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Mapping subterranean resources: The cave invertebrates distribution as indicator of food availability

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Abstract. The trophic dynamic in cave ecosystems is poorly known, even being essential for understanding the structure and function of an entire cave ecosystem. The determination of sites of resource availability in caves is the first step to understand its trophic dynamic. We propose here methods to indicate resource accumulation sites in caves. The overlap of distribution of a pair of invertebrate scavenger species can indicate the sites of resource accumulation. It was assumed that sites where these organisms are more abundant are probably those with higher resource availability. To be good indicators, these species should not exclude one another competitively. In addition, species populations must be generalist, abundant, wide distributed into the cave and easily sampled by pitfall traps. The distribution of invertebrates as a method we propose is very important, since the structure of cave communities are strongly resource dependent. Hence, the detection of sites with greater resource availability is fundamental to understand the trophic dynamics of cave communities.

Key words: Caves, resources, bioindication, invertebrate distribution

Introduction

The cave environment is highly stable and permanently aphotic (POULSON & WHITE 1969; BARR & KUEHNE 1971; CULVER 1982). The physical cave environment is usually less variable than the epigean (external) one. The temperature in caves approaches the average of annual external temperatures, and the humidity is high, tending towards saturation (GILBERT *ET AL.* 1994). Primary producers are absent in caves, except for eventual chemoautotrophic bacteria. Therefore, most of the resources existing in a cave came from outside.

Organic matter comes into caves continuously or intermittently, carried by physical or biotic agents (CULVER 1982). The entrance and dissemination of particulate organic matter take place in streams or through vertical openings (when these exist) in the ceiling and walls. Besides, the dissolved organic matter, together with bacteria and protozoan present in percolation waters, penetrate through the limestone. Finally, feces or corpses of animals that use caves regularly are also important source of resources, specially in permanently dry caves (POULSON 1972, BERNARTH & KUNZ 1981, HERRERA 1995, FERREIRA & MARTINS 1998, FERREIRA & MARTINS 1999A, FERREIRA & MARTINS 1999B). The kind and way of resource dissemination are important in determining composition, abundance and distribution of the cave fauna.

The communities associated to ephemeral resources in caves are usually structured like other communities that use similar resources in the epigean environment (CORNABY 1974, DOUBE 1986). There are, however, many caves in which the organic matter enter continuously, mainly carried by streams. In these cases, the resources are not ephemeral and the communities associated to them show different dynamics (energy flux) when compared to those previously cited.

Cave organisms can be categorized in three classes (HOLSINGER & CULVER 1988, based on the system of Schiner-Racovitza): The trogloxens use the interior of caves but go outside regularly to feed. Thus, many of them import energy from the epigean environment to the cave, being often the main responsibles for energy flux in cave systems, as it occurs in permanently dry caves. The troglophiles can complete their life cycle in the hipogean and/or the epigean environments. Some species can even be trogloxens under certain circumstances (in caves with low amount of resources) and troglophiles in others (in caves with a great food availability). Troglobites are constrained to the cave environment, especially due to specializations originated under genetic isolation. Such specializations (morphologic – e.g. reduction of ocular structures and despigmentation – physiologic or behavioral) probably evolved under selective pressures found in caves and/or due to the absence of selective pressures commonly found in the epigean environment.

Most of cave species depend on the availability and quality of resources in caves systems. Many species are even spatially distributed according to the distribution of available resources (FERREIRA *et al*. 2000). Population growth is also dependent on nutrient availability. Thus, structures and processes related to a continuous availability of food resources for the maintenance of the biotic integrity of a habitat are very important. In epigean ecosystems, the processes related to primary production must be maintained as a whole, aiming their conservation, what is not true for cave ecosystems. In caves, resource importation and accumulation dynamics are the bases on which hypogean communities are structured (POULSON & CULVER 1969, POULSON & WHITE 1969, BERNARTH & KUNZ 1981, CULVER 1982, DECU, 1986). Secondary productivity plays also a fundamental role in caves and, as it depends essentially on debris availability (such debris being carried from the epigean environment), the detection of regions with higher resource availability in caves is important to evaluate the degree of community conservation of these systems.

