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Structure and interactions in a cave guano–soil continuum community

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ABSTRACT

Bat guano represents an important food resource for cave-dwelling organisms, hosting up to entire communities in a single deposit. Sampling conducted in guano and its interface with the adjacent soil revealed a wide variation in physicochemical parameters (nitrogen, phosphorus, organic matter, pH and moisture) along that continuum. The invertebrate orders that showed the greatest abundance and species richness were: Mesostigmata, Sarcoptiformes and Trombidiformes, all belonging to subclass Acari. The results clearly showed that mite species are the most abundant group in guano deposits. Such species can directly or indirectly feed on this food resource. The abiotic factors of the guano significantly explained some community parameters. Furthermore, moisture was the parameter that best explained the abundance distribution for the most common mite species. Lastly, a trophic web of the most abundant species in the guano was devised based on literature data, interspecies correlation, preferences for microhabitats and abundance rates of the populations. It was possible to observe that the temporal changes in the guano deposit determine a successional process in the community, including the trophic web structure.

1. Introduction

The condition of total absence of light and the resulting inexistence of photosynthetic organisms require cave environments to depend on resources from the outside. That condition gives rise to a tendency toward oligotrophy in most of these systems [1]. Nevertheless, that condition is not always prevalent in caves, especially those in which guano deposits can be found. Guano from birds, invertebrates and most commonly bats, can form extensive deposits in caves; in those cases, it represents the main food resource for cave-dwelling organisms [2,3].

Bats can produce considerably large deposits. Guano deposits vary with regard to dietary quality and microclimate, characterized by the high variability of microhabitats, with variable pH, moisture and organic matter percentage [4]. This heterogeneity in the chemical conditions of guano deposits mainly takes place due to the variations this substrate undergoes over time. Fresher guano is generally more alkaline and moist; as it ages, it becomes drier and more acidic [5,6]. However, studies by Ferreira et al. [3] demonstrated that moisture and pH data alone are not sufficient to infer the age of a guano deposit. According to those authors, guano deposits are open systems and are therefore affected by chemical, physical and biological processes, such as percolating water, physical and biological movement, and incorporation of animal bodies and exuviae.

Guano deposits have a strong influence on the distribution pattern of certain cave-dwelling populations, sometimes hosting large communities at different successional stages [7,6]. These communities include such diverse organisms as bacteria, fungi, protozoa, nematodes, mites, coleopterans, dipterans, lepidopterans, collembola and spiders [4]. Among those, mites are the most abundant organisms in guano [6].

The majority of studies on the communities associated with guano deposits in caves have been food chain descriptions and species lists e.g., [4,7–9]. Few studies consider the interrelations with the physicochemical parameters of the substrate under study [10].

Moreover, there have been no studies taking into consideration the continuums of variation in the physicochemical parameters of the substrate in the guano–soil interface area. Therefore, there is a need to understand the interference of this change in the substrate properties on associated invertebrate communities. As such, in

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order to understand the structure of a given community associated with bat guano, it is important to relate richness and abundance patterns to abiotic parameters of those organic deposits.

The objective of the present study was to determine the composition of the invertebrate community associated with a large guano deposit and its interface with the adjacent soil in a Neotropical cave. Furthermore, the study aimed to assess whether abiotic factors of the guano and soil (pH, organic matter percentage, moisture content, total nitrogen and total phosphorus) influence the structure of the invertebrate community associated with those substrates. Finally, the possible existing interactions were represented in a trophic web of the most abundant species in the guano.

2. Materials and methods

2.1. Study area

The work was carried out in a large bat guano deposit located in Lapa Nova cave. This dolomitic cave is located in the municipality of Vazante, northwestern Minas Gerais state, Brazil (UTM-23 299811 – 8010693) [11]. Although it is not set up for mass tourism, Lapa Nova has been visited annually by pilgrims for several decades, thereby serving as local tourist hub.

The guano under study is located in an area far from the main entrance to the cave. It is in continuous deposition and is characterized as guano from omnivorous bats of the genus *Phyllostomus*. The deposit is, on average, 15 m long and 5 m wide, representing an important source of feeding resources for the organisms of that cave.

