

Ecotone delimitation: Epigean–hypogean transition in cave ecosystems

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Abstract The ecotone zone between epigean and hypogean environments has been delimited for two limestone caves using a new method proposed herein. The richness and the diversity of the ecotone, epigean and hypogean environments and their similarities have also been determined. The ecotones were delimited using a similarity matrix between the inner and outer sectors of each cave. The ecotone of Dona Rita's cave was estimated to be 12 m long and the ecotone of Retiro's cave 16 m. The richness (S) of arthropods in Dona Rita's cave was higher in the ecotone ($S = 131$), intermediate in the epigean environment ($S = 75$) and lower in the hypogean system ($S = 45$). The invertebrate diversity (H') was lower in the hypogean environment ($H' = 2.89$) and not statistically different between the epigean environment and the ecotone ($H' = 3.56$ and $H' = 3.76$, respectively). The richness in Retiro's cave was higher in the ecotone ($S = 86$), intermediate in the epigean environment ($S = 39$) and lower in the hypogean system ($S = 12$). The invertebrate diversity was lower in the hypogean environment ($H' = 0.48$), intermediate in the ecotone ($H' = 3.02$) and higher in the epigean region ($H' = 3.29$). Species migration patterns, differential environmental barriers and determination of accidental versus troglobenes/troglophylous species are topics that are primarily approached by establishing ecotone zones in caves. The aim of the present paper is to establish the delimitation of these zones.

Key words: arthropods, Brazil, boundaries, caves, communities, diversity, ecotone, neotropics.

INTRODUCTION

An ecotone has been defined as a ‘transition zone between adjacent ecological systems, having a set of unique features defined by a spatial–temporal scale and by the strength of the interactions between the systems’ (Hansen *et al.* 1988a), and is characterized as a dynamic region subject to modifications in space and time. Thus, such a region is part of an ecological unit in which the processes of the ecosystem as a whole occur. Therefore, these areas are important in the energy flow between the environments (Naiman *et al.* 1988; Naiman & Decamps 1990; Risser 1990, 1995).

Organisms may specialize themselves to live in ecotones either because in these places they can find suitable supporting conditions unavailable in other environments or because they depend on two or more structurally different and contiguous habitats (Gates & Gysel 1978; Odum 1983; Dunning *et al.* 1992).

The ecotone has frequently been considered an area with greater richness and diversity than each one of the systems that gave rise to it (Petts 1990; Delcourt & Delcourt 1992; Hansen & di Castri 1992; Lloyd *et al.*

2000). Nevertheless, Hansen *et al.* (1988a) suggest that such an increase in diversity is only one possibility for ecotones, and the diversity can be greater, intermediate or lower than that of the neighbouring areas.

The diversity can be higher in the ecotone in those instances when it provides shelter for species from both neighbouring environments and for those specific to the ecotone itself. A high migration rate between the adjacent habitats would also favour greater diversity in the transition area.

An intermediate diversity can be found in ecotones if one of the neighbouring areas is relatively poor in species, so that the ecotone is colonized mainly by species that come from the richest area.

Finally, an ecotone can support a lower diversity if resources vary broadly within it, as in the interfaces of estuaries between freshwater and salt water, or if it is located in an area under the influence of strong disturbances, such as the wave-battered region of the intertidal zone.

Cave ecosystems are, in general, stable and characterized by a permanent absence of light, similar temperatures to the annual external means and moisture tending to saturation. The cave entrances are regions in which environmental variables are under strong influence from the external environment.

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Temperature, moisture and luminosity vary during the day and during the year in such regions (Culver 1982). The presence of light, even in an indirect way, allows the growth of photosynthetic organisms that might result in an increase of resource availability, making the local fauna richer or modified. Thus, regions close to the entrance might show gradients of structural, biological or physical modifications, creating a transition zone between epigean and hypogean systems. Therefore, cave entrances can be characterized as ecotones.

The terrestrial cave communities can be divided into three groups based on their dependence on resources and spatial distribution (Ferreira & Martins 2001): the ‘resource-space-dependent’, the ‘resource-space-independent’ and the ‘para-epigean’ communities.

The resource-space-dependent communities are those formed by organisms that are generally small (smaller than 5 mm in size) with low mobility and are found preferentially within the limits of the resource pile (e.g. bat guano deposits, decomposing trunks), such as Acari (e.g. Uropodidae), wingless Psocoptera (e.g. Psyllipsocidae), Diptera larvae (e.g. Phoridae), Isopoda (e.g. Platynarthridae) and pseudo-scorpions (e.g. Chernetidae) (Ferreira 1998; Ferreira & Martins 1999).

The resource-space-independent communities are those in which organisms are not obligatorily associated with a single resource deposit. Such organisms can move through long areas in the cave in a short time interval (e.g. Phoridae, Reduviidae, Phalangopsidae, Sicariidae, Ctenidae) (Ferreira & Martins 1999).

Para-epigean communities are those occurring near the cave entrance and are composed of epigean and hypogean organisms.

Features such as the influence of energy flow between neighbouring environments and the lack of knowledge on the effects of human impact on this environment make ecotones an important source for ecological studies (Wiens *et al.* 1985; Hansen *et al.* 1988b; Risser 1990, 1995; Neilson 1993). However, most studies on ecotones have been carried out with vegetal communities or aquatic–terrestrial ecotones (Naiman & Decamps 1990; Holland 1993; Bretschko 1995; Lloyd *et al.* 2000). Studies conducted in ecotone zones between epigean and hypogean environments focus mainly on the aquatic environment, and studies with a terrestrial approach are rare (Culver & Poulsen 1970; Skalski 1973; Peck 1976; Gers 1998; Gibert *et al.* 1990, 1997).

