Sharing the space: coexistence among terrestrial predators in Neotropical caves

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ABSTRACT

The subterranean environment has a set of unique characteristics, including low thermic variation, high relative humidity, areas with total absence of light and high dependence on nutrient input from the epigean environment. Such characteristics promote distinct ecological conditions that support the existence of unique communities. In this work, we studied seven caves in the Presidente Olegário municipality, Minas Gerais state, Southeast Brazil, to determine their richness of predatory species, to understand how they are spatially distributed in the cave and whether their distribution is influenced by competition and/or predation. We carried out five surveys of the caves, with each cave divided into sampling plots. We collected fauna within the plots using a manual search method. The collected animals were fixed in 70% ethanol for later identification. We performed a canonical correspondence analysis to verify the spatial distribution and substrate preference of each species, and selected five species for agonistic interaction testing in the laboratory. We found a great richness of predators in the caves, with 79 species distributed among 22 families of spiders, five families of pseudoscorpions, three families of chilopods, two families of opilionids and one family each of scorpions and heteroptera. Spiders were the most species diverse and abundant of all arthropods we found in the caves. We recorded evidence of competition among some pairs of species but, in general, the spatial distribution of the predatory community in the interior of the caves seems to be unrelated to interspecies competition. The laboratory pairings support our field observations that most species merely share space, rather than exhibiting aggressive or predatory behaviour.

Introduction

The subterranean environment or hypogean realm is defined as the interconnected spaces of the subsurface, varying in size from millimetres to hundreds of metres (Culver and Pipan 2009). These spaces can be filled with air or water and exhibit a set of unique environment characteristics, including low thermic variation, high relative humidity, the total absence of

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light and dependence on nutrient input from the epigean environment (Juberthie 2000; Culver and Pipan 2009).

Terrestrial subterranean habitats include air pockets, caves, crevices, cracks, burrows, mines (artificial subterranean environments) and the interfaces between these habitats and soil (superficial subterranean environment) (Camacho 1992). Zonation in subterranean environments is a function of distance from the epigean environment interface. Identified zones include the entrance zone, where there is direct light and climate influence from the exterior; the twilight zone, where there is no direct incidence of solar light; and the aphotic zone, where there is a total and permanent absence of light. The aphotic zone is the least affected by surface conditions (Poulson and White 1969; Howarth 1979).

The classification of subterranean organisms, according to Schiner (1854), and modified by Racovitza (1907), is based on the degree of association with, and dependence on, the hypogean environment. This classification includes the trogloxenes, which often occupy the hypogean realm but must periodically return to the surface to acquire the necessary resources to complete their life cycle; troglophiles, which may complete their life cycle in either hypogean or epigean environments; and troglobites, which are restricted to the subterranean environment, and often exhibit troglomorphy.

The absence of photosynthetic organisms in the deepest and darkest areas of caves results in food scarcity, and animals that live in these habitats primarily depend on allochthonous energy resources, brought into caves by wind, floods, rivers and accidental and/or trogloxenic animals (Poulson 2012). This lack of primary producers limits the subterranean trophic chains to consumers, including predators and/or detritivores (Gibert and Deharveng 2002). The resultant reduction in trophic diversity found in caves, compared with the epigean environment, reduces its complexity, making cave communities excellent natural laboratories for ecological studies (Poulson and White 1969; Culver 1982, 2012).

Most studies of ecological interactions in Brazilian caves have focused on proposed food webs, potential predation or observations of interactions (Trajano and Gnaspini 1991; Gnaspini 1992; Ferreira and Martins 1998; Gnaspini and Trajano 2000; Ferreira et al. 2011; Souza-Silva and Ferreira 2014). Indeed, most studies concerning competition in cave habitats have been conducted using aquatic communities in temperate zones (Culver 1970a, 1970b, 1971a, 1971b, 1973, 1975, 1994; Sket 1977; Howarth 1983; Culver and Pipan 2009), and have not addressed terrestrial communities. The population approach is most commonly used for these studies, wherein the growth of two interacting populations is observed during contact or, when contact is prevented, through experimental manipulation (Gause 1934, 1935; Connell 1961; Tilman 1977; Damgaard 2008).

In Neotropical caves, the invertebrates considered true terrestrial predators (*sensu* Begon et al. 2006) include arachnids, such as Araneae, Scorpiones, Pseudoscorpiones, Opiliones and Amblypygi; insects, such as Heteroptera and Coleoptera; and Chilopoda (centipedes), such as Scolopendromorpha, Geophilomorpha, Scutigeromorpha and Lithobiomorpha (Trajano and Gnaspini 1991; Culver and Shear 2012; Reddell 2012).

Although some studies have suggested that subterranean organisms are generalists in terms of dietary preferences (Huppop 2012; Poulson 2012), arachnids, such as spiders and scorpions, some reduviids (Heteroptera) and several groups of centipedes remain strict predators in this environment and are generally considered the top predators (Culver and Shear 2012; Reddell 2012).

The presence of more than one species occupying the same trophic level in a food- and space-limited environment suggests the potential for interspecific competition, defined as the utilisation of one common resource by two or more distinct species, with a consequence of limitations of population size for both of them (Gause 1934, 1935; Milne 1961; Culver 2012).

This study was a preliminary survey to examine the ecological processes that may drive the spatial distribution, habitat occupation and interactions among the species-rich terrestrial predatory communities of Neotropical caves.

Materials and methods

Study area

We conducted five surveys (between September 2013 and September 2014) in seven caves (Table 1) located within an approximately 20 km long limestone outcrop, in the Presidente Olegário municipality, Minas Gerais State, Southeast Brazil (Figure 1 (a–c)). The karst of the region belongs to the Bambuí group, dating from the Later Proterozoic (Grupo Pierre Martin de Espeleologia, GPME 2009, 2011).

The altitude is ca. 900 m, and the climate is predominantly tropical sub-warm and semi-humid, with a five-month dry season (from April to August) (Nimer 1989). According to Ab'Saber (1977), the municipality is within the Morphoclimatic Domain of the Cerrado (savannah-like vegetation).