Therefore, we aim to evaluate the potential indication of resource richer sites in caves through the overlap of scavenger species distribution. For this purpose, the following questions should be answered:

1. Are the distributions of different scavenger species correlated in a cave?
2. Are the visible and quantifiable organic deposits the most important as food resource for cave invertebrates?
3. The overlap in distribution of certain scavenger species can indicate richer resource sites in caves?

METHODS

Study site

The study was carried out in five caves, located in Minas Gerais, Bahia and Goiás states, Brazil (Fig. 1). The caves were placed in very distinct biomes, and were chosen aiming to verify the applicability of the method proposed in caves submitted to different the external environmental conditions. Tree caves have streams (Taboa cave, Salitre cave, and Passa Três cave), and the other two are permanently dry (Morrinho cave and Lavoura cave). Geological information for each cave are given elsewhere: Taboa cave (44⁰19'16"W 19⁰28'31"S - Ferreira & Pompeu, 1997), Morrinho Cave (40⁰55'05''W 10⁰12'32''S - Ferreira & Martins, 1998), Lavoura Cave (44⁰02'14.17"W 19⁰31'26.74"S – Ferreira *et al*., 2000), Passa Três cave (46⁰23'26''W 13⁰36'14''S) and Salitre cave (44⁰22'44"W 19⁰07'25"S – Travassos, 1999).

Methods

Samplings were conducted in January 1997 in Lavoura and Morrinho; July 1999 in Salitre and Taboa, and August 2000 in Passa Três cave.

Morrinho and Lavoura were divided in 10-meter-linear-sections (due to the relatively small size of these caves in relation to the others) A pitfall trap was placed

Figure 1. Location of each studied cave in Brazil.

in the center of each section. All bat guano piles present in each section had their surface areas estimated through Simpson's Index, which integrates the lengths of parallel segments took from the largest longitudinal distance of each deposit (FERREIRA & MARTINS, 1998). The areas of all deposits were summed, giving the total guano area present in each section. The total area was divided by 1000 cm^2, giving the number of deposits (with a standardized area) present in each section. The number of 1000 cm^2 deposits was correlated to the number of *Endecous* sp. (Ensifera: Phalangopsidae) individuals captured in each section. This procedure aimed to verify the importance of the visible and quantifiable organic sources in determining the distribution of a very common cave scavenger invertebrate.

In the remaining caves, pitfall traps were put in 25-meter-intervals (Taboa and Salitre) and 7.5-meter-intervals (Passa Três), due to size differences among caves (Passa Três had a sample area six times smaller than the remaining caves). In the first two caves (Taboa and Salitre), the invertebrate fauna was also collected manually, in each 25-meter-intervals, each section possessing a pitfall trap in a single transect. In these caves, simple correlations tests were performed between abundances of scavenger species caught in each trap (ZAR 1996). The compared pair of species were not always the same among different caves. All the analyzed species are generalist scavenger troglophiles, which can feed upon guano, corpses, vegetal debris, and fungi (personal observation). Such species were chosen also due to their wide distributions into the caves. Restricted or local distributed species were excluded from the analysis. In Salitre and Taboa caves, a Pearson's correlation test between *Endecous* sp. (Ensifera: Phalangopsidae) and *Conicera* sp. (Diptera: Phoridae) abundances was performed. In Passa três cave, a Pearson's correlation test between *Conicera* sp. (Diptera: Phoridae) and Entomobryidae sp1 (Collembola) abundances was performed. Non-normally distributed data were log-transformed (Log_{10}). On the other hand, the sites of resource accumulation were determined by estimating the mean abundance of scavenger indicator invertebrates along the conduct of each cave. We are assuming that sites where scavenger species are more abundant are probably those with higher resource availability.