2.2. Experiment layout

First, a linear transect was established in the direction of the greatest length of the deposit until reaching an area with no visible guano. Next, two samples were collected every meter of that transect. The same volume of guano was collected at all points for biological analyses. The samples were taken from 400 cm^2 squares, 5 cm deep. For the analysis of community structure, the samples were individually placed in plastic jars, which were then sealed, labeled and taken to the lab. The other set of samples were used to quantify the percentage of organic matter, moisture level, pH, nitrogen and phosphorus.

The first set of samples was previously triaged to remove the larger organisms. Next, those samples were place in Berlese–Tullgren funnels for one week to extract the invertebrates that could not be collected visually [5]. The extracted fauna was fixed in 70% alcohol for later identification down to the lowest possible taxonomic level and separation into morphospecies. From the numbers obtained by the triage, the richness, equitability, diversity and abundance values were calculated for each point. The calculation of diversity was done using the Simpson index [12]. Besides being one of the most applied indices for diversity, this index is more sensitive to the most abundant species, while being less sensitive to species richness [12]. Considering that in this study some species occurred in just one or in a few collected points, Simpson is an appropriated index to be used.

The percentage of moisture was obtained by subtracting the weight before and after the drying process (100 °C for 48 h) from a fraction of the second set of collected samples [2]. The pH analyses were carried out in the chemistry laboratory of the Federal University of Lavras; 10 g of each sample were diluted in 10 ml of distilled water and homogenized for about 1 min. The determination of nitrogen was done by the *Kjeldahl* method [13]. The extraction of phosphorous was done by an ion exchange procedure [14]. Finally, the organic matter analysis was done by dichromate oxidation in acidic medium, and organic matter determination was performed by colorimetry [15]. The Soils Laboratory of the Federal University of Lavras performed those last three analyses.

2.3. Statistics

In order to confirm the efficiency of the sampling of the deposit under study, a collection curve was calculated along with its confidence interval, with 100 simulations of cumulative richness observed throughout the 25 sampling points, using *EstimateS* software. Using the same program, the richness and abundance expected in the guano deposit were calculated using the average of Jackknife 1 and 2 and Chao 1 and 2 estimators.

The similarity between the fauna at the different points in the guano was compared using non-metric multidimensional scaling – n-MDS. The n-MDS was built based on the abundances of the invertebrate fauna, using the Bray–Curtis index. The aim of the analysis was basically to compare possible differences in the composition of organisms in guano, in the guano–soil interface and in the soil. The existence of significant differences between n-MDS groups was evaluated by ANOSIM. Lastly, SIMPER analysis was used to evaluate which species were responsible for those differences. All above-mentioned analyses were carried out using *Primer* software.

The relationship between abiotic parameters (pH, moisture, levels of nitrogen and phosphorus, and organic matter availability) and biotic variables (richness, equitability and invertebrates diversity) were evaluated by *General Linear Models* (GLM) using *Statistica* software. The relationship between the abundance of the most representative species and the abiotic parameters was evaluated through Canonical Correlation Analysis (CCA) using *PC-ORD 5.0* software. Lastly, a correlation matrix was obtained between the most abundant/best distributed species and environmental parameters using *BioEstat 5.0* software. Next, a correlation matrix was built only among the most abundant species in the guano using *Statistica*.

The possible interactions between the most abundant species present in the guano deposit were also assessed. That task was performed using information on the biology of each group found in the literature [16,17], the correlations among the species, the abundance rates and their preferences for microhabitats obtained from *CCA*.

3. Results

Among the abiotic parameters under analysis, organic matter (OM) and nitrogen (N) showed the most significant reduction at the transition from guano to soil predominance. Conversely, phosphorus (P) behaved in an opposite way to nitrogen and organic matter. Points with predominance of soil had higher phosphorus concentrations. The pH showed three distinct patterns along the analyzed transect. From points 1 to 11, pH was more neutral, ranging from 5.6 to 7.1; from point 12 to 17, pH became more acidic, with values from 5.2 to 5.8; in the final part of the deposit (and its interface with the adjacent soil), pH became alkaline, with values surpassing 7.8. Moisture peaked at points 3 and 4 (Fig. 1).

