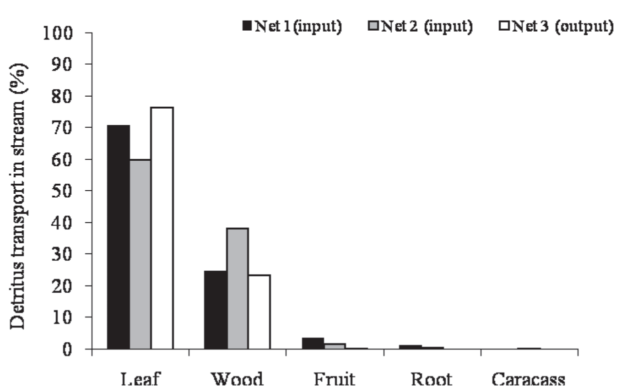

Fig 4 - Types of detritus input (nets 1 and 2) and output in a short cave stream.

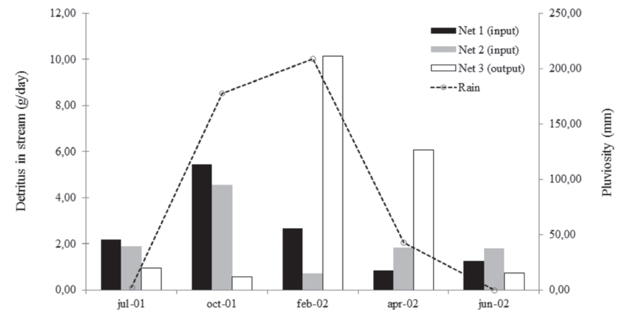

Fig 5 - Variation in the rain, amount of input (nets 1and 2) and output (net 3) of detritus transported in a short cave stream.

about 80 percent of the plant mass (Figs 6A and 6B). In the terrestrial environment, the plant detritus processing rate was slow (Table 2). At 31 days of exposure, the plant detritus mass loss was approximately 50 percent in relation to the initial mass. After 31 days, there was only an additional 15 percent loss of the initial mass (Figs. 6C and 6D). The processing rate of the guano of carnivorous bats can be considered fast in the cave (Table 2). At the 44 days of exposure there was a fast guano weight loss (72 % loss). After this period, the weight loss was slow (Fig. 7).

Considering all the organic matter (100 %) that enters daily in the cave, 61.7 percent is carried by the stream water. The roots that grow in the sediment represent 23.8 percent of this matter and the remaining 76.2 percent include detritus. In spite of this larger contribution of detritus, only 10.7 percent is retained by the sediment of the stream. The experiment of the leaf liberation-recapture reveal that retainment of detritus by the sediment is higher in the dry season of the year (79%). However, larger volumes of water and flood pulses in the rainy season impose lower retainment rates for the sediments (42%). In this period, the detritus banks are frequently washed and tend to be less available for the invertebrate fauna in function of this water flow instability (Fig. 8).

On the other hand, of all the organic matter (100%) that enters the cave daily, 38.3 percent is carried through the terrestrial environment, by the bats that deposit feces and carcasses (Fig. 8). The organic resource carrier species were the bats *Chrotopterus auritus*, *Natalus stramineurus*, *Furipterus horrens* and *Loncophylla* sp. (Fig. 8). This carrying process represents secondary production, since the carried detritus (guano) is of animal origin (carnivorous habits).

Those food resources are not carried to the exterior of the cave, remaining available for a long time for invertebrate use. However, the guano deposited in the cave is an ephemeral resource demonstrating a fast weight loss rate (Fig. 8). In spite of plant detritus (litterbag method) having registered slow processing rates, it was not found in sediment banks in the terrestrial environment of the cave (Fig. 7).

The number of species present in the several "*habitat compartments*" of the aquatic system was variable, although, in all of them, the orders Coleoptera and Diptera showed to be the richest (Table 3 and 4). The highest richness was sampled in eight root tufts (111 spp).