Field methodology

We divided each cave into sampling plots (Table 1) based on the number of chambers in each cave. Plots were made as large as possible in each room to maximise floor and wall coverage. Sampling effort was proportional for each plot based on the mean plot area for each cave (Table 1). Within each plot we recorded the location of each observed individual, including the type of substrate (Figure 2 (a–d)); we estimated the developmental stage (juvenile or adult) and defined a behaviour category (e.g., stationary, walking about or feeding) for each individual.

Table 1. Geographical location, environmental features and sampling plot parameters defined for the seven caves in this study in Presidente Olegário, Minas Gerais state, Southeast Brazil. Legend: GC = geographical coordinates; CL = cave length; AZ = aphotic zone; G = guano; PR = penetrating plant roots; N = number of sampling plots; PA = plot area (mean); TSE = total sampling effort (mean); SEP = sampling effort by plot (mean).

| Caves	GC	CL (m)	AZ	G	PR	N	PA	TSE	SEP
Lapa Vereda da Palha	18°15′18.77″S, 46°07′33.63″W	2500	X	X		6	33.9 m^2	6 h	1 h
Lapa da Fazenda São Bernardo	18°16′36.83″S, 46°06′45.52″W	2000	X		X	5	35.6 m^2	6 h	1 h/12 min
Gruta da Juruva	18°19′19.20″S, 46°04′52.90″W	1103	X	X		4	22.8 m^2	3 h	45 min
Lapa Zé de Sidinei	18°05′62.48″S, 46°05′40.64″W	650	X	X		3	159 m^2	4 h	1 h/20 min
Lapa Arco da Lapa	18°12′31.3″S, 46°08′53.3″W	500	X	X	X	4	30.8 m^2	5 h	1 h/15 min
Lapa do Moacir	18°11′09.68″S, 46°09′34.50″W	200		X	X	2	28.6 m^2	2 h	1 h
Toca do Charco	18°11′05.64″S, 46°09′39.31″W	80			X	1	24.4 m^2	1 h	1 h
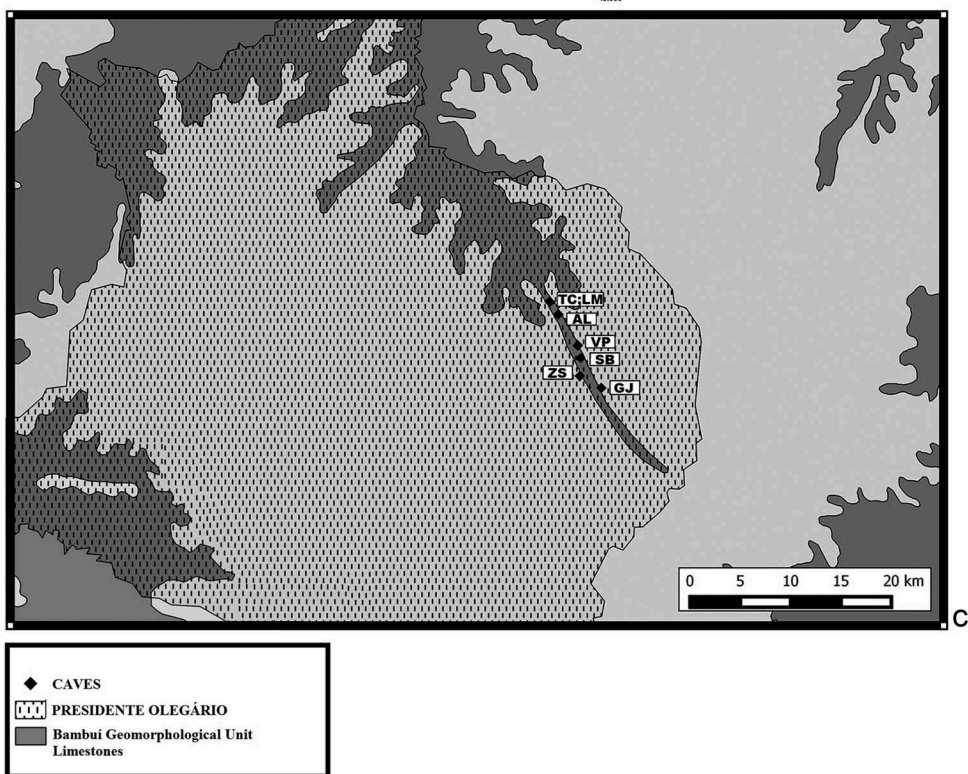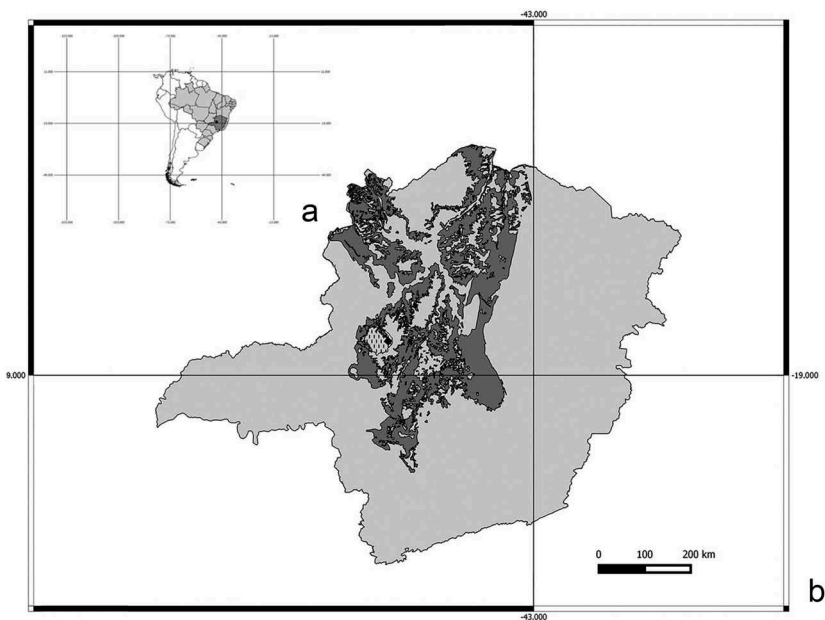
Figure 1. (a) Neotropical region, showing the location of Brazil and the state of Minas Gerais. (b) Minas Gerais and Bambuí Geomorphological Unit, showing the location of the Presidente Olegário municipality. (c) Presidente Olegário municipality with the studied caves. Legend: TC:LM = Toca do Charco and Lapa do Moacir; AL = Lapa Arco da Lapa; VP = Lapa Vereda da Palha; SB = Lapa da Fazenda São Bernardo; ZS = Lapa Zé de Sidinei and GJ = Gruta da Juruva.