A total of 157,271 individuals were sampled, distributed into 61 morphospecies belonging to 12 different orders: Mesostigmata, Sarcoptiformes, Trombidiformes, Araneae, Pseudoscorpiones, Geophilomorpha, Diptera, Coleoptera, Hymenoptera, Lepidoptera, Psocoptera and Collembola, as well as Oligochaeta. Subclass Acari (comprising orders Mesostigmata, Sarcoptiformes and Trombidiformes) was the most abundant, with 156,319 individuals, representing 99.34% of total individuals. That subclass was represented by 36 morphospecies. Among arthropods excluding mites, the most

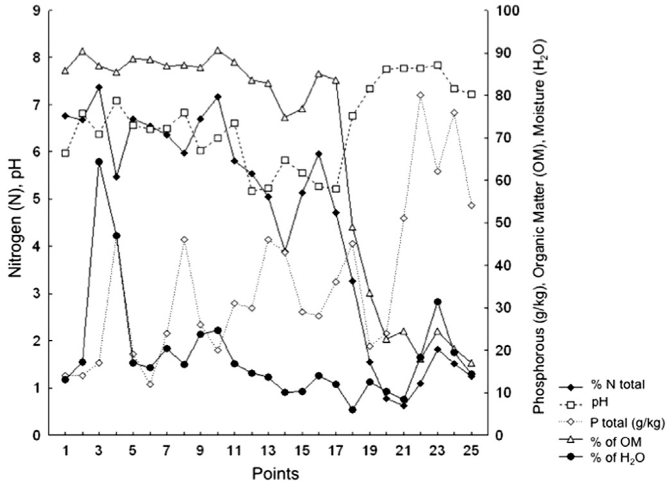

Fig. 1. Values of pH, amount of nitrogen and percentages of phosphorous, organic matter and moisture found at each point in the guano.

abundant order was Lepidoptera, with two identified species, totaling 393 individuals. Araneae and Geophilomorpha were the least abundant orders, with only 1 individual each (Appendix I–II).

Among the best distributed organisms along the guano deposit, the orders with the following species stood out: the **Trombidiformes** (*Tarsonemus* sp. (Tarsonemidae) (25 points), *Lorryia* sp. (Tydeidae) (21), *Cheyletus cacahuamilpensis* (Cheyletidae) (18), *Imparipes* sp. (Scutacharidae) (17)); **Sarcoptiformes** (*Tyrophagus* sp. (Acaridae) (24), Oribatida sp.2 (15) and Acaridae sp. (15)); and **Mesostigmata** (*Androlaelaps* sp. (Laelapidae) (18)). The orders with the following species with largest number of individuals were: **Trombidiformes** (*Tarsonemus* sp. (Tarsonemidae) (64,817), *Lorryia* sp. (Tydeidae) (35,065), *C. cacahuamilpensis* (Cheyletidae) (6782), *Imparipes* sp. (Scutacharidae) (2638), Eupodidae sp. (1792), and Stigmaeidae sp. (1132)); **Sarcoptiformes** (Oribatida sp.2 (17,932), Histiostomatidae sp. (4060), *Tyrophagus* sp. (3906), and Oribatida sp.1 (2712)); and **Mesostigmata** (Uropodina sp.2 (5434), *Proctolaelaps* sp. (Melicharidae) (1607), Trachytidae sp. (1413), *Androlaelaps* sp. (Laelapidae) (1045), and Rhodacaridae sp.1 (1017)). Combined, those organisms represented 24.5% of the total richness found and 96% of the total abundance counted in the deposit.