Table 2 - Breakdown rates (k) from time and mass for leaves and guano in cave.

Site	Resource	Mesh (mm)	K	Use	Cases	Starting weight	Final weight
Ground	Leaf	0.1 x 0.1	0.007	Slow	34	0.673	0.262
Ground	Leaf	1 x 1	0.006	Slow	34	0.655	0.272
Ground	Leaf	5 x 7	0.007	Slow	35	0.615	0.245
Ground	Guano	1 x 1	0.017	Fast	24	2.031	0.490
Stream	Leaf	0.1 x 0.1	0.043	Fast	33	0.645	0.035
Stream	Leaf	1 x 1	0.0521	Fast	33	0.623	0.020
Stream	Leaf	5 x 7	0.598	Fast	33	0.591	0.017

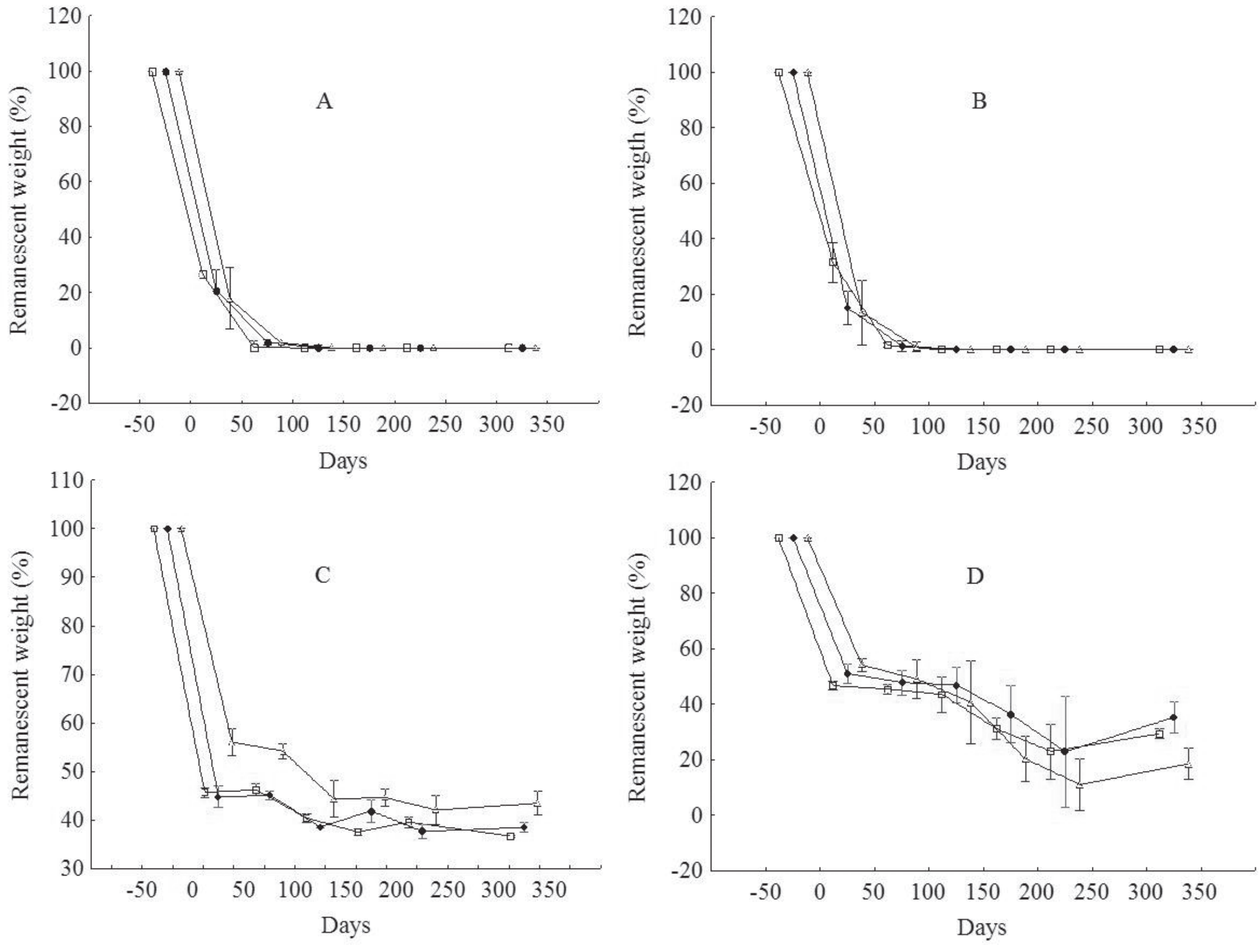

Fig 6 - Plant detritus processing in a cave stream (A and B) and terrestrial cave habitat (C and D). A, B, C, D refer to different sites in the cave.

The group of the shredders stood out in the plant detritus collected in the contention nets and litter bags. In the root tufts, the grazer organisms showed more representatives (Table 5).

The diversity was higher in root tufts 2 (H' = 2.78) and the highest dominance in root tufts 5 (d = 0.35) (Table 6). Roots tufts closer to each other and also those closer to the upstream entrance were the more similar in fauna composition than those located in the inner portions of the cave (Table 7).

The abundance ($\log_{10}$) ($R^2 = 0.63$; $P < 0.02$) and richness ($\log_{10}$) ($R^2 = 0.63$; $P < 0.01$) related positively with

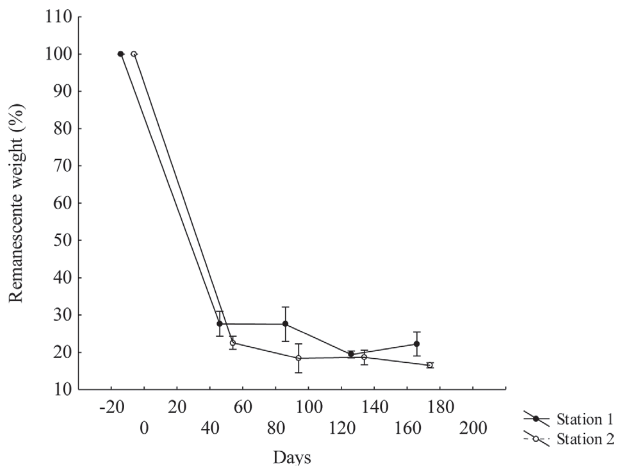

Fig 7 - Bat feces processing in terrestrial environment in a tropical limestone cave.