Figure 2. Substrate categories utilised for the field observations and the canonical correspondence analysis (CCA). Rocky substrates: (a) wall and (b) unconsolidated substrate (scale = 5 cm). Organic substrates: (c) guano (forceps for scale) and (d) leaf litter. Photographs by the authors.

During these observations, we measured the temperature and relative humidity of the air at each plot using a digital thermohygrometer (*THAL-300*; precision, RH: ±1.2%; temp: ±1.2°C) to obtain a gradient for those variables. The observed individuals were collected and fixed in 70% ethanol for later identification.

Laboratory tests: agonistic interactions

We selected the following five species as models for agonistic behavioural testing: *Enoploctenus cyclothorax* and *Isoctenus* sp. (both Araneae: Ctenidae); *Loxosceles similis* (Araneae: Sicariidae); *Eusarcus hastatus* and *Mitogoniella taquara* (both Opiliones: Gonyleptidae). Species selection was made based on body sizes large enough to permit accurate species identification and observations in the field, species whose abundance was relatively high, and that occurred in at least two of the studied caves (Table 2).

Table 2. Terrestrial predatory species from the caves of Presidente Olegário, Minas Gerais, Southeast Brazil, selected to perform the agonistic behavioural tests in the laboratory. Legend: VP = Lapa Vereda da Palha; SB = Lapa da Fazenda São Bernardo; ZS = Lapa Zé de Sidinei; AL = Lapa Arco da Lapa; LM = Lapa do Moacir; TC = Toca do Charco and GJ = Gruta da Juruva; N = number of captured individuals; FG = functional group; Trp = troglophile; Trx = trogloxene; SUBS = substrate; R = rocky substrates; OM = organic substrates.

Species	Occurrence							N	FG	SUBS
	VP	SB	ZS	AL	LM	TC	GJ			
Araneae										
Enoploctenus cyclothorax	X	X	X	X	X	X	X	25	Trp	R
Isoctenus sp.	X	X	X	X	X	X	X	20	Trp	R
Loxosceles similis	X			X			X	25	Trp	R
Opiliones										
Eusarcus hastatus		X				X		20	Trp	OM
Mitogoniella taquara	X	X		X				20	Trx	R

Five individuals of each species, captured during each visit to the caves, were transported to the laboratory, with the following exceptions: opilionids were not collected during the second survey, and one spider species (*Isoctenus* sp.) was not collected during the fourth survey (Table 2). The animals were placed in 200-ml plastic bottles or Styrofoam boxes, containing moistened cotton, and transported to the laboratory in thermal bags. In the laboratory, the individuals were accommodated in terraria

Figure 3. (a, b) Terraria with substrates for housing individual test animals in the laboratory (scale = 30 cm). (c, d) Terraria used for the agonistic interaction tests in the laboratory. Photos: L.P.A. Resende.

containing cave substrates under controlled conditions of temperature and humidity, and in total and permanent darkness (Figure 3 (a–b)). The spiders were fed small crickets, and opilionids were fed lyophilised (freeze-dried) chironomid larvae (Diptera: Chironomidae) once a week.

In order to develop the agonistic tests, the individuals were first submitted to a starvation period of two weeks. After this period, one individual of each species pair was placed in the same terrarium (Figure 3 (c–d)), and they were monitored for two distinct periods: a short period (eight hours) and a long period (72 hours). The paired animals were observed at one-hour intervals during the short period and at 12-hour intervals during the long period. If one individual ate the other, the experiment was ended.

Data analysis

We performed canonical correspondence analysis (CCA; Ter Braak 1986) on our field observations and environmental parameters to determine the spatial segregation among the species in the caves. This test was also applied to the abundance data set of the predatory community as a whole, and for the five model species individually. To calculate CCA, we divided each sampling plot into two main substrate categories (rocky substrates and organic substrates) and assigned a numerical value for each one (Table 3). Furthermore, we added the zonation of the caves as an additional environmental variable, assigning a numerical value for each zone according to its light level, determined by our visual perception of luminosity (Table 3).

We calculated the percentage of predation and agonistic interaction among the paired species. We compared the frequency of occurrence of agonistic events between the species using the Kruskal-Wallis test and applied the post-hoc Mann-Whitney test (Zar 1996). We adapted the definition of agonistic behaviour from Schuck-Paim (2007) and Riechert (1979, 1984, 1986) who considered it to be ritualised displays that organisms manifest when faced with conflicting interests, often the access of some limited resource that is vital for both of them. Aggression: physical contact in which the purpose is to harm the opponent. Submission: when one individual, often the biggest one, wins a contest and repels the opponent. Predation/cannibalism: when one individual just preys on and eats the other without any ritualised intimidation display; this is called cannibalism when the individuals belong to the same species. Avoidance/coexistence was considered to be when the individuals remain in the same place without interacting

Table 3. Numerical values and gradients attributed to the substrate categories and zonation presents in the studied caves in Presidente Olegário, Minas Gerais state, Southeast Brazil, for the development of the canonical correspondence analysis (CCA). Legend: Subs Cat = substrate categories; R = rocky substrates; OM = organic substrates; N = numerical value; Grad = gradient; L-OM = lack of organic matter; W-OM = with organic matter. Zone: Ent = entrance; Tw = twilight; Aph = aphotic. L = intense light level; LL = low light level and WL = without light.

Subs Cat	N	Grad	Zone	Grad	N
R	0	L-O.M	Ent	L	2
			Tw	LL	1
OM	1	W-OM			
			Aph	WL	0

with each other, this definition being made by us. The tests were performed using the PAST 3.02 program (Hamer et al. 2001).

Results

Predatory richness

We detected a high richness of predators in the caves, with a total of 79 species, including 55 spiders within 22 families (54 Araneomorphae and one Mygalomorphae species), eight pseudoscorpions in five families, five opilionids in two families, five centipedes in three families, five heteropterans in one family and one scorpion. The species list is presented in Appendix 1.