The temperature and moisture content were also measured in Taboa and Salitre caves, in each sector of 25 meters. These measurements were maid with a termohigrometer, placed in the floor.

The total richness and total abundance obtained by manual collection and pitfall traps were tested by linear regression upon the mean abundance of scavenger species in Taboa and Salitre caves. The goal was to determine if there is an actual indication of resource availability by the scavenger species in each system. The invertebrate species found in the first 25 meters (near the entrance) were excluded from this analysis, since most of them were not actually cave species, using the entrance only as a shelter.

Results

A total of 5.882 individuals belonging to 133 morphospecies of 48 families of: Acarina, Pseudoscorpionida, Araneida, Opilionida, Amblypygi, Isopoda, Spirostreptida, Polydesmida, Coleoptera, Collembola, Diptera, Ensifera, Heteroptera, Hymenoptera, Lepidoptera and Psocoptera was collected. The orders Diptera (11 families), Coleoptera (7 families) and Araneida (6 families) were the richer in families; the others have just been represented by a maximum of 5 families. The species richness was variable; Taboa cave had 53 species while Salitre 83 species. The populations' distribution of the different morphospecies inside each cave was variable. Some populations had a restricted distribution (e.g. those associated to guano deposits) while other were more widespread (as those scavenger species used as resource indicators).

The abundance of *Endecous* sp. varied along the ducts of Lavoura and Morrinho caves, as did the number of standardized guano deposits per section. There was not a significant correlation between the number of guano deposits and the abundance of *Endecous* sp. per section in none of the caves.

The potential indicator scavenger species in the remaining caves showed very similar distributions along the extension of each cave, but varied among different caves (Fig. 2a,b,c; 3a,b,c; 4a,b,c). In Taboa cave, *Endecous* sp. abundance in each sampling point correlated positively with the $\log_{10}$ of *Conicera* sp. abundance at the same points ($r = 0.77$; $p<0.05$). In Salitre cave, the $\log_{10}$ of *Endecous* sp. abundance correlated positively with the $\log_{10}$ of *Conicera* sp. abundance along the cave duct ($r = 0.53$; $p<0.05$). Finally, *Conicera* sp. abundance correlated positively with the $\log_{10}$ of Entomobryidae sp1 abundance along the duct of Passa Três cave ($r = 0.63$; $p<0.05$).

The mean abundance of scavenger species (Log_{10}) in Taboa cave correlated positively with total richness ($F_{1,23}=6.5$; $R=0.47$; $p<0.018$ – Figure 5a) and with the $\log_{10}$ of total abundance of invertebrates ($F_{1,24}=11.2$; $R=0.56$; $p<0.003$ – Fig. 5b). The mean abundance of scavenger species in Salitre cave correlated positively with the total abundance of invertebrates ($F_{1,29}=22.4$; $R=0.66$; $p<0.000$ – Fig. 5c).

The sites with greatest resource availability (which may coincide with those of greater resource accumulation) also varied along the extension of each cave and among different caves, but did not become more or less abundant while becoming far from cave's entrance (Fig. 6).