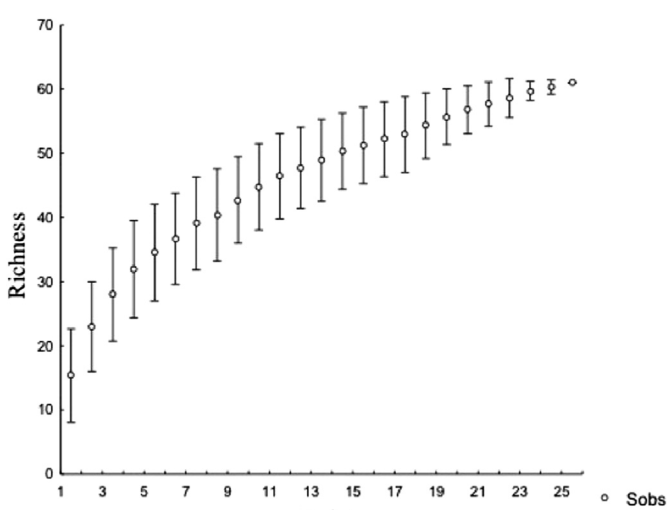

Fig. 2. Simulation of the cumulative richness (total number of morphospecies) observed, ± standard deviation, for the guano deposit.

Table 1
Values of the biotic variables found at each sampling point of Lapa Nova guano.

Point	Richness	Evenness	Diversity	Total abundance
1	11	0.4664	1.118	1,557
2	28	0.2971	0.9899	19,089
3	33	0.5644	1.974	19,341
4	28	0.442	1.473	13,813
5	20	0.2934	0.8789	19,524
6	19	0.3364	0.9906	7,725
7	17	0.4074	1.154	3,380
8	18	0.204	0.5895	17,296
9	18	0.4863	1.405	3,187
10	23	0.5368	1.683	9,518
11	20	0.4128	1.237	10,039
12	20	0.3459	1.036	10,064
13	17	0.3118	0.8834	6,687
14	12	0.4345	1.08	3,766
15	8	0.5407	1.124	1,016
16	12	0.4019	0.9986	5,967
17	13	0.378	0.9695	965
18	6	0.3647	0.6534	1,133
19	19	0.4472	1.317	1,113
20	11	0.3483	0.8353	1,261
21	6	0.2943	0.5273	283
22	8	0.5912	1.229	513
23	5	0.9463	1.523	9
24	5	0.8787	1.414	11
25	5	0.7891	1.27	14

The collection curve created from the simulations did not reach the asymptote with the sampling of 25 points in the guano deposit (Fig. 2). The richness values obtained from the estimators were 78, 85, 70 and 75 for Jacknife 1 and 2 and Chao 1 and 2, respectively. The average of the estimators was 77 species. The observed richness comprised 61 species, which represents 79% of the expected richness.

The values for richness, diversity, equitability and abundance varied along the guano–soil continuum (Table 1). Fig. 3 represents the continuum in the transition from more recent guano (with two current deposition stains) toward older guano, and then on to soil. The sudden decrease in the percentage values of organic matter at points 18, 19 and 20 corresponds to the sites where the guano concentration is progressively lower. The first two peaks in moisture and richness correspond to the sites where guano is currently

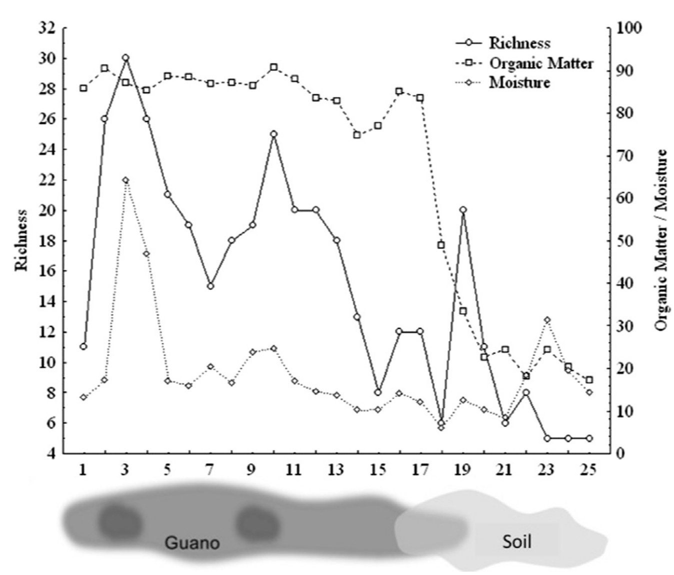

Fig. 3. Percentage of organic matter, moisture and invertebrate community richness in a transition continuum from guano to soil. The darker stains in the guano deposit represent the current deposition sites.