The spiders were dominant in both number of species (55 species, 68.3%) and abundance (705 individuals, 75.8%), in which the ctenid spider *Enoploctenus cyclothorax* was the most abundant with 140 individuals (15% of the total).

Field observations

We observed 228 spiders building webs on cave walls, within all cave zones, particularly those belonging to the families Pholcidae, Theridiidae and Theridiosomatidae. On three occasions, we found emesine reduviids associated with pholcid webs.

Approximately 170 ctenid spiders, *Isoctenus* sp. and *Enoploctenus cyclothorax* were observed on the walls, usually motionless (76% of the observations), with legs extended in a typical resting posture. Nevertheless, we did observe these spiders feeding on crickets (three observations) and walking from one hunting territory to another (40 observations). A third ctenid species, *Ancylometes concolor*, was less abundant (only four individuals) on the walls close to water bodies.

Individuals of other spider families (Anapidae; Caponiidae; Hahniidae; Lyniphiidae; Symphytognathidae and Tetragnathidae) were observed less frequently, mainly because these are cryptic species, that hide under rocks and concretions, and in leaf litter. The same pattern was detected for centipedes (Scolopendromorpha, Geophilomorpha and Lithobiomorpha) that were found only among damp vegetal debris.

About 63% of the pseudoscorpion *Spelaeochernes* sp. were found on guano deposits, along with small populations (less than 20 individuals) of the theridiid spiders *Nesticodes rufipes* and *Cryptachea parana*. These two theridiids never shared the same guano pile.

The opilionids *Mitogoniella taquara* and *Discocyrtus* sp. were frequently observed on parietal substrates; the former was exposed on the walls in 96% of the observations, and the latter primarily hidden in rock crevices (75% of the observations). A third opilionid species, *Eusarcus hastatus*, was associated with vegetal debris; it was observed foraging on the trunks of rotting trees in 80% of the observations.

Canonical correspondence analysis (CCA)

The results of the CCA analysis for the predatory community are presented in ordering diagrams for sampling plots (Figure 4) and species (Figure 5). The eigenvalues for the
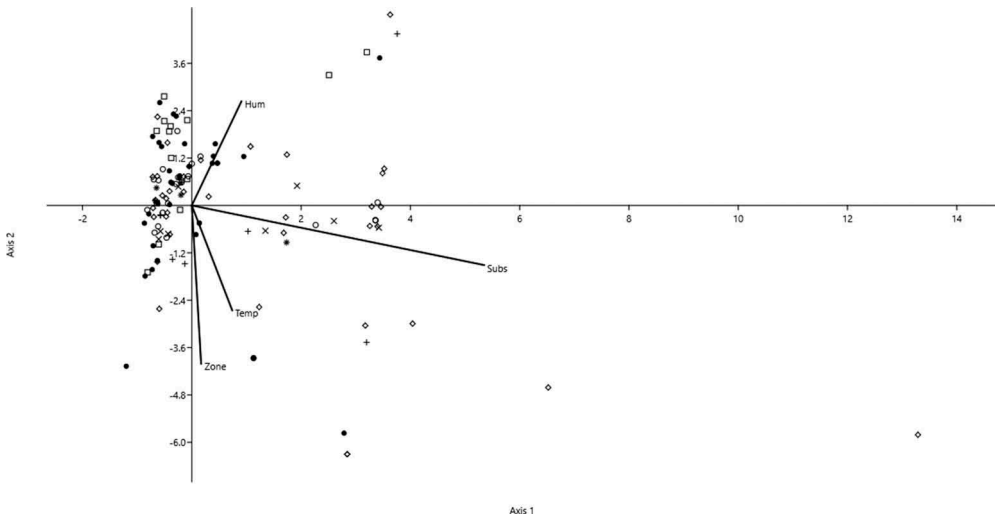
Figure 4. Ordering diagram of the sampling plots produced by the canonical correspondence analysis (CCA). The plots are represented by symbols and the environmental variables by vectors. Legend: • = Lapa Vereda da Palha; □ = Lapa Zé de Sidinei; ◊ = Lapa da Fazenda São Bernardo; ○ = Lapa Arco da Lapa; x = Toca do Charco; * = Gruta da Juruva + = Lapa do Moacir; Hum = humidity; Temp = temperature; Subs = substrate.
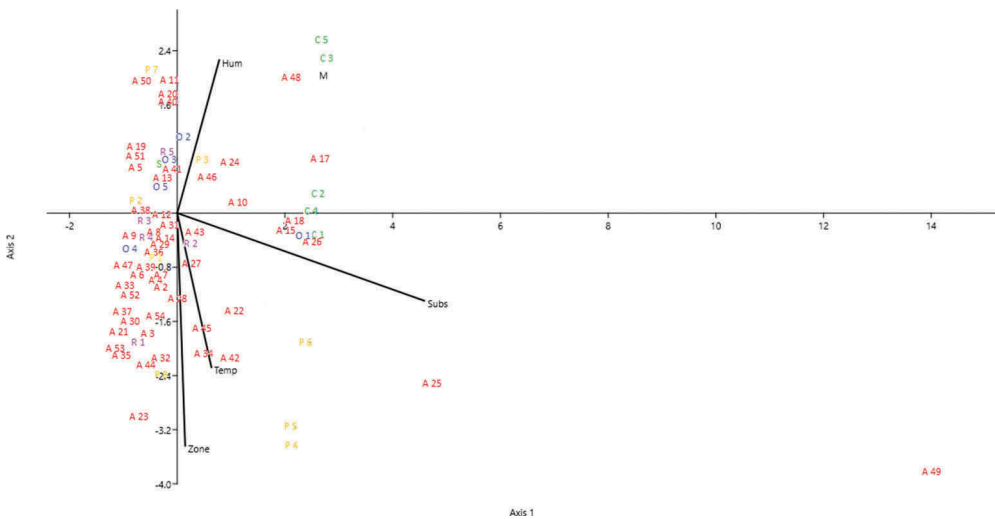

Figure 5. Ordering diagram of the species produced by the canonical correspondence analysis (CCA). Legend: Hum = humidity; Temp = temperature; Subs = substrate. The codes for species are given in Appendix 1.

first two axes of the ordering were 0.470 and 0.289, respectively, with the first axis explaining 51.68% of the total variance and the second axis explaining 31.86%.