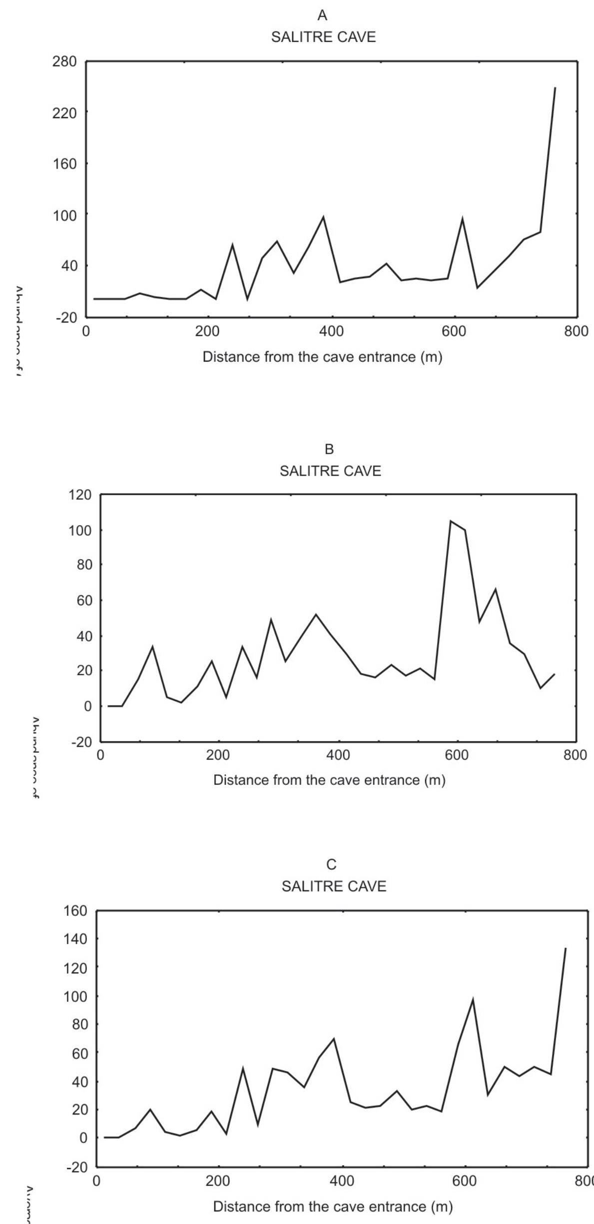

Figure 2. Spatial distribution of the scavenger species in Salitre cave: A. Distribution of *Conicera* sp.(Phoridae sp1); B. Distribution of *Endecous* sp.; C. Avarage distribution of the two scavenger species.

The sites in witch the indicator species were most abundant were not environmentally similar, as one could suppose. The temperature and moisture content were variable along Taboa and Salitre caves, not coinciding in any point (Tab. 1).

Table 1. Temperature and moisture content along the conduit in Taboa and Salitre caves. This parameters were taken in 25 meters intervals from the caves´ entrances. The values in bold indicate the temperature an moisture content in areas of organic resource accumulation.

	Salitre cave		Taboa cave	
Sector	Temperature (^{0}C)	Moisture (%)	Temperature (^{0}C)	Moisture (%)
External	16,80	60,00	31,40	33,00
Entrance	17,30	60,00	22,70	50,00
1	17,70	65,00	21,40	66,00
2	17,00	66,00	**20,00**	**75,00**
3	18,60	68,00	19,20	80,00
4	18,90	69,00	18,70	83,00
5	18,40	70,00	19,10	84,00
6	18,40	70,00	19,50	85,00
7	18,40	72,00	19,60	86,00
8	16,90	80,00	19,80	87,00
9	17,00	83,00	19,80	87,00
10	18,10	83,00	19,90	89,00
11	**18,40**	**84,00**	**19,90**	**92,00**
12	**18,30**	**87,00**	20,10	91,00
13	18,20	89,00	20,10	91,00
14	18,70	91,00	20,20	93,00
15	**18,60**	**92,00**	20,30	94,00
16	18,90	92,00	20,50	95,00
17	19,20	92,00	**20,80**	**96,00**
18	19,10	93,00	21,00	97,00
19	**19,60**	**96,00**	21,70	98,00
20	20,00	97,00	22,30	96,00
21	20,30	97,00	22,00	95,00
22	20,10	97,00	22,20	95,00
23	20,40	98,00	**22,60**	**94,00**
24	21,00	98,00	23,00	94,00
25	**21,30**	**98,00**	23,10	93,00
26	21,30	98,00	22,20	95,00
27	21,40	99,00	-	-
28	21,60	99,00	-	-
29	21,70	99,00	-	-
30	21,80	99,00	-	-
31	**21,60**	**99,00**	-	-

Discussion

The most widespread morphospecies in all the studied caves (e.g. *Endecous* sp and *Conicera* sp.) are extremely common troglophiles in Brazilian caves (DESSEN *et. al*. 1980, TRAJANO 1987, PINTO-DA-ROCHA 1995, FERREIRA, 2004). So, their use as indicators is appropriate. The other families observed in the studied caves are also commonly found in other caves in Brazil (TRAJANO & MOREIRA 1991, BICHUETTE & SANTOS 1998, FERREIRA & MARTINS 1999A, B, FERREIRA *et al*. 2000, FERREIRA, 2004).