Here, we propose a method to delimit the boundaries of the ecotone zone between the epigean and the hypogean environments, by comparing invertebrate similarity. More specifically, we aim to answer the following questions: (i) what is the length of the ecotone zone in the studied caves?; (ii) are ecotones richer and more diverse than their neighbouring systems?; (iii) how do organisms distribute themselves in these

different environments?; (iv) what are the similarities among the external, internal and ecotone zones of the caves?; and (v) which of the regions, epigean or hypogean, contribute most to the composition of the arthropod fauna in the ecotone zone?

METHODS

Study sites

Dona Rita’s cave is located at Pains municipality ($20^{\circ}22'S$, $45^{\circ}44'W$) in the centre–west of Minas Gerais state, Brazil. It belongs to a limestone outcrop covered by a semideciduous forest at its top. A pasture surrounds the cave entrance.

The linear projection of the cave is approximately 140 m. The entrance is 5 m wide and 3 m high. Eight metres from the entrance, the main gallery narrows into two small ducts, opening again 4 m ahead. A fordable gallery extends through approximately 60 m before bifurcating.

Bat guano piles are the main food source in this permanently dry cave. Shrubs and grasses cover all the terrain in front of the cave entrance. This vegetation extends 6 m into the cave. The soil in the entrance is rocky and extends for 30–40 m onto the pasture.

Retiro’s cave, also located in Pains, has two entrances at different levels on the same outcrop. The lower entrance is at the level of the water table. In front of the cave entrance, there is a secondary forest with medium sized trees more than 10 m high.

The only conduct of the cave extends for approximately 150 m. Close to the entrance, there is a collapsed saloon covered by huge rocky blocks. In the median portion of this saloon, there is a large calcite-deposit column. A watercourse comes from an external lake, enters through the lowest entrance of the cave, flowing through a short distance of approximately 20 m to form a siphon. This watercourse emerges initially in a short space of 5 m and again in the posterior portion of the collapsed saloon, where it runs for 60 m until the end of the cave.

Besides the organic matter carried by the watercourse, other food sources found are bat guano piles (especially from haematophagous bats, *Desmodus rotundus*) distributed around the whole cave. Litter covers the soil outside the cave. The soil of the first 10 m of the upper entrance of the cave is covered by earth and vegetal debris brought from the external environment.

Measurements

A linear transect was placed through each cave and projected 20 m into the external environment from the

cave entrance. In the external environment, temperature, air moisture and luminosity were measured every 2 m along the whole transect. These variables were also measured inside the caves in the same way until the luminosity reached zero lux. From this point on, temperatures and air humidity were measured at 20-m intervals.

The 20-m transect outside the cave and the first 20 m inside cave were divided into 2-m sections. Outside the caves, the sections had a constant width, corresponding to the mean value of the widths of the internal sections of each cave.

In every 2-m section, a manual sampling of arthropods was performed using tweezers and brushes. The samples were collected on February 2001 during the day and each section was sampled taking the necessary time for a complete visual scan (at least 25 min). During the sampling procedure, all the potential microhabitats (under rocks and trunks) were meticulously inspected. The arthropods were fixed in 70% ethanol and deposited in the laboratory of Ecologia e Comportamento de Insetos of the Instituto de Ciências Biológicas of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. Special attention was paid to microhabitats, such as under stones and trunks in the external environment. The organisms collected were identified to the lowest taxonomic level possible and then separated into morphospecies to record the richness of each section. The Sorensen qualitative similarity ($C_s = 2j/(a + b)$ where C_s is the similarity value, a is richness in

first site, b richness in second site and j shared species) among the sections, and the Shannon diversity index ($H' = -\sum p_i \ln p_i$, where p_i is the proportion of total sample belonging to i th species) of the environments (epigean, hypogean and ecotone) were used (Magurran 1988).

Linear regressions were performed between the measured environmental variables and the richness and diversity of each sampled section. Hutcheson's *t*-test (Magurran 1988) was used to test for significant differences between the Shannon diversity indexes of the external, internal and ecotone environments of the caves.

Determining the ecotone zone

To delimit the ecotone zone, a comparison between elements of the communities of the sectors from each side of the cave entrance (inside and outside the cave) was performed. It is assumed that the cave entrance is the 'central part' of the ecotone; thus, we would expect to find a reduction in the similarity values of correspondent sectors (in the epigean and hypogean zones) equidistant from the cave entrance as they are far from this centre. Thus, the limits of the ecotone are defined by the total dissimilarity between the communities of the adjacent systems (similarity corresponding to zero). The community present on the sectors in which the similarity values are higher than zero are considered to be in the ecotone.