All variables, except for substrate, showed a strong correlation with the second axis (temperature = axis 2: −0.379; humidity = axis 2: 0.376; zone = axis 2: −0.572; substrate = axis 1: 0.764). The Monte Carlo permutation test showed that the correlations

among the abundance of species and the environmental variables were significant ($p < 0.05$ for axes 1, 2 and 3).

The ordering diagram for sampling plots on axis 2 (Figure 4) presents a temperature gradient from the lower to the upper side of the diagram, in which the lower plots represent the warmest temperatures and the upper plots the colder. For the humidity, we observed the opposite trend, where the upper plots represent higher humidity and the lower plots lower humidity. Axis 2 shows a light-level gradient, in which the lighter plots are located on the lower side of the diagram and the darker plots on the upper side. Most of the plots were located in the centre of the diagram. These are the in the twilight zone, with mild temperatures, moderate humidity and intermediate light levels.

Axis 1 in Figure 4 shows the influence of the two different substrate categories in the sampling plots. The sampling plots located on the left side of the diagram include rocky substrates, walls, concretions and unconsolidated substrates (Figure 2a–b). Sampling plots located on the right side of the diagram contain organic substrates, such as guano and leaf litter (Figure 2 (c–d)).

The ordering diagram of the species (Figure 5) shows a pattern similar to that observed for the sampling plots, in which most of the species were located at the centre of the diagram. This finding suggests a preference for the twilight zone, with intermediate conditions of temperature and humidity, primarily on rocky substrates with a low organic matter content. A more detailed view of the distribution of the taxa in relation to substrates and zones is presented in Appendix 2.

The results of the CCA for the five modeled species are shown in the ordering diagram in Figure 6. The eigenvalues for the first two axes were 0.301 and 0.073, respectively, with the first axis explaining 74.30% of the total variance and the second axis explaining 18.02%. The environmental variables show a relatively weak relation with the axis when compared with that observed in the community analysis (temperature = axis 2: −0.063; humidity = axis 2: −0.045; zone = axis 2: 0.077; substrate = axis 1: 0.456). Nevertheless, the Monte Carlo permutation test shows a significant correlation among the abundance of the species and the environmental variables ($p < 0.05$ for axes 1, 2 and 3).

Corroborating the field observations, the ordering diagram (Figure 6) shows a preference for rocky substrates by the three spider species and the opilionid *Mitogoniella taquara*, and a preference for organic substrates by the opilionid *Eusarcus hastatus*. It is also evident that *Loxosceles similis* has a preference for drier, cooler and darker environments, while *Enoploctenus cyclothorax* and the two opilionid species preferred mild temperatures and moderate humidity and are found in the twilight zones. *Isoctenus* sp. is found more frequently in habitats that are warmer, more humid and more photic.

Laboratory tests: agonistic interactions

A unique record of an agonistic event occurred between the opilionid *Mitogoniella taquara* and the spider *Enoploctenus cyclothorax*, which was classified as submission, in which the opilionid approached the spider with its pedipalps raised and its legs positioned to the rear. Subsequently, the opilionid stretched its legs, partially launching its body forward and striking the cephalothorax of the spider with its pedipalps. In response, the spider rapidly moved away from the opilionid.
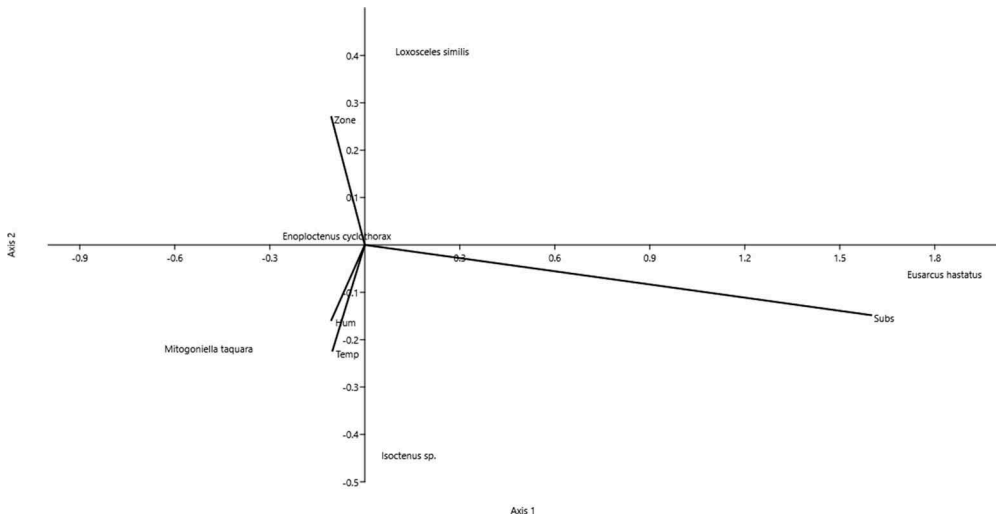
Figure 6. Ordering diagram for the five model species produced by the canonical correspondence analysis (CCA). Legend: Hum = humidity; Temp = temperature; Subs = substrate.

Predation and cannibalism events were common (Table 4): we observed cannibalism events among *Enoploctenus cyclothorax* in 75% of the pairings, and equal results were obtained for *Isoctenus* sp. For *Loxosceles similis*; 100% of the pairings resulted in cannibalism. We did not observe cannibalism among the opilionids.

In relation to predation, we observed that opilionids are not a preferred food item in the diet of either *Enoploctenus cyclothorax* or *Isoctenus* sp., as no predation events were observed. However, *Loxosceles similis* fed on *Eusarcus hastatus*, showing predation in 25% of the pairings. No predation events were observed among the opilionids. The spider *Isoctenus* sp. predated *Loxosceles similis* in 25% of the pairings, and *Enoploctenus cyclothorax* predated *Loxosceles similis* in 20% of the pairings.

Table 4. Agonistic behaviour interaction results among five species of terrestrial predators that were selected for the laboratory tests. The percentages indicate the proportion of positive results for either agonistic or predatory behaviour.