the root tuft biomass (log_{10}). The dominance related negatively with distance from the upstream entrance (log_{10}) ($R^2 = 0.76$ $p < 0.004$). The diversity ($R^2 = 0.87$, $p < 0.0005$) and the richness (log_{10}) ($R^2 = 0.75$, $p < 0.004$) were positively related with the distance from the upstream entrance. The root tuft biomass (log_{10}) related positively with the distance from the upstream entrance (log_{10}) ($R^2 = 0.52$, $p < 0.04$).

In the submerged roots tufts, Lepidoptera larvae (Pyralidae), Coleoptera larvae (Elmidade and Ptylodactylidae), Mollusca (Gastropoda) and as phytophagous Acari (Hydrachnidae, Smarididae and Rhynchohydracaridae) and Homoptera (Ortheziidae) were found as primary consumers (grazerss and scrapers). These, in turn, can serve as food for Trichoptera (Leptoceridae, Hydroptilidae and Hydropsychidae), Megaloptera (Corydalidae**)**, Odonata (Calopterygidae and Gomphidae), Heteroptera (Naucoridae, Hebridae and Belostomatidae) and fishes (*Ancystrus* sp and *Astyanax scabripinnis*). Other taxa can use the roots or detritus only as stable substrate (Ephemeroptera (Baetidae), Diptera (Ceratopogonidae, Chironomidae, Simuliidae, Stratiomyiidae and Tipulidae) Heteroptera (Veliidae), Coleoptera (Carabidae, Coccinellidae, Dytiscidae, Elmidae, Ptilodactylidae and Staphylinidae), Plecoptera (Perlidae), Rotifera (*Lecane* sp., *Bdelloidela* sp., *Cephalodela* sp., *Collotheca* sp., *Filinia* sp., *Keratella* sp., *K. Americana, Lepadella* sp., *Lepadella Patella,* and *Ptygura* sp) e.g. Annelida, Amphipoda, etc), Platyhelminthes (Planariidae) and Nematomorfa (Gordioidea).