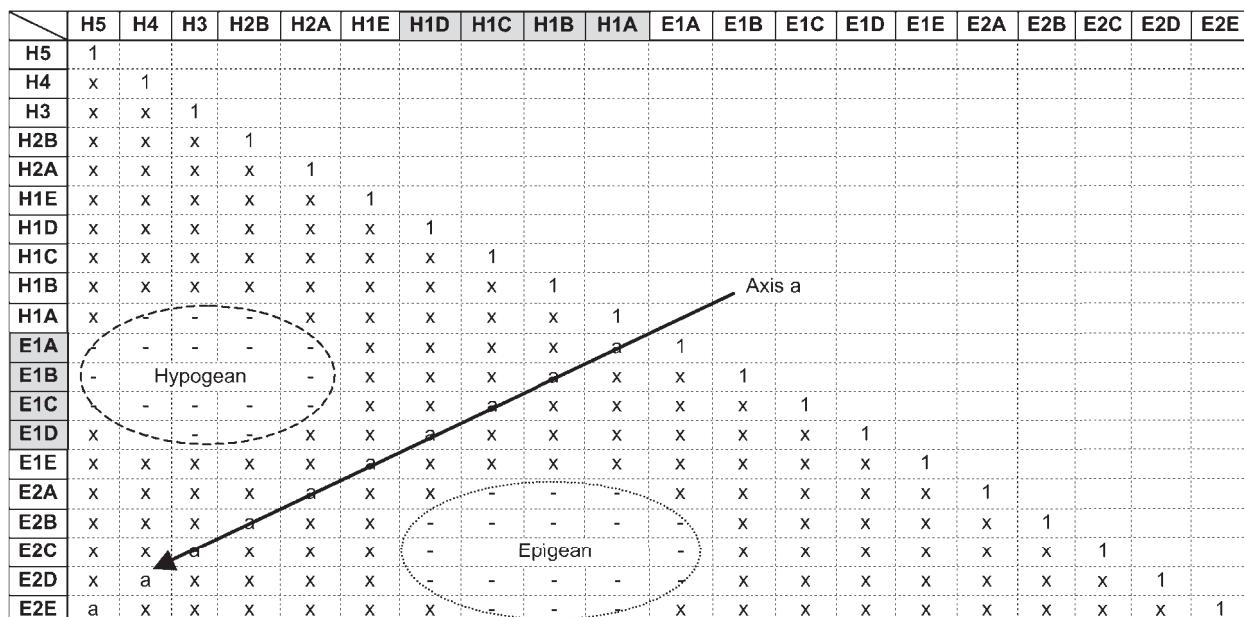


Fig. 1. Similarity matrix. H, (---) hypogean sections; E, (...) epigean sections. Axis a represents the similarity between the equidistant cave entrances sections. (□) The ecotone zone is defined by the sectors with positive similarity on axis a before it reaches zero. (—) values = 0; (x) values = / 0.

A similarity matrix was built among all the sampled sections, as in the example in Figure 1. The analysis of similar values in axis a (similarity between the epigean and hypogean sections at the same distances from the entrance) determined the extension of the momentary ecotone.

RESULTS

Dona Rita's cave

Environmental variables

The sections of Dona Rita's cave showed variability regarding temperature, moisture and luminosity (Table 1). Temperature and luminosity correlated significantly to distance from the entrance ($R = -0.91$, $P < 0.01$, $F_{1,20} = 41.95$ and $R = -0.94$, $P < 0.01$, $F_{1,20} = 42.26$, respectively). Relative air humidity also correlated significantly to the distance from the entrance ($R = 0.96$, $P < 0.01$, $F_{1,20} = 107.54$).

One hundred and ninety-seven morphospecies of 24 orders were found in Dona Rita's cave. Species richness correlated significantly to distance from the entrance of the cave ($R = -0.79$, $P < 0.05$,

$F_{1,20} = 10.40$), air moisture ($R = -0.83$, $P < 0.01$, $F_{1,20} = 14.07$) and temperature ($R = 0.77$, $P < 0.05$, $F_{1,20} = 8.84$).

Similarity matrix

The similarity matrix for Dona Rita's cave can be seen in Figure 2a. Observing the diagonal similarity axis between each external section and its corresponding section into the cave in relation to the distance from the entrance (axis a from Fig. 1), it can be observed that the similarity reaches zero in the intersection of the sections H1D and E1D (8 m from the entrance). This suggests that the zone between sections H1C and E1C (the last point of axis of the matrix in which there is similarity between the faunas present) is the momentary ecotone, with an extension of 12 m.

Richness (S) was higher in the ecotone zone ($S = 131$), intermediate in the epigean environment ($S = 75$) and lower in the hypogean environment ($S = 45$).

Diversity indexes (H') in the hypogean, epigean and ecotone regions of the cave were $H' = 2.89$, $H' = 3.56$ and $H' = 3.76$, respectively. The diversities were significantly different between the hypogean and epigean ($t = 6.86$, degrees of freedom (d.f.) = 462.1, $P < 0.05$) and the hypogean and ecotone zones

Table 1. Temperature, moisture and luminosity measurements for Dona Rita's and Retiro's caves

Distance (m)	Temperature (°C)	Retiro's cave			Dona Rita's cave		
		Moisture (%)	Luminosity (lux)	Temperature (°C)	Moisture (%)	Luminosity (lux)	
Hypogean							
20	22.4	93	0	20.3	89	0	
18	22.4	92	1	21.1	88	0	
16	22.5	91	2	21.5	85	0	
14	22.5	92	6	21.3	84	9	
12	22.3	92	12	21.4	84	36	
10	22.6	92	30	21.1	82	170	
8	22.4	92	55	22.0	80	560	
6	23.5	88	160	22.9	74	860	
4	24.2	88	315	23.3	73	1170	
2	24.3	84	670	24.0	70	1390	
Entrance							
0	24.7	84	720	24.4	70	1300	
Epigean							
2	25.2	82	855	25.2	71	1330	
4	25.1	81	1411	25.7	70	1360	
6	24.8	82	950	25.6	69	1290	
8	24.9	82	830	25.9	70	1380	
10	25.1	82	1030	26.0	69	1356	
12	25.2	82	950	25.4	69	1379	
14	25.4	82	613	25.6	70	1338	
16	26.0	80	521	25.6	69	1269	
18	26.0	80	726	26.0	70	1340	
20	26.1	79	940	25.9	70	1312	

($t = 9.97$, d.f. = 986.2, $P < 0.05$) and not different between the ecotone and the external environment ($t = 1.84$, d.f. = 565.3, $P > 0.05$).