	Agonistic behaviour			
Pairings	Aggression	Submission	Predation/cannibalism	Avoidance/coexistence
Isoctenus sp. × *Isoctenus* sp.	0%	0%	75%	25%
Isoctenus sp. × *E. cyclothorax*	0%	0%	0%	100%
Isoctenus sp. × *L. similis*	0%	0%	25%	75%
Isoctenus sp. × *E. hastatus*	0%	0%	0%	100%
Isoctenus sp. × *M. taquara*	0%	0%	0%	100%
E. cyclothorax × *E. cyclothorax*	0%	0%	75%	25%
E. cyclothorax × *L. similis*	0%	0%	20%	80%
E. cyclothorax × *E. hastatus*	0%	0%	0%	100%
E. cyclothorax × *M. taquara*	0%	20%	0%	80%
L. similis × *L. similis*	0%	0%	100%	0%
L. similis × *E. hastatus*	0%	0%	25%	75%
L. similis × *M. taquara*	0%	0%	0%	100%
E. hastatus × *E. hastatus*	0%	0%	0%	100%
E. hastatus × *M. taquara*	0%	0%	0%	100%
M. taquara × *M. taquara*	0%	0%	0%	100%

The Kruskal-Wallis test showed significant differences between the occurrences of predation events among pairings ($p < 0.05$). The Mann-Whitney test showed that these differences occurred among the spiders and opilionids, reflecting cannibalism among the spiders, but not in the opilionids.

Discussion

Since the pioneering studies about competition, such as Gause (1934, 1935) and Connell (1961), which introduced the concepts of competitive exclusion and competition by resource use or by interference, the principal evidence of the action of competition among populations of the competing species has been the spatial segregation that exists among them.

There are many examples of subsequent studies that corroborate this premise, in which the distributions of ecologically and phylogenetically similar species are adjacent, but non-overlapping (Brown 1971a; Chappell 1978; Paterson 1980; Bowers and Brown 1982; Johanson and Keddy 1991; Taniguchi and Nakano 2000). Even though many distinct organisms were tested – both vertebrates and invertebrates, animals and plants, and in different environments – the general rule of spatial segregation could be seen in the great majority of these studies. In subterranean environments the same principle was present, as demonstrated by the studies developed by Culver, the only models of competition developed for caves (Culver 1970a, 1970b, 1971a, 1971b, 1973, 1975, 1982).

Thus, it is reasonable to conclude that in order to access the presence of competition among species in a given community, on a preliminary basis, the first step would be to observe whether there is spatial segregation among species within that community.

With few exceptions (the theridiid spiders *Nesticodes rufipes* and *Cryptachea* parana) the absence of spatial segregation among the terrestrial predatory species in the Presidente Olegário caves suggests that the competition is not present. If competition is present, it is apparently not strong enough to promote the patterns of spatial distribution expected in a community where its presence is more significant.

Another kind of evidence of competition, that does not involve population aspects, is the presence of agonistic behaviour among the competing species (Schuck-Paim 2007). Such behaviours are characterised by the presence of intimidation rituals and/or physical aggression in the form of fights, which could result in the death of one of the individuals (Parker 1974; Enquist and Leimar 1983, 1987; Schuck-Paim 2007). The presence of such behaviours has been observed and associated with competition for space and food for many predatory species (Riechert 1978, 1979, 1984, 1986; Burgess and Uetz 1982).

Thus, observing two species showing agonistic behaviour, or fighting with each other, would be strong evidence in favour of the presence of interspecific competition. Except for the submission behaviour observed between the opilionid *Mitogoniella taquara* and the spider *Enoploctenus cyclothorax*, none of the species in this study showed such behaviour. This reinforces the hypothesis that competition does not have an important role in the studied terrestrial predatory community.

One hypothesis that may explain the presence of these two antagonist ecological patterns would be associated with the physical characteristics of the caves. The caves have many openings to the epigean environment, and entrances contain large

quantities of organic matter. Additionally, there are many plant roots penetrating the caves, and guano of both hematophagous and frugivorous bats.

The huge abundance of food for detritivores, and even for herbivores such as planthoppers (Auchenorrhyncha: Cixiidae), that is associated with the presence of plant roots (Stone et al. 2012), suggests the existence of enough prey to sustain a community rich in both species and numbers of predators, without their having to compete with each other for food. Competition may be absent or inconsequential in these situations where food resources are not a limiting factor (Tilman 1982; Kadmon 1995).

Many studies, both in tropical and in temperate caves, have associated the diversity of the subterranean communities with the abundance of food. Caves that have a great quantity and quality of nutrients may support more diverse and robust animal communities (Poulson and White 1969; Gnaspini-Netto 1989; Juberthie and Decu 1994; Ferreira and Pompeu 1997; Gnaspini and Trajano 2000; Deharveng and Bedos 2012; Deharveng et al. 2012; Poulson 2012).

Subterranean faunistic surveys conducted in other Brazilian caves, in which similar sampling and collection methods were used, have also shown a great richness in terrestrial predatory communities. Gallão and Bichuette (2015) found 64 species in the sandstone caves of the Serra do Espinhaço region, Bahia state Northwest Brazil; Simões (2013) found 166 species in the limestone caves of São Domingos, Bahia state. The results of those studies demonstrate the species richness of terrestrial predators found in Neotropical caves, but they did not address the significance of available nutrients in those caves.

There are other factors besides food availability that may mitigate the effects of competition among species living in caves. One of these factors is niche differentiation, with its consequent occupation of distinct habitats by different species (MacArthur and Levins 1967; May 1973; Pianka 1974; Abrams 1976, 1983). This could be the case in the study caves for the ctenid spider *Ancylometes concolor*, which lives in the same caves with other ctenid species; the first species occupies microhabitats close to water bodies and the latter mainly inhabits the cave walls.

However, in order to determine if such observed niche differentiation in the community is caused by actual ecological processes or is simply a vestige of historic competition (Connell 1980), additional studies would be required.

In conclusion, the Presidente Olegário caves have a high terrestrial predatory species richness and, based on study results, these species show spatial distribution and habitat occupation that are not determined by competition. Two factors that could explain this pattern are: (1) the huge amount of food available in the caves; and (2) residual effects of historic competition. The importance of these factors in the community structure of the studied caves, and other Neotropical caves that sustain diverse communities, is still an open field for future studies.