Resource availability is an important selective pressure in cave ecossystems (DECOU & DECOU 1964, POULSON & CULVER 1969, POULSON 1972, BERNARTH & KUNZ 1981, CULVER 1982, DECU 1986, HERRERA 1995, FERREIRA *et al.* 2000). Understanding resources dynamics is therefore important in such habitats, since the amount of resources availability in larger or smaller amounts determine the structure of cave communities and the evolution of troglobites (PARK 1951, BREDER 1953, MITCHELL 1969, DYKHUIZEN 1978, CULVER 1982).

The trophic dynamics in caves is based in three inter-dependent factors. The first one refers to resource importation, which is dependent on frequency they are imported, on the ways by which the resources enter into the system and on the amount of imported resources (POULSON & WHITE 1969, NEGREA & NEGREA 1971, POULSON 1972, DECU & TUFESCU 1976, MARTIN 1976, BERNARTH & KUNZ 1981, DECU 1986, FERREIRA 1998, FERREIRA *et al*. 2000). In spite of being essential to understand resources dynamics in caves, the last two factors have been poorly discussed. The second one is determined by the accumulation and modification dynamics of resources in the cave system. These processes probably depend on the cave's topography and on the meso or microclimatic variations among different sites in a cave (SOUZA-SILVA, 2003). Sites prone to accumulate organic matter or to promote microorganisms growth (moister sites) can show up into these systems as sites with greater resource availability.

The third factor refers to the difficulty of differentiate between resources quality and quantity. A site with an apparent greater quantity of resources (but that are poor in organic matter) may be less attractive than another one in which resource is low but richer in organic contents.

The visible and quantifiable organic deposits are not those necessarily most used in the system. The lack of correlation between *Endecous* sp. abundance and the number of guano deposits in two caves corroborates this assumption. Thus, mapping