The highest similarity was between the ecotone and the epigean environment ($C_s = 0.340$); there was an intermediate level of similarity between the ecotone and the hypogean environment ($C_s = 0.193$); and the lowest similarity was between the epigean and hypogean environments ($C_s = 0.117$).

Retiro's cave

Environmental variables

Similar to Dona Rita's cave, the sections of Retiro's cave varied regarding temperature, air moisture and luminosity (Table 1). Temperature, luminosity and moisture correlated significantly to the distance from the entrance ($R = -0.70$, $P < 0.01$, $F_{1,20} = 19.65$,

(a)

	H5	H4	H3	H2B	H2A	H1E	H1D	H1C	H1B	H1A	E1A	E1B	E1C	E1D	E1E	E2A	E2B	E2C	E2D	E2E
H5	1																			
H4	0.15	1																		
H3	0.39	0.10	1																	
H2B	0.23	-	0.29	1																
H2A	0.13	-	0.17	0.62	1															
H1E	0.12	-	0.15	0.32	0.53	1														
H1D	0.07	-	0.10	0.15	0.22	0.17	1													
H1C	0.11	-	0.27	0.17	0.10	0.18	0.12	1												
H1B	0.10	-	0.16	0.09	0.05	0.09	0.06	0.30	1											
H1A	0.17	-	0.20	0.14	0.15	0.14	0.05	0.21	0.51	1										
E1A	0.06	-	0.07	0.04	-	-	0.04	0.07	0.18	0.18	1									
E1B	-	-	-	0.04	-	0.04	-	0.08	0.09	0.14	0.30	1								
E1C	0.03	-	0.04	0.08	-	0.04	-	0.10	0.06	0.13	0.22	0.37	1							
E1D	0.04	-	-	-	-	-	-	0.06	0.07	0.07	0.15	0.27	0.29	1						
E1E	-	-	0.06	-	-	-	-	-	0.08	0.12	0.13	0.23	0.21	0.30	1					
E2A	-	-	0.05	-	-	0.06	-	-	0.03	0.10	0.18	0.17	0.13	0.25	0.24	1				
E2B	-	-	-	-	-	-	-	-	-	0.05	0.08	0.14	0.04	0.20	0.25	0.26	1			
E2C	-	-	0.05	-	-	-	-	-	0.06	0.07	0.15	0.22	0.21	0.17	0.33	0.22	0.27	0.22	1	
E2D	0.05	-	-	-	-	0.07	-	-	0.04	0.11	0.19	0.29	0.14	0.19	0.17	0.23	0.15	0.41	1	
E2E	0.06	-	-	0.09	-	-	-	0.17	0.09	0.09	0.15	0.21	0.16	0.29	0.21	0.17	0.11	0.26	0.27	1

(b)

	H5	H4	H3	H2B	H2A	H1E	H1D	H1C	H1B	H1A	E1A	E1B	E1C	E1D	E1E	E2A	E2B	E2C	E2D	E2E
H5	1																			
H4	0.40	1																		
H3	0.50	0.40	1																	
H2B	0.40	0.33	0.40	1																
H2A	0.29	0.50	0.29	0.25	1															
H1E	0.33	0.57	0.33	0.57	0.44	1														
H1D	0.25	0.67	0.25	0.22	0.36	0.40	1													
H1C	0.14	0.40	0.14	0.13	0.23	0.25	0.44	1												
H1B	0.05	0.16	0.05	0.10	0.10	0.15	0.24	0.34	1											
H1A	-	0.07	-	-	-	-	0.12	0.26	0.35	1										
E1A	-	-	-	-	-	-	-	0.07	0.19	0.27	1									
E1B	-	0.14	-	-	-	-	0.12	0.17	0.13	0.21	0.34	1								
E1C	-	0.12	-	-	-	-	0.10	0.08	0.09	0.20	0.19	0.33	1							
E1D	-	0.15	-	-	-	-	0.12	0.18	0.09	0.11	0.07	0.29	0.26	1						
E1E	-	-	-	-	-	-	-	0.10	0.09	-	-	0.10	0.09	0.11	1					
E2A	-	0.12	-	-	-	-	0.10	0.31	0.24	0.19	0.12	0.24	0.15	0.33	0.27	1				
E2B	-	0.12	-	-	-	-	0.10	0.23	0.24	0.19	0.31	0.24	0.22	0.33	-	0.43	1			
E2C	-	-	-	-	-	-	-	0.16	0.17	0.10	0.19	-	-	-	0.19	0.37	0.37	1		
E2D	-	-	-	-	-	-	-	0.11	0.10	0.06	0.17	0.12	0.10	0.12	0.14	0.10	0.20	0.10	1	
E2E	-	-	-	-	-	-	-	0.08	0.17	0.10	0.19	-	0.23	-	0.09	0.15	0.22	0.31	-	1

Fig. 2. Arthropod similarity matrix between the sections of each cave. (a) In Dona Rita's cave, the similarity on axis a reaches zero on E1D × H1D; therefore, the ecotone in this cave is located between E1C and H1C (12 m). (b) In Retiro's cave, the similarity on axis a reaches zero on E1E × H1E; therefore, the ecotone in this cave is located between E1D and H1D (16 m).