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Appendix 1

List of the terrestrial predatory species from caves of the Presidente Olegário municipality, state of Minas Gerais, Southeast Brazil. Legend: VP = Lapa Vereda da Palha; SB = Lapa da Fazenda São Bernardo; ZS = Lapa Zé de Sidinei; AL = Lapa Arco da Lapa; LM = Lapa do Moacir; GJ = Gruta da Juruva and TC = Toca do Charco.

Class	Order/suborder	Family	Species/morphotype	VP	FB	ZS	AL	LM	GJ	TC	N	CCA code
Arachnida	Araneomorphae	Anapidae	Anapidae sp. 1	0	2	0	1	0	0	0	3	A1
		Araneidae	Araneidae sp.	0	0	0	1	0	1	0	2	A2
			Alpaida sp.	0	0	1	1	0	0	0	2	A3
			Araneus sp. 1	0	0	0	1	1	0	0	2	A4
			Araneus sp. 2	0	0	0	4	0	0	0	4	A5
			Araneus sp. 3	0	0	0	1	0	0	0	1	A6
			Cyclosa sp.	0	0	0	1	0	0	0	1	A7
			Eustala sp.	16	4	3	3	2	0	0	28	A8
			Mangora melanocephala	0	1	0	1	0	0	0	2	A9
		Caponiidae	Nops sp.	0	2	0	0	0	0	0	2	A10
		Ctenidae	Ancylometes concolor	1	1	1	0	0	0	1	4	A11
			Enoploctenus cyclothorax	20	58	9	32	6	13	2	140	A12
			Isoctenus sp.	8	18	14	2	4	2	4	52	A13
		Deinopidae	Deinops sp.	0	0	0	0	0	0	1	1	A14
		Hahniidae	Hahniidae sp.	0	4	0	0	1	0	6	11	A15
		Linyphiidae	Linyphiidae sp.	0	0	0	1	0	0	0	1	A16
			Mermessus sp.	4	2	0	0	0	0	0	6	A17
			Smermisia sp.	0	2	0	2	0	0	0	4	A18
			Scolecura parilis	0	0	0	16	0	0	0	16	A19
			Vesicapalpus simplex	0	1	0	0	0	0	0	1	A20
		Nephilidae	Nephila clavipes	1	0	0	1	0	0	0	2	A21
		Oonopidae	Cynetomorpha sp. 1	0	1	0	0	1	0	0	2	A22
			Cynetomorpha sp. 2	0	0	3	0	0	0	0	3	A23
			Neotrops sp.	2	1	0	1	0	1	0	5	A24
			Triaeris stenaspis	0	5	0	0	0	0	0	5	A25
		Palpimanidae	Fernandesina sp.	0	2	0	0	0	0	0	2	A26
		Pholcidae	Pholcidae spp.	5	12	3	11	9	5	5	50	A27
			Mesabolivar aff. tandilicus	0	0	0	27	13	0	23	63	A28
			Mesabolivar aff. togatus	12	3	9	1	0	0	0	25	A28
			Mesabolivar undes. sp.	8	18	5	0	0	0	0	31	A30
			Metagonia sp.	0	6	0	0	0	0	0	6	A31

(Continued)

Appendix 1 (Continued).

Class	Order/suborder	Family	Species/morphotype	VP	FB	ZS	AL	LM	GJ	TC	N	CCA code
		Salticidae	Salticidae sp. 1	3	18	3	1	0	0	2	27	A32
			Salticidae sp. 2	3	0	0	0	0	0	2	5	A33
			Salticidae sp. 3	0	0	0	0	2	0	0	2	A34
			Salticidae sp. 4	0	0	0	0	2	0	1	3	A35
			Coritalia sp.	0	2	0	0	0	0	0	2	A36
		Scytodidae	Scytodes fusca	0	0	0	1	0	0	0	1	A37
			Scytodes aff eleonorae	0	8	0	0	0	0	3	11	A38
		Segestriidae	Ariadna sp.	0	0	0	3	0	0	0	3	A39
		Selenopidae	Selenops sp.	1	0	0	0	0	0	0	1	A40
		Sicariidae	Loxosceles similis	6	0	0	45	0	13	0	64	A41
		Symphytognathidae	Symphytognathidae sp.	1	0	0	1	0	0	0	2	A42
		Tetragnathidae	Tetragnathidae sp. 1	4	1	0	0	0	0	0	5	A43
			Tetragnathidae sp. 2	2	0	0	0	0	0	0	2	A44
		Theridiidae	Cryptachaea sp.	2	1	0	0	0	0	0	3	A45
			Cryptachaea parana	9	7	0	0	1	1	5	23	A46
			Dipoena santaritadopassaquatrensis	0	0	0	1	0	0	0	1	A47
			Nesticodes rufipes	2	0	0	0	0	0	0	2	A48
			Thymoites aff. ebus	0	1	0	0	0	0	0	1	A49
		Theridiosomatidae	Plato sp.	13	4	16	5	0	0	0	38	A50
			Theridiosoma sp.	10	5	0	3	6	0	0	24	A51
		Uloboridae	Migramops sp.	0	2	0	0	0	0	0	2	A52
			Uloborus sp.	1	1	0	0	0	0	0	1	A53
			Zoziz sp.	0	2	0	2	0	0	0	4	A54
	Mygalomorphae	Theraphosidae	aff. Catanduba sp.	0	1	0	0	0	0	0	1	M
	Opiliones	Gonyleptidae	Discocyrtus sp.	0	7	3	0	0	0	0	10	O1
			Eusarcus cavernicola	3	1	4	0	0	0	0	8	O2
			Eusarcus hastatus	0	16	0	0	0	1	3	20	O3
			Mitogoniella taquara	2	9	0	16	0	0	0	27	O4
		Zalmoxidae	Zalmoxidae sp.	0	2	0	0	0	0	0	2	O5
	Pseudoscorpiones	Atemnidae	Atemnidae sp.	0	1	0	2	0	0	0	3	P1
		Cheiridiidae	Cheiridiidae sp.	1	1	0	17	0	7	0	26	P2
		Chernetidae	Spelaeochernes sp.	9	2	18	14	0	0	1	44	P3
		Chthoniidae	Chthoniidae sp. 1	0	3	0	0	0	0	0	3	P4
			Chthoniidae sp. 2	2	0	0	0	0	0	0	2	P5
			Chthoniidae sp. 3	0	0	0	0	1	0	0	1	P6
			Chthoniidae sp. 4	0	0	1	0	0	0	0	1	P7
		Geogarypdae	Geogarypus sp.	0	7	0	0	0	0	0	7	P8
	Scorpiones	Buthidae	Tityus sp.	1	0	1	0	0	0	0	2	S

(Continued)

Appendix 1 (Continued).