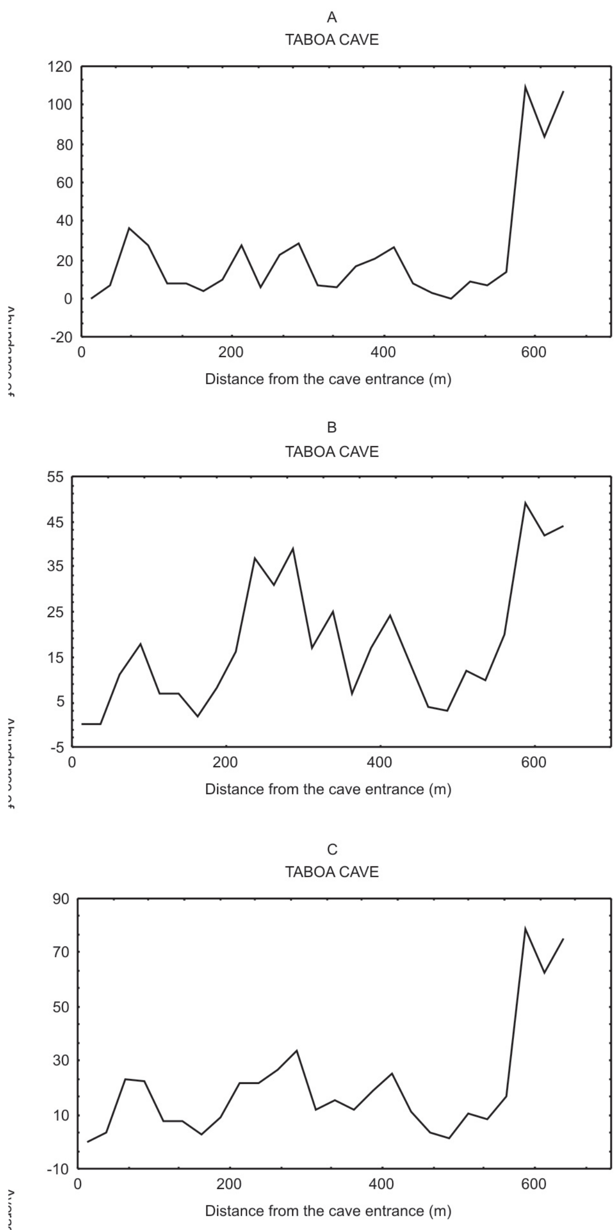

Figure 3. Spatial distribution of the scavenger species in Taboa cave: A. Distribution of *Endecous* sp.; B. Distribution of *Conicera* sp. (Phoridae sp1); C. Avarage distribution of the two scavenger species.

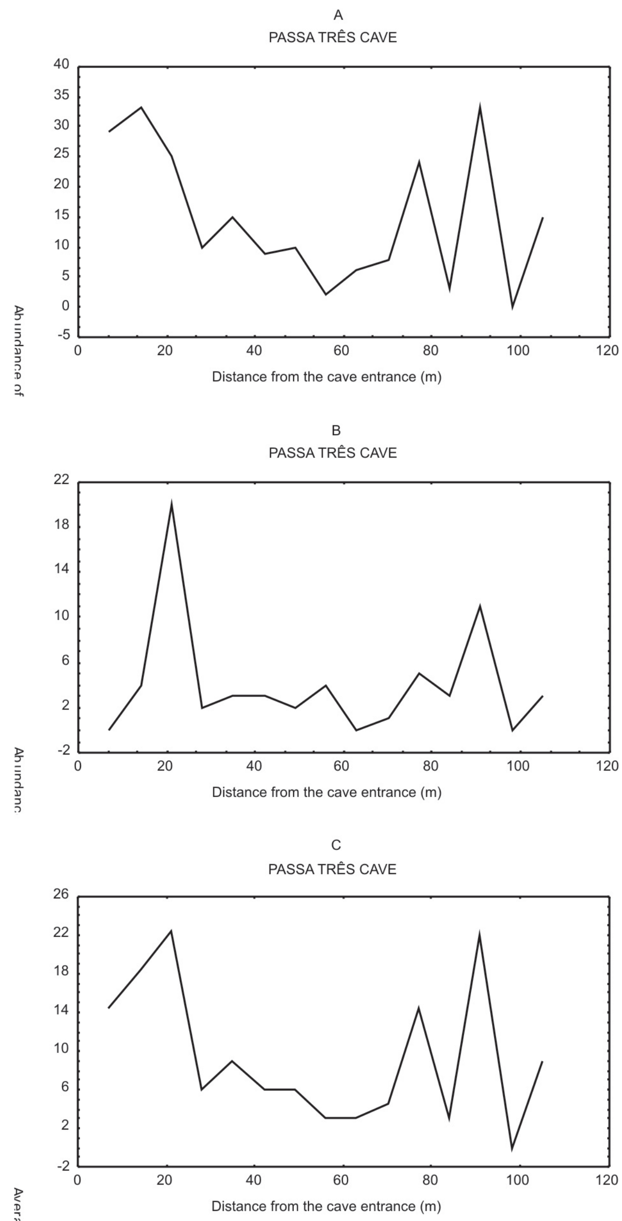

Figure 4. Spatial distribution of the scavenger species in Passa Três cave: A. Distribution of *Conicera* sp.(Phoridae sp1); B. Distribution of Entomobryiidae sp 1; C. Avarage distribution of the two scavenger species.

organic deposits alone may not reflect the trophic status of a cave, since the organic matter assessed may have a low nutritional value. Bat guano deposits, for instance, become less attractive as they turn older (FERREIRA, 1998; FERREIRA & MARTINS, 1998; FERREIRA & MARTINS, 1999A; FERREIRA & MARTINS, 1999B).