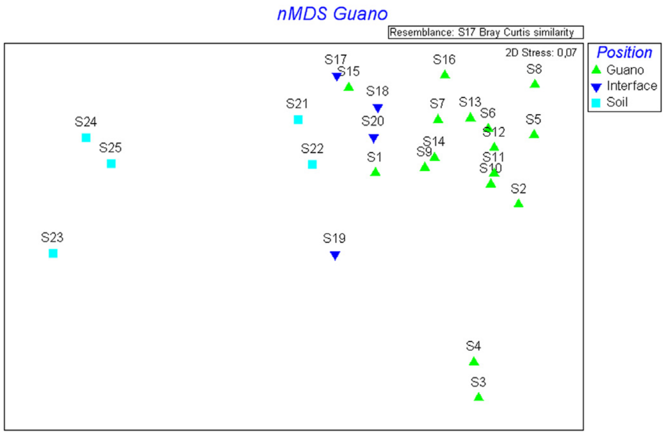

Fig. 4. Multidimensional scaling (n-MDS) of the different points inserted in: triangles, in guano (1–16); upside down triangles, in the guano–soil interface (17–20); square, in the soil (21–25). Jaccard similarity coefficient.

being deposited. There is also a peak in richness, corresponding to the exact location of the transition from guano to soil. Finally, there is peak in moisture at an area with high predominance of soil.

The *n-MDS* analysis (using the Bray–curtis index – stress equal to 0.07) showed that the points located in the guano–soil interface are in an intermediate situation between guano and soil, even if they are more similar to guano. However, guano and soil points were highly different (Fig. 4). The differences between the groups analyzed by the Bray–curtis index were significant in ANOSIM ($R = 0.52$, $p = 0.002$).

According to SIMPER analysis, the species that most contributed to the average dissimilarities between the guano and soil points were: *Tarsonemus* sp, responsible for approximately 42.4% of those differences; followed by *Lorrya* sp, with close to 21.5%; *C. cacahuamilpensis*, with 8.3%; Oribatida sp2, with 7.6%; and *Tyrophagus* sp, with 5.0% (Table 2). Those species combined accounted for over 80% of the differences in similarity between the sampled points. Besides that, *Tarsonemus* sp, was responsible for 38.9% of the differences presented by guano and its interface and also responsible for 42.9% for the soil interface dissimilarities. Moreover, all of the species listed above showed a decreased abundance in the guano–soil interface area and an even more pronounced decrease in the area of soil predominance.

Species richness was explained by total phosphorus, organic matter and moisture ($F = 7.79$, $p = 0.011$; $F = 8.91$, $p = 0.007$; $F = 18.92$, $p < 0.001$ respectively), while the whole model explained 77% of the variation ($F = 16.74$, $p < 0.001$). The Simpson diversity variation was significantly explained among the points by nitrogen, organic matter, pH and moisture ($F = 7.54$; $p = 0.012$; $F = 13.22$; $p = 0.001$; $F = 5.74$; $p = 0.027$; $F = 6.68$; $p = 0.018$ respectively), and the whole model also explained 50% of the variation ($F = 5.76$, $p = 0.002$). Finally, nitrogen, total phosphorous and organic matter significantly explained the equitability variance ($F = 9.87$; $p = 0.004$; $F = 4.61$; $p = 0.044$; $F = 19.42$; $p < 0.001$ respectively), and the whole model explained 57% of the variation ($F = 5.01$, $p = 0.004$).