$R = -0.90$, $P < 0.01$, $F_{1,20} = 73.25$; and $R = 0.89$, $P < 0.01$, $F_{1,20} = 80.19$, respectively).

One hundred and nineteen morphospecies of 20 orders were collected in Retiro's cave. Species richness correlated significantly to the distance from the cave entrance ($R = -0.71$, $P < 0.01$, $F_{1,20} = 20.65$), moisture ($R = -0.73$, $P < 0.01$, $F_{1,20} = 24.96$), luminosity ($R = 0.90$, $P < 0.01$, $F_{1,20} = 73.54$) and temperature ($R = 0.84$; $P < 0.01$, $F_{1,20} = 49.80$).

Similarity matrix

The similarity matrix for Retiro's cave can be seen in Figure 2b. Observing axis a represented in Figure 1, note that the similarity drops to zero at the intersection of sections H1E and E1E (10 m from the entrance). This result suggests that the zone between sections H1D and E1D (the last point of axis of the matrix in which there is similarity between the faunas present) is the momentary ecotone (16 m long).

The richness of Retiro's cave was higher in the ecotone zone ($r = 86$), intermediate in the epigean environment ($r = 39$) and lower in the hypogean environment ($r = 12$).

Diversity indexes for the hypogean, epigean and ecotone regions were $H' = 0.48$, $H' = 3.29$ and $H' = 3.02$, respectively. The diversities were significantly different between the hypogean and epigean ($t = 22.47$, d.f. = 217.9, $P < 0.05$), hypogean and ecotone ($t = 22.96$, d.f. = 570.1, $P < 0.05$) and epigean and ecotone zones ($t = 2.27$, d.f. = 199.5, $P > 0.05$).

Similarity, as in Dona Rita's cave, was higher between the ecotone and the epigean environments ($C_s = 0.320$), intermediate between the ecotone and the hypogean environments ($C_s = 0.102$) and lower between the epigean and hypogean environments ($C_s = 0.039$).

Total abundance and distribution of organisms

A total of 2078 individuals (841 in Retiro's cave and 1237 in Dona Rita's cave), belonging to at least 88 families of the orders Acarina, Araneida, Opilionida, Pseudoscorpionida, Chilopoda, Diplopoda, Pauropoda, Archeognatha, Caelifera, Coleoptera, Collembola, Dermaptera, Dictyoptera, Diptera, Ensifera, Heteroptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Mantodea, Neuroptera, Phasmida, Psocoptera, Thysanoptera, Zygentoma and Isopoda were sampled.

Some families were found exclusively in one of the environmental compartments: hypogean, epigean or ecotone. Those families exclusively from the ecotone were separated according to their presence in the internal (hypogean) or external (epigean) compartments.

Sparassidae and Gnaphosidae (Araneida), Pauropoda, Acrididae (Caelifera), Chrysomelidae, Melandryidae (Coleoptera) and an unidentified Lepidoptera were found only in the epigean environment.

The groups present exclusively in the epigean compartment of the ecotone were Dipluridae and Theraphosidae (Araneida), Chthoniidae (Pseudoscorpionida), Geophilomorpha (Chilopoda), Scarabaeidae (Coleoptera), Fanniidae (Diptera), Scutelleridae, Lygaeidae, Pentatomidae and Alydidae (Heteroptera), and Mantidae (Mantodea).

In the hypogean compartment of the ecotone, the exclusive groups found were Mimetidae and Miturgidae (Araneida), Geogarypidae (Pseudoscorpionida), Cerambycidae (Coleoptera), Milichiidae, Tachinidae and Tephritidae (Diptera), Myrmeleontidae (Neuroptera), and Thysanoptera. The families Segestriidae (Araneida), Chernetidae (Pseudoscorpionida), Leiodidae (Coleoptera), Hesperiidae (Lepidoptera) and Porcellionidae (Isopoda) were found exclusively in the hypogean environment.

The groups found in at least two different environments were Ctenidae, Sicariidae, Tetragnathidae, Theridiosomatidae, Araneidae, Pholcidae, Corinidae, Scytodidae, Lynphiidae, Salticidae, Theridiidae, Deinopidae, Lycosidae, Philodromidae and Thomisidae (Araneida), Acarina, Lithobiomorpha (Chilopoda), Spirostreptida, Glomeridesmida, Polydesmida, Spirobolida and Polyxenida (Diplopoda), Machilidae (Archeognatha), Staphylinidae, Curculionidae, Tenebrionidae and Carabidae (Coleoptera), Entomobryidae and Tomoceridae (Collembola), Psycidae, Cecidomyiidae, Phoridae, Tipulidae, Drosophilidae, Mycetophilidae and Culicidae (Diptera), Phalangopsidae (Ensifera), Reduviidae, Ploiaridae, Tingidae and Pyrrhocoridae (Heteroptera), Cixiidae (Homoptera), Formicidae (Hymenoptera), Nasutitermitidae (Isoptera), Noctuidae and Tineidae (Lepidoptera), Chrysopidae (Neuroptera), Phasmidae (Phasmida), Psyllipsocidae (Pscooptera), Nicoletiidae (Zygentoma), Dubioniscidae (Isopoda), Dictyoptera and Dermaptera.