Table 3 - Invertebrate species composition, distribution and richness (i.e. number) associated in distinct cave "*habitat compartments*". in stream and ground.

	Stream			Ground				
	Roots	Detritus	Litterbags	Guano	Owl pellets	litterbags	Guanobags	Carcass
Acari	8	1	3	9				
Annelida	5	2		1				
Amphipoda	1							
Araneae				5		2		
Coleoptera	28	21	17	8				
Diplopoda				1		2	1	
Diptera	26	18	7	3				
Blattodea						1	1	
Ephemeroptera	6	4	5					
Heteroptera	4	5		1		1		
Homoptera							1	
Hymenoptera				4	1	1		
Isopoda				1				
Isoptera				1		1	1	
Lepidoptera	3	2		2	1	4	2	1
Megaloptera	1	1	2					
Mollusca	5	2	3					
Odonata	7	3	2					
Ostracoda	3	1	2					
Plecoptera	3	2						
Pseudoscorpiones				1				
Psocoptera				4			1	
Trichoptera	10	5	3					
Turbellaria	1	1		1				
Total	111	68	44	42	2	12	7	1

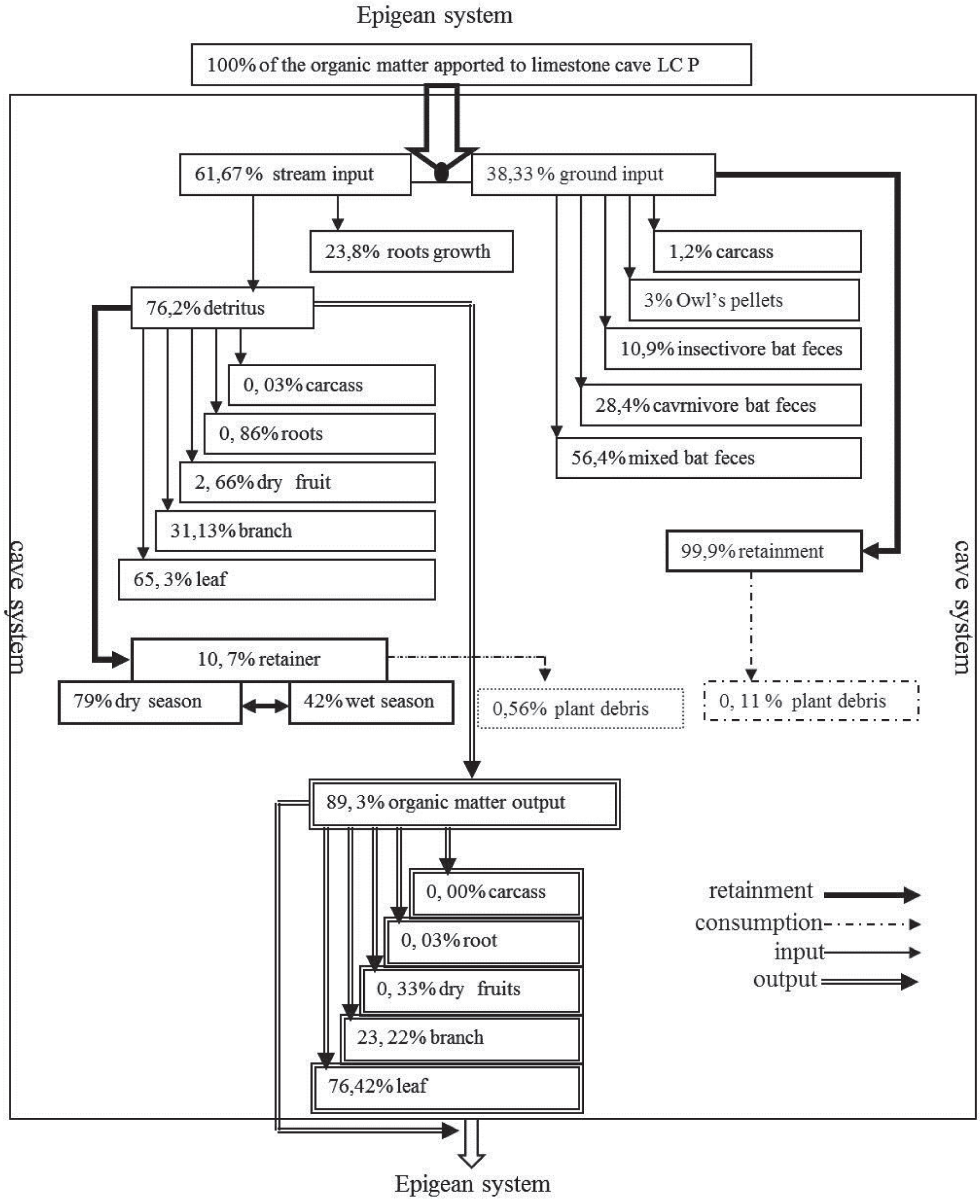

Fig 8 - Terrestrial and aquatic detritus budgets through a short tropical limestone cave.

For the terrestrial system, the richness of species was also variable, although always inferior to the values observed in the aquatic system (Table 3 and 4). However, there was no preponderance of a same taxon in the diverse compartments, as observed for the aquatic system. The shredder groups dominated all of the organic substrate observed in the terrestrial system (Table 5).

Therefore, in the terrestrial environment, the invertebrates have only associated to the bat guano, the carcasses of birds and owl regurgitate. Such invertebrates,