Table 2
SIMPER analysis. Species that contributed to the differences at points in the guano, guano–soil interface and soil.

Taxon	Contribution	Cumulative %	Guano	Interface	Soil
Tarsonemus sp	36.53	41.21	3888	529	100
Lorrya sp	17.2	60.61	2184	30.3	1
Cheyletus cacahuamilpensis	8.965	70.72	366	227	2.6
Oribatida sp2	6.199	77.72	1121	0.25	0.6
Tyrophagus sp	5.752	84.21	198	178	6

Table 3
Correlation matrix between the abiotic parameters of guano; correlations in bold are significantly correlated, $p < 0.05$.

Correlation matrix	N	P	OM	pH	Moisture
N	1.00	**−0.68**	**0.96**	**−0.64**	0.32
P	**−0.68**	1.00	**−0.66**	**0.42**	−0.05
OM	**0.96**	**−0.66**	1.00	**−0.73**	0.21
pH	**−0.64**	**0.45**	**−0.73**	1.00	0.11
Moisture	0.32	−0.05	0.21	0.11	1.00

The correlation matrix of abiotic parameters showed that organic matter and nitrogen are highly correlated (Table 3). Therefore, it was decided that organic matter would be excluded from the Canonical Correlation Analyses (CCA), due to the fact that this parameter did not have a normal distribution. Nitrogen, phosphorus, organic matter and pH are also correlated to one another, although at a lower intensity. Only moisture was not correlated to any of the analyzed parameters.

The CCA analyses revealed significant relationships between the most abundant/best distributed species and abiotic variables ($p = 0.001$). Combined, the two axes of the CCA explained 42.0% of the variation in species abundance and environmental variables (Fig. 5; Table 4). Axis1 by itself explained 33.3% of the variance, and that axis was determined mainly by moisture. The abundance values for most species are related to moisture differences. On the second axis, nitrogen, phosphorus and pH mostly explained the variations in the abundance of the species under analysis. Nevertheless, the impact of those abiotic parameters was low (8.7%).

The correlation matrix built from the abiotic parameters and the most abundant/best distributed species along the entire deposit confirmed that moisture is the factor that most influences species abundance. That parameter was positively correlated to Aacridae sp., Oribatida sp.2, Histiostomatidae sp., *Proctolaelaps* sp., Rhodacaridae sp., Stigmaeidae sp. and Uropodina sp.2, all highly significant ($p < 0.001$). Nitrogen was positively correlated to *Tarsonemus* sp. and Rhodacaridae sp.1 ($p < 0.05$). Finally, phosphorus and pH

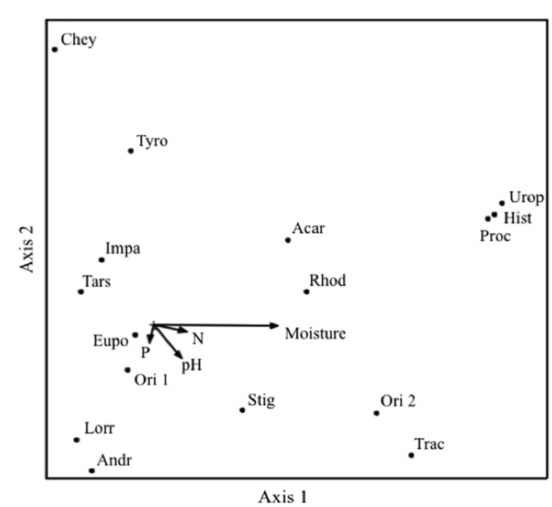

Fig. 5. Distribution pattern of species as a function of environmental variables, based on the rule of canonical correlation analyses. Captions: Andr = *Androlaelaps* sp; Acar = Acaridae sp; Chey = *Cheyletus cacahuamilpensis*; Lorr = *Lorryia* sp; Ori 2 = Oribatida sp 2; Impa = *Imparipes* sp; Tars = *Tarsonemus* sp; Tyrp = *Tyrophagus* sp; Trac = Trachynidae sp; Eupo = Eupodidae sp; Hist = Histiostomatidae sp; Ori1 = Oribatida sp1; Proc = *Proctolaelaps* sp; Rhod = Rhodacaridae sp 1; Stig = Stigmaeidae sp; Urop = Uropodina sp 2.