DISCUSSION

In most studies concerning ecotones, the delimitation of the ecotone zone is subjective and is often difficult to precisely define the ecotone area and quantify its importance in the functioning underground systems (Gibert 1997). There are few empirical studies indicating ecotone dimensions and none has been carried out in caves (Hobbs 1986; Delcourt & Delcourt 1987; Lloyd *et al.* 2000). The first assay to identify the exact position of the ecotone was performed by Lloyd *et al.* (2000) using detrended correspondence analysis. The use of the similarity matrix to delimit

ecotones is proposed for the first time in the present study.

It is important to stress that this method allows the definition of a momentary ecotone, but it does not mean that the ecotone is static. In fact, ecotones can be as ephemeral as their contiguous environments (Hansen *et al.* 1988a,b). Eventual expansions or retractions of the ecotone could be linked to external environmental changes. Thus, the different compartments of the ecotone might expand in moist seasons and retract in dry seasons. However, the dynamics of arthropod movements between the different ecotone compartments remain largely unknown and merit further research.

A criticism regarding ecotone dimensions is that they are frequently seen only in two dimensions and do not consider that the landscape is 3-D (Hansen *et al.* 1988a). In a pasture, a third dimension is negligible, as vegetation height is very low. Conversely, height must be considered in a forest (and great importance must be given to the third dimension). In the present study, the ecotone characterizations were based on ground arthropod communities, and assumed a minimum third dimension. This approach has been adopted considering that, in the cave environment, almost the whole fauna is associated with the organic matter brought from the external environment and concentrated on the soil surface. Therefore, most of the

invertebrate cave organisms are found in this region. The methodology for ecotone delimitation can thus be applied in many different situations, from pastures to forests, as long as the kind of sampling design considers the correct dimensional approach.

The more extensive ecotone of Retiro's cave might be a result of the dense vegetation covering the outer region of the cave. Because the area in front of Dona Rita's cave is a pasture with sparse vegetation, the diversity of microhabitats potentially suitable to the hypogean fauna is reduced. Many studies have already demonstrated the positive correlation between plant diversity and arthropod diversity (Murdoch *et al.* 1972; Southwood *et al.* 1979; Siemann 1998; Lambrinos 2000). As Retiro's cave has a rainforest close to its entrance (which reduces the impact of sunlight and temperature variation, and increases humidity and availability of microhabitats), a higher superposition between both communities (epigean and hypogean) is possible, increasing the ecotone area.

The relatively low diversity found into both caves is not surprising, because cave systems are very restrictive environments to many invertebrate species (e.g. because of the permanent lack of light, absence of primary producers and consequent low availability of food resources; Poulson & White 1969; Culver 1982). Transition areas have already been identified as being responsible for preventing the movement of animals

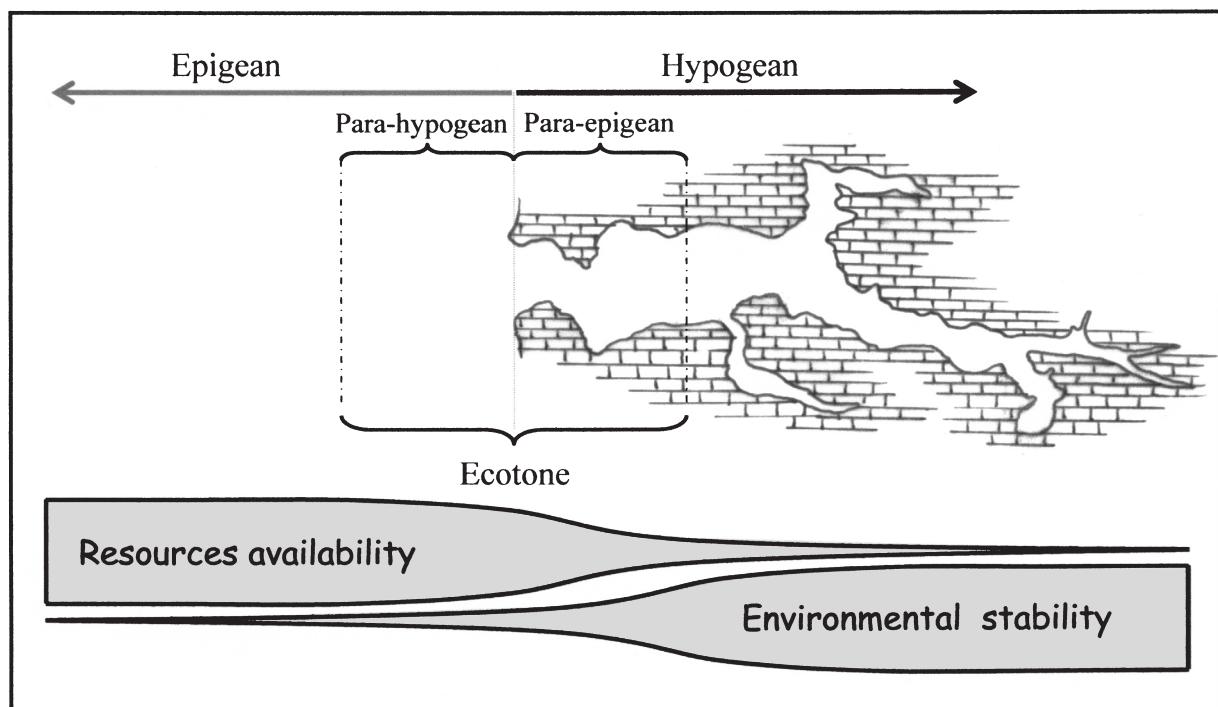


Fig. 3. Different regions of the epigean–ecotone–hypogean system. The ecotone is located in a zone characterized by an equilibrium between environmental stability and resource availability. Hypogean and epigean communities are located in opposite extremes – the former on a stable environment in a zone of low resource availability and the latter in a zone of low environmental stability with high resource availability.

between adjacent systems (Gates & Gysel 1978; Wunderle *et al.* 1987; Hansen *et al.* 1988b). The ecotone between the epigean and hypogean environments works as a selective filter, or as a differentially permeable membrane, as suggested by Hansen *et al.* (1988a), through which only species pre-adapted to the cave environment are able to pass.