Table 4 - Cave fauna richness and abundance in different cave "*habitat compartments*".

Site	*"habitat compartments"*	*Richness*	*Abundance*
Stream	Root	111	1163
	Detritus	68	880
	Litterbags	44	785
	Watercourse	24	160
Ground	Wall and floor	62	136
	Guano	42	763
	Litterbags	12	26
	Guanobags	7	126
	Owl pellets	2	13
	Carcass	1	39
Total		270	4091

in turn, are prey of a large number of predator species. In the guano, the main scavengers are composed of species from the Armadillidiidae, Tineidae, Psyllipsocidae Pseudocaecillidae, and Dermestidae families, besides mites, composing the base of the trophic web. In the terrestrial environment there are organisms that do not associate directly to the guano patches, but they occur dispersed throughout the cavity. These were located on the floor or walls of the cave (Heteroptera (Ploiaridae and Reduviidae), Collembola (Entomobryidae), Ensifera (Phalangopsidae), Opiliones (Cosmetidae), Polydesmida (Cryptodesmidae), Homoptera (Cixiidae), Hymenoptera (Apidae, Evaniidae, Formicidae and Sphecidae), Coleoptera (Carabidae, Curculionidae, Scarabeidae and Sthaphylinidae), Blattodea, Diptera, Diplura (Campodeidae), Neuroptera (Chrysopidae), Isoptera (Termitidae), Psocoptera (Psyllipsocidae and Pseudocaecillidae), Acari (*Ornithodoros* sp).

Table 5 - Functional groups (% abundance) associated in distinct cave "*habitat compartments*" in stream and ground.