Class	Order/suborder	Family	Species/morphotype	VP	FB	ZS	AL	LM	GJ	TC	N	CCA code
Chilopoda	Geophilomorpha		Geophilomorpha sp.	0	9	0	0	0	0	0	9	C1
		Geophilidae	Geophilidae sp.	0	3	0	0	0	0	0	3	C2
	Lithobiomorpha	Henicopidae	*Lamyctes* sp.	0	0	10	0	1	0	0	11	C3
	Scolopendromorpha		Scolopendromorpha sp.	0	1	0	0	0	0	0	1	C4
		Cryptopidae	*Cryptops* sp. 1	0	1	0	0	0	0	0	1	C5
Insecta	Hemiptera	Reduviidae	*Emesa mourei*	0	0	0	2	0	0	0	2	R1
			Ploiaria sp.	7	6	0	6	0	0	0	19	R2
			Ploiaria aff. *carvalhoi*	0	0	0	0	0	0	1	1	R3
			Phasmatocoris sp.	0	0	0	0	0	0	1	1	R4
			Zelurus zikani	5	1	9	4	0	0	1	20	R5
											929	

Appendix 2

List of the terrestrial predatory species from caves of Presidente Olegário, Minas Gerais state, Southeast Brazil, with the substrates and zones where they were collected. Legend: AZ = aphotic zone; EZ = entrance zone; OM = organic substrates; R = rocky substrates; Subs = substrate; TZ = twilight zone; Zo = zonation.

Order	Species/morphotype	Subs		Zo		
		R	OM	EZ	TZ	AZ
Araneae	Anapidae sp. 1	1	2		2	1
	Araneidae sp.	2		2		
	Alpaida sp.	2		1	1	
	Araneus sp. 1	2		2		
	Araneus sp. 2	4			4	
	Araneus sp. 3	1		1		
	Cyclosa sp.	1		1		
	Eusatala sp.	28		9	18	1
	Mangora melanocephala	2		1	1	
	Nops sp.	2			2	
	Ancylometes concolor	4		1	3	
	Enoploctenus cyclothorax	124	16	49	77	14
	Isoctenus sp.	45	7	13	28	11
	Deinops sp.		1	1		
	Hahniidae sp.	2	9	1	8	2
	Linyphiidae sp.		1		1	
	Mermessus sp.		6		5	1
	Smermisia sp.		4		2	2
	Scolecura parilis		16	3	13	
	Vesicapalpus simplex		1		1	
	Nephila clavipes	2		2		
	Cynetomorpha sp. 1		2	1	1	
	Cynetomorpha sp. 2	3		3		
	Neotrops sp.		5		4	1
	Triaeris stenaspis	1	4	4	1	
	Fernandesina sp.	2		2		
	Pholcidae spp.	42	8	32	16	2
	Metagonia sp.	6		4	2	
	Mesabolivar aff. tandilicus	57	6	28	35	
	Mesabolivar aff. togatus	25		18	7	
	Mesabolivar undes. sp.	30	1	15	12	4
	Salticidae sp. 1	27		27		
	Salticidae sp. 2	5		5		
	Salticidae sp. 3	2		2		
	Salticidae sp. 4	3		3		
	Coritalia sp.	2		2		
	Scytodes fusca	1			1	
	Scytodes aff. eleonorae	6	5	3	7	1
	Ariadna sp.	3			3	
	Selenops sp.	1			1	
	Loxosceles similis	54	10	16	22	27
	Symphytognathidae sp.		2	2		
	Tetragnathidae sp. 1	5		3	2	
	Tetragnathidae sp. 2	2		2		
	Cryptachaea sp.	3		2	1	
	Cryptachaea parana	13	10	4	10	9
	Dipoena santaritadopassaquatrensis	1		1		
	Nesticodes rufipes		2			2
	Thymoites aff. ebus	1			1	
	Plato sp.	34	4	5	20	13
	Theridiosoma sp.	16	8	4	11	9
	Migramops sp.	2		1	1	
	Uloborus sp.	1		1		
	Zozis sp.	4		3	1	

(*Continued*)

Appendix 2 (Continued).

Order	Species/morphotype	Subs		Zo		
		R	OM	EZ	TZ	AZ
	aff. *Catanduba* sp.		1			1
Opiliones	*Discocyrtus* sp.	10		7	2	1
	Eusarcus cavernicola	5	3	1	4	3
	Eusarcus hastatus	4	16	1	18	1
	Mitogoniella taquara	27		9	15	3
	Zalmoxidae sp.		2		2	
Pseudoscorpiones	Atemnidae sp.	3		2	1	
	Cheiridiidae sp.	26			26	
	Spelaeochernes sp.	16	28	5	26	13
	Chthoniidae sp. 1		3	3		
	Chthoniidae sp. 2		2		2	
	Chthoniidae sp. 3		1		1	
	Chthoniidae sp. 4	1			1	
	Geogarypus sp.	7		7		
Scorpiones	*Tityus* sp.	2				2
Geophilomorpha	Geophilomorpha sp.		9		7	2
	Geophilidae sp.		3		3	
Lithobiomorpha	*Lamyctes* sp.		11	1		10
Scolopendromopha	Scolopendromorpha sp.		1		1	
	Cryptops sp. 1		1			1
Hemiptera	*Emesa mourei*	2		1	1	
	Ploiaria sp.	19		11	8	
	Ploiaria aff. *carvalhoi*	1			1	
	Phasmatocoris sp.	1			1	
	Zelurus zikani	17	3	7	6	7
	Total abundance	715	214	335	451	144