Culver and Poulson (1970) found, in the entrance of Cathedral cave, Kentucky, USA, a species diversity value slightly higher than that inside or outside the cave. Compared to Culver and Poulson's finding, two different situations were observed at the caves in the present study.

The ecotone in Retiro's cave showed a slightly lower diversity index compared with the epigean environment. Nevertheless, the 16-m area of the ecotone was larger than the 12 m sampled in the epigean environment, and the dimensions of the area could influence richness and diversity (higher food resource and micro-habitat availability; Ferreira 1998). Therefore, the value for the diversity of the ecotone might have been overestimated. The real diversity should probably be intermediate if compared with the two environments (epigean and hypogean).

The diversity of Retiro's cave supports the hypothesis of Hansen *et al.* (1988a) to explain an intermediate diversity in the ecotone. An intermediate diversity could be expected in those ecotones where one of the adjacent areas is relatively poor in species, as was found in the restrictive environment inside Retiro's cave, and the other is rich in species, as was found outside Retiro's cave.

The diversity in the ecotone of Dona Rita's cave was slightly higher than that of the epigean environment, even considering that the sampling area of the former was smaller than that of the latter (12 and 16 m, respectively). The environmental conditions at the entrance of Dona Rita's cave are more stable than those of the pasture outside the cave, and the resource availability apparently did not suffer a great decrease. Therefore, the ecotone is more suitable for organisms, and this could explain the greatest diversity in the ecotone.

Culver and Poulson (1970) demonstrated that the fauna at the entrance zone of Cathedral cave had a higher similarity to the fauna inside than outside the cave. However, in the present study, a higher similarity was observed between the epigean environment and the ecotone region in both caves, suggesting that the external environment in tropical systems is more important as a source of potential species to colonize the ecotone. This also indicates that the ecotone could function as a filter between the two adjacent environments, allowing only pre-adapted organisms to cross it and thus to colonize the cave.

The three types of communities proposed by Ferreira and Martins (2001) refer to hypogean com-

munities. In the present study, we suggest the addition of another component to this classification, considering that the ecotone can be divided into epigean and hypogean zones. The para-epigean community previously mentioned, is part of the hypogean compartment, and the 'para-hypogean' community proposed here is present in the epigean compartment of the ecotone. In spite of being located in the epigean compartment, the para-hypogean community is important to the ecotone dynamics, as it can provide a constant flux of organisms from the entrance zone.

Coleoptera (Leiodidae), Isopoda (Platyarthridae), Psocoptera (Psyllipsocidae) and Pseudoscorpionida (Chernetidae) are commonly found inside caves, being therefore components of hypogean communities. Species in the hypogean environment have an advantage in terms of environmental stability, but share lower quantities of available resources. Conversely, organisms in epigean regions live in an environment with abundant resources but lower environmental stability. These organisms are able to exploit the moderate resource availability associated with the intermediate environmental stability of cave entrances. Neuroptera (Myrmeleontidae), spiders (Salticidae and Pholcidae) and Diptera (Culicidae and Psychodidae) form the para-epigean and para-hypogean communities. Thus, the ecotone zone where the para-epigean and para-hypogean communities occur functions as a selective barrier between organisms able to exploit each habitat type.

We suggest a graphical model representing the different regions of the epigean-hypogean system and the location of different communities in relation to stability levels and resource abundance in a hypothetical cave (Fig. 3).

The delimitation of an ecotone is fundamental to the study of different processes that exist in such zones and this new methodology aims to make new studies encompassing these regions easier and more stimulating.

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REFERENCES

- Bretschko G. (1995) River/land ecotones: scales and patterns. *Hydrobiologia* **303**, 83–91.