	Stream			Ground				
	Litterbags	Roots	Detritus	Carcass	Guano	Guanobags	Litterbags	Owl pellets
Collector	8	7.8	6,7	0	0	0	0	0
Filter feeding	0	2.4	0.1	0	0	0	0	0
Grazers	0	47.9	0					
Parasites	0	0	0	0	2.4	0	0	15
Predator	19,2	18.8	33.9	0	24.5	0,8	11.5	0
Scrapers	0,4	0.9	1.4					
Shredder	71,5	15.4	56.7	100	73.1	99.2	88.15	84
Sucker	0	2.4	0					

Table 6 - Macroinvertebrate community structure in root tufts submerged in a short subterranean stream.

	Root 1	Root 2	Root 3	Root 4	Root 5	Root 6	Root 7	Root 8
Richness (s)	27	19	38	34	10	8	5	4
Abundance	100	51	410	260	34	30	24	9
Dominance	0.11	0.08	0.17	0.17	0.38	0.32	0.37	0.26
Diversity (H)	2.73	2.75	2.58	2.31	1.49	1.48	1.19	1.37
Evenness(J)	0.83	0.93	0.71	0.65	0.65	0.71	0.74	0.99

Table 7 - Qualitative similarity of macroinvertebrates in discrete roots submerged in subterranean stream.

Root tufts	1+	2	3	4	5	6	7	8*
1+	-	**0.304**	0.123	0.164	0.216	0.171	0.125	0.194
2		-	0.281	0.264	0.207	0.074	0.083	0.087
3			-	**0.444**	0.042	0.087	0.093	0.048
4				-	0.136	0.146	0.103	0.105
5					-	**0.222**	0.267	**0.429**
6						-	0.154	0.167
7							-	**0.444**
8*								-

The sequence of numbers indicates the neighbors
** indicates root closest to the upstream entrance*
+ indicates root farthest from the upstream entrance

Species of the orders Pseudoscorpiones (Chernetidae) Scutigeromorpha**,** Scorpiones (Buthidae) and Araneae (Pholcidae*,* Theraphosidae, Salticidae, Scicariidae, Theridiidae, Mysmetidae and Oonopidae) were the top predators in the terrestrial environment.

DISCUSSION

The vegetation of tropical limestone outcrops frequently has a high proportion of deciduous species, which provide a higher accumulation of leaves in the litter during the dry season (Crowther 1987, Brina 1998).

This accumulated plant detritus in the soil during the dry season is carried in great amounts to the cave in the rainy season.

High detritus retainment rates in the sediment occur especially during the dry season. However, these retainment rates are higher than the processing speed of the detritus in the stream. In case the detritus was not removed by the current, certainly it would accumulate in large sediment banks on the underground stream bed. In relation to the LCP cave, what actually removes detritus from the stream bed is not the constancy of the outflow, but the flood pulses that are frequent in the rainy periods. Such a fact can be evidenced through the high output values and the detritus retainment rate falls during the rainy season.

Flood pulses make up one of the few environmental characteristics common to natural lotic ecosystems (Lake 2000, Robinson et al. 2002, Olsen and Townsend 2005). These floods frequently result from great storms, causing large volumes of water to move quickly down stream (Minshall et al. 1983). The volume and the speed of the water create high shearing tension in the channel and banks of a stream, moving substrata and sediment (Carling 1987, Matthaei and Townsend 2000). Those changes in the habitat structure have corresponding effects on the biotic environment (Fisher et al. 1982, Bunn and Arthington 2002, Downes and Street 2005).

For the LPC hypogean stream, the primary productivity (via submerged plant roots tufts) is what sustains the highest number of species in the invertebrate communities. Such a fact differs from the epigean aquatic ecosystems, where the trophic webs are based mainly on allochthonous detritus (Allan and Castillo 2007, Webster et al. 1999) and hypogean aquatic ecosystems, where the trophic webs are based on dissolved organic matter (Simon et al. 2007).

Roots are important resources for invertebrate animals in the terrestrial and aquatic environments of many caves (Jasisnka et al. 1996, Howarth 1983, Ferreira 2005). Besides offering food resources, the submerged roots are also microhabitats with structures different from those that the sediment offers (Jasinska et al. 1996).