In spite the restrictions above, the determination of areas with greater resource availability could be done through the knowledge of the distribution of scavenger species. However, a single population of a given scavenger species is not enough to indicate

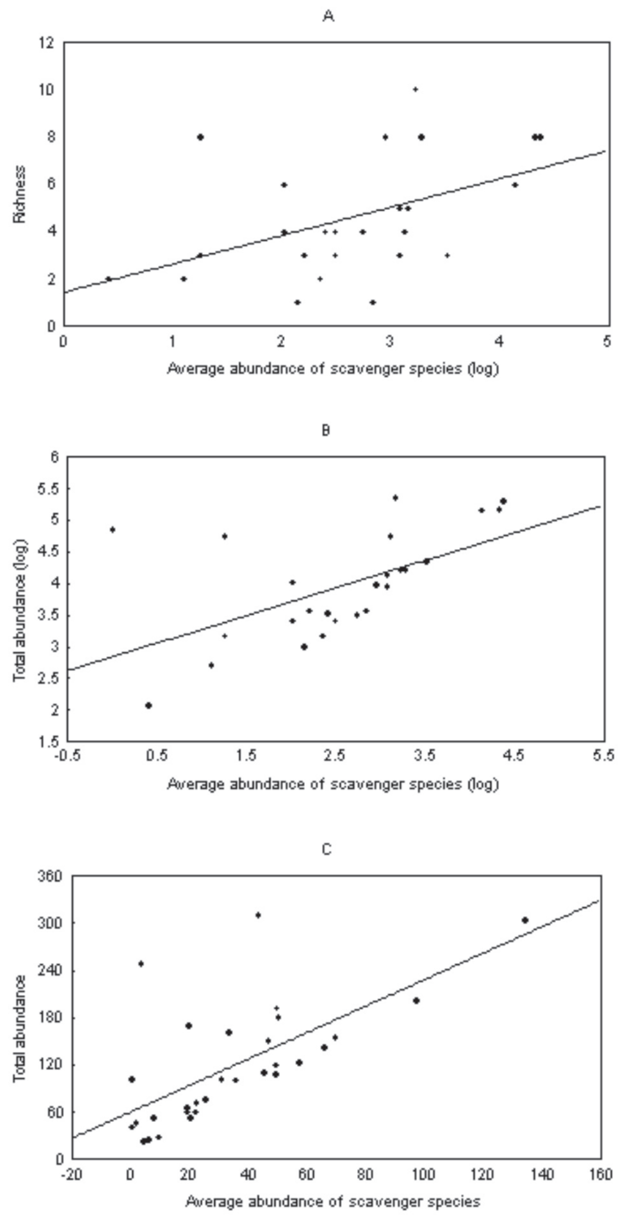

Figure 5. A) Correlation between richness and average abundance of scavenger species (log) in Taboa cave; B) Correlation between total abundance (log) and average abundance of scavenger species (log) in Taboa cave; C) Correlation between total abundance and average abundance of scavenger species in Salitre cave.