- Culver D. C. (1982) *Cave Life. Evolution and Ecology*. Harvard University Press, Cambridge, MA.
- Culver D. C. & Poulsen T. L. (1970) Community boundaries: Faunal diversity around a cave entrance. *Annales Spéléologie* **25**, 853–60.
- Delcourt P. A. & Delcourt H. R. (1987) *Long-Term Forest Dynamics of the Temperate Zone*. Springer-Verlag, New York.
- Delcourt P. A. & Delcourt H. R. (1992) Ecotone dynamics in space and time. In: *Landscape Boundaries: Consequences for Biotic Diversity and Landscape Flows* (eds A. J. Hansen & F. di Castri); Ecological Studies 92; pp. 19–54. Springer-Verlag, New York.
- Dunning J. B., Danielson B. J., Pullian H. R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos* **65**, 169–75.
- Ferreira R. L. (1998) Ecologia de comunidades cavernícolas associadas a depósitos de guano de morcegos. Dissertação de Mestrado em Ecologia, Conservação e Manejo de Vida Silvestre da Universidade Federal de Minas Gerais, MG, Brasil.
- Ferreira R. L. & Martins R. P. (1999) Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Trop. Zool.* **12**, 231–52.
- Ferreira R. L. & Martins R. P. (2001) Cavernas em risco de ‘extinção’. *Ciência Hoje* **29**, 20–28.
- Gates J. E. & Gysel L. W. (1978) Avian nest dispersion and fledgling success in field-forest ecotones. *Ecology* **59**, 871–83.
- Gers C. (1998) Diversity of energy fluxes and interactions between arthropod communities: from soil to cave. *Acta Oecologica* **19**, 205–13.
- Gibert J. (1997) The importance of ecotones in karstland. In: *Conservation and Protection of the Biota of Karst* (eds D. Sasowsky, D. W. Fong & E. L. White) pp. 17–19. Karst Water Institute, University of Akron, Akron, OH.
- Gibert J., Dole-Olivier M. J., Marmonier P., Vervier P. H. (1990) Surface water-groundwater ecotones. In: *The Ecology and Management of Aquatic-Terrestrial Ecotones* (eds R. J. Naiman & H. Decamps) pp. 199–204. Parthenon Publications, Carnforth.
- Gibert J., Mathieu J., Fournier F. (1997) *Groundwater/Surface Water Ecotones: Biological and Hydrological Interactions and Management Options*. International Hydrobiolgy Series. Cambridge University Press, Cambridge.
- Hansen A. J. & di Castri F. (1992) *Landscape Boundaries: Consequences for Biotic Diversity and Landscape Flows*. Ecological Studies 92. Springer-Verlag, New York.
- Hansen A. J., di Castri F., Naiman R. J. (1988a) Ecotones: what and why? *Biol. Int. Special Issue* **17**, 9–46.
- Hansen A. J., di Castri F., Risser P. G. (1988b) A new SCOPE project. Ecotones in a changing environment: The theory and management of landscape boundaries. *Biol. Int. Special Issue* **17**, 137–63.
- Hobbs E. R. (1986) Characterizing the boundary between California annual grassland and coastal sage scrub with differential profiles. *Végetatio* **65**, 115–26.
- Holland M. M. (1993) Management of land/inland water ecotones: needs for regional approaches to achieve sustainable ecological systems. *Hydrobiologia* **251**, 331–40.
- Lambrinos J. G. (2000) The impact of invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered Mediterranean-type shrub land in California. *Divers. Distrib.* **6**, 217–31.
- Lloyd K. M., McQueen A. A. M., Lee B. J., Wilson R. C. B., Walker S., Wilson J. B. (2000) Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. *J. Vég. Sci.* **11**, 903–10.
- Magurran A. E. (1988) *Ecological Diversity and its Measurement*. Croom-Helm Limited, London.
- Murdoch W. W., Evans F. C., Peterson C. H. (1972) Diversity and pattern in plants and insects. *Ecology* **53**, 819–29.
- Naiman R. J. & Decamps H. (1990) *The Ecology and Management of Aquatic-Terrestrial Ecotones*. United Nations Educational, Scientific and Cultural Organization (UNESCO), Parthenon Press Publications, Carnforth.
- Naiman R. J., Holland M. M., Décamps H., Risser P. G. (1988) A new UNESCO program: Research and management of land/inland water ecotones. *Biol. Int. Special Issue* **17**, 107–36.
- Neilson R. P. (1993) Transient ecotone response to climatic change: some conceptual and modeling approaches. *Ecol. Applic.* **3**, 385–95.
- Odum E. P. (1983) *Basic Ecology*. Saunders College Publishing, Philadelphia, PA.
- Peck S. B. (1976) The effect of cave entrances on the distribution of cave-inhabiting terrestrial arthropods. *Int. J. Speleol.* **8**, 309–21.
- Petts G. E. (1990) The role of ecotones in aquatic landscape management. In: *The Ecology and Management of Aquatic-Terrestrial Ecotones* (eds R. J. Naiman & H. Decamps). pp. 227–61. United Nations Educational, Scientific and Cultural Organization (UNESCO), Parthenon Press Publications, Carnforth.
- Poulsen T. L. & White W. B. (1969) The cave environment. *Science* **165**, 971–81.
- Risser P. G. (1990) The ecological importance of land/land-water ecotones. In: *The Ecology and Management of Aquatic-Terrestrial Ecotones* (eds R. J. Naiman & H. Decamps) pp. 7–21. United Nations Educational, Scientific and Cultural Organization (UNESCO), Parthenon Press Publications, Carnforth.
- Risser P. G. (1995) The status of the science examining ecotones. *Bioscience* **45**, 318–25.
- Siemann E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* **79**, 2057–70.
- Skalski A. W. (1973) A study on the immigration of epigean invertebrates into caves. In: *International Speleology. Proceedings of the 6th International Congress of Speleology; August 31–September 18 1973, Olomouc, Czechoslovakia* (ed. Vladmir Panos) pp. 243–51. Olomouc, Czechoslovakia.
- Southwood T. R. E., Brown V. K., Reader P. M. (1979) The relationships of plant and insect diversities in succession. *Biol. J. Linn. Soc.* **12**, 327–48.
- Wiens J. A., Crawford C. S., Gosz J. R. (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* **45**, 421–7.
- Wunderle J. M., Diaz A., Velazquez I., Schawon R. (1987) Forest openings and the distribution of understory birds in a Puerto Rican rainforest. *Wilson Bull.* **99**, 22–37.