The richness and diversity increase pattern and reduction of dominance with the increase of the distance from the cave entrance can be due to the influence of the root tuft biomass or the effect of the drift on the fauna transport. The benthic invertebrate species penetrate in the cave through the upstream entrance and apparently use the water currents to reach the roots farthest away from that entrance. Thus, it may not be the distance from the cave entrance that directly influences the structuring of the invertebrate communities in roots of this stream, but the available biomass of each root (that was shown casually related to the distance from the entrance) that can maintain abundant, richer and uniform populations.

The dispersion by drift is a frequent condition in benthic macroinvertebrate communities in streams, and the increase of the water flow works as one of the main determinants in the increase of the taxa richness under drift (Waters 1981, Callisto and Goulart 2005). According to Waters (1981), the number of individuals under drift can be reduced or stabilize with the increase of the distance traveled from the entrance. Such a fact can explain an increase of the diversity and reduction of the dominance in roots farther away from the entrance.

The guano makes up one of the main organic resources for the terrestrial invertebrate fauna in caves, mainly those permanently dry (Ferreira and Martins 1999). Such a fact was corroborated by the present study, keeping in mind the enormous contribution of the guano as a main food resource for terrestrial communities in the terrestrial LCP system.

Since seasonal variations in the external vegetation can influence the bat food resource use patterns, the highest guano deposition inside the cave in the rainy season could be associated to an increase in the food availability for these animals (Faria 1996). The forests on limestone outcroppings in tropical karst terrain present well defined seasonal phenophases, with an increase of flowering and fructification in the beginning of the rainy season (Crowther 1987, Brina 1998). In the tropics, the insect species are more active in humid periods, seemingly in function of the higher availability of food, flowers and fruits (Wolda 1988).

In LCP, the bats are fundamental for the structuring of the terrestrial invertebrate communities, because they contribute to the maintenance of a considerable number of invertebrate scavenger and predator species. The guano, deposited in places not accessible by water, seems not to have a means of transport to the exterior of the cave, which can make it available for a long period of time. However, as it is an ephemeral resource, the guano can become dehydrated or to have its nutritional value quickly reduced for the invertebrate fauna (Ferreira et al. 2000). Therefore, a continuous deposition, to allow the maintenance of its humidity and nutritient quality, which is essential for maintenance of the scavenger fauna and their predators, is necessary.

The plant detritus processing rates in the hypogean stream of the cave were similar to those observed in other epigean streams (Allan and Castillo 2007). Initially, fast nutrient loss rates occur, as observed in this study, due to the lixiviation by the abrasive force of the water associated to the action of shredder invertebrates (Simon and Bienfield 2001).

The low consumption rates of the plant detritus in the terrestrial environment of the cave can be related to the unfavorable temperature and mainly humidity conditions of the substrata in the soil. Those variables are essential to regulate the metabolism of decomposer organisms, besides being able to act differentially in the liberation of phenolic compounds and lixiviation elements during decomposition (Goley 1978, Wieder and Lang 1982, Nicolai 1988, Humphreys 1991).

The plant organic matter degradation process in the terrestrial environment of LCP can be compared to that observed in epigean environments with low water availability (e.g. deserts).

Thus, the higher carnivorous bat guano consumption speed, compared to plant detritus consumption speed, is probably due to the higher attractiveness and nutrient quality of the guano, usually richer in organic compounds (Ferreira et al. 2000). Another factor to be considered is the ephemeral characteristic of the guano that deteriorates due to the volatilization of ammonia compounds (Mcfarlane et al. 1995).

There is an historical assumption that organic resources imported by water are more available in caves in rainy seasons but, as shown in this work, the stochastic pulse flows continually disturb and remove the previously accumulated resource.

It is clear that the trophic dynamics in LCP cave have been influence by external seasonal events. The strong dependence of the cave ecosystem on the epigean environment that surrounds it is also clear. Thus, the necessity of preservation of the entire external surroundings, when we intend to preserve some caves or caves species, is obvious.

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