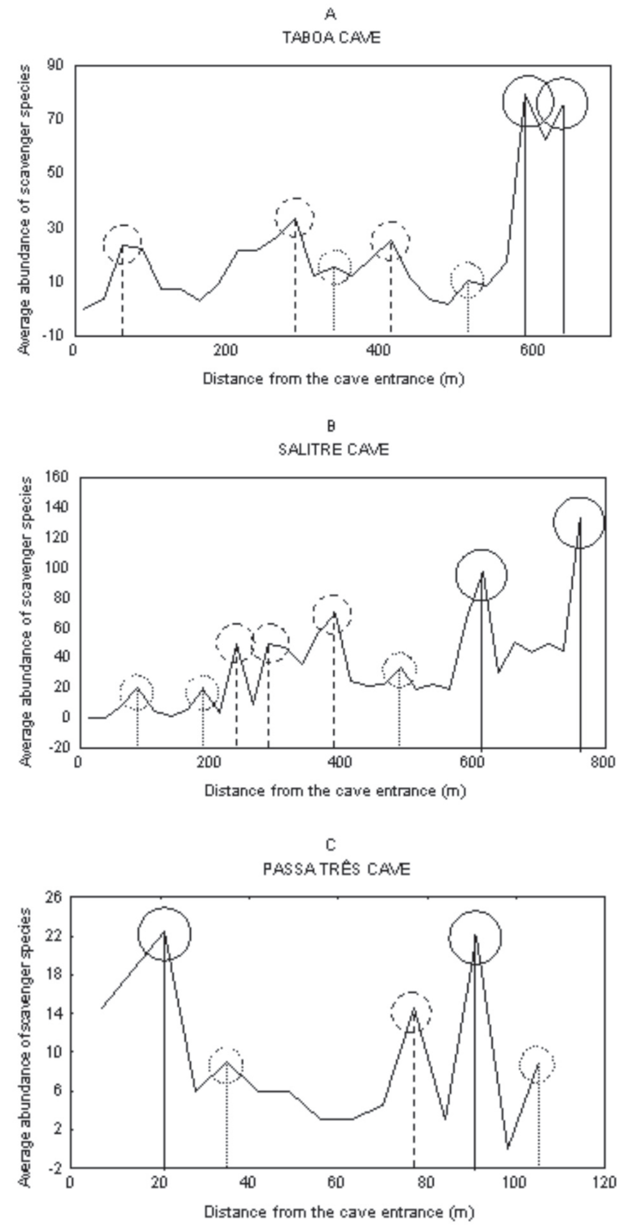

Figure 6. Areas of organic resource accumulation in the studies caves. The circles indicate the areas with probably different amounts of resource. A) Taboa cave; B) Salitre cave; C) Passa Três cave.

resource accumulation sites. This population may have its distribution pattern altered by some change in the epigean environment (overflows) or hipogean (habitat colonization by a new species). Then, sampling a single species may be not enough to infer which the resource richest sites are. So, the trophic system must be considered under this approach superposing the distribution areas of two or more scavenger species, which will hardly be similarly altered by an unexpected event (e.g. a flooding in a cave stream). If distributions of these species coincide, it might be a strong evidence of resource accumulation in the corresponding sites.

One could think that the coincidence in the distribution of the scavenger species could be reflecting a microhabitat selection, instead of resource accumulations sites. However, in both caves in which topoclimatic features were assessed, the sites where the species are most abundant are quite different in temperature and moisture content, witch indicates that the invertebrate distribution is not related to microenvironment conditions.

The positive correlation among the distribution of scavenger species in three sampled caves indicates the richer sites in resource availability. Such sites are identified by the means of distribution values of scavenger species used as indicators in each system (Figure 6). An important factor that must be pointed out is that *Conicera* sp. was never seen feeding on *Endecous* feces, as could be thought by someone. All the species that were used as resource indicators are scavenger generalists, not feeding on an exclusive type of resource. Nevertheless, to be good resources' indicators, these species must not exclude one another competitively. Besides, populations must be abundant and broadly distributed into the cave, and also easily sampled by pitfall traps.

The significant correlation found between total richness and total abundance with the average abundance of "indicator species" in Taboa and Salitre caves is evidence that these species are actually indicators of sites with greater resource availability in these caves.

We can sometimes understand some environmental features which we are not adapted to. But, many times, we can produce a deformed interpretation of a situation, since that is a human way to understand the nature. However, if we can "see through the organism's eyes" these mistakes are quietly reduced, since we do not have to "intermediate" situations, only describe them.

The methods proposed, notwithstanding restricted, are important, as the structure of cave communities are basically resource dependent (FERREIRA & MARTINS 1998, FERREIRA *et al* 2000). Hence, the detection of sites with greater resource availability is fundamental to understand the trophic dynamics of cave communities.

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