Table 4
Results of the canonical correlation analyses (CCA) of mite species abundance and environmental variables.

Variable/axis	1	2	3
Nitrogen	−0.137	−0.366	−0.126
Phosphorous	−0.018	−0.384	−0.137
pH	0.020	−0.361	0.153
Moisture	0.949	0.166	0.057
Axis			
Eigenvalue	0.828	0.216	0.106
Cumulative explained variation (%)	33.3	42.0	46.2
Species variable correlation (Pearson)	0.991	0.775	0.629

were negatively correlated to Scutacharidae sp. and *C. cacahuamilpensis* respectively ($p < 0.05$).

Using the same figure generated by the CCA analyses, we represented the abundances of each of the most abundant species by the circle sizes, and it was possible to see that there is a transition from the fresh to the old guano, with a species substitution (Fig. 6). As expected, generalist detritivorous species were much more abundant than predators. Finally, the trophic web proposed has demonstrated that there are changes in the predator/prey relationship over time. In the old guano *C. cacahuamilpensis* is the main predator while in the fresh guano Rodacharidae is the main predator (Fig. 6).

4. Discussion

Although there are many studies regarding cave guano communities that have proposed trophic webs (e.p. 18; 6; 19), none of them was based on differences observed in species abundance or even in preferences shown by the species for specific conditions of the guano. Accordingly, many proposed models are too generalist, and can eventually fail in describing the actual relations between species in such communities. Species preferences for specific conditions are poorly investigated. Some studies have shown

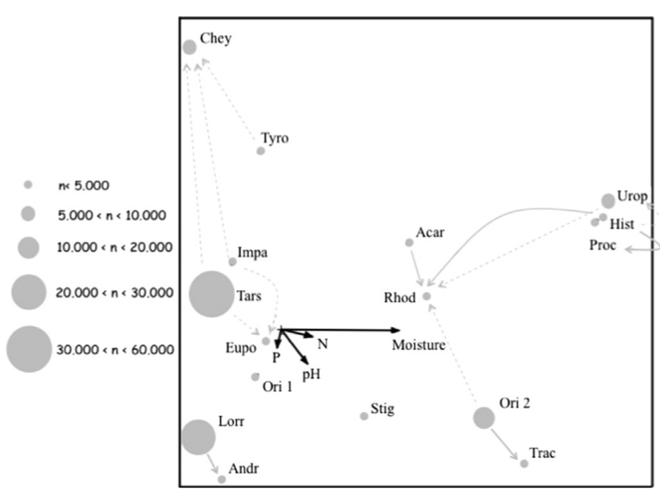

Fig. 6. Possible predator–prey interactions at Lapa Nova. The bold arrows indicate stronger interactions (with higher probability of occurring); light arrows indicate weaker interactions (with lesser probability of occurring); and the dotted arrows indicate the interactions least likely to occur. Gray circles indicate the abundance of each population found at the sampled points in the guano. Captions: Andr = *Androlaelaps* sp; Acar = Acaridae sp; Chey = *Cheyletus cacahuamilpensis*; Lorr = *Lorryia* sp; Ori 2 = Oribatida sp 2; Impa = *Imparipes* sp; Tars = *Tarsonemus* sp; Tyrp = *Tyrophagus* sp; Trac = Trachynidae sp; Eupo = Eupodidae sp; Hist = Histiostomatidae sp; Ori1 = Oribatida sp1; Proc = *Proctolaelaps* sp; Rhod = Rhodacaridae sp 1; Stig = Stigmaeidae sp; Urop = Uropodina sp 2.

correlations among bat guano invertebrate communities and some guano parameters [19], but to access species preferences and niches a multivariate approach is needed [20]. For this purpose, more detailed information about specific environmental conditions under which species are found is required [20].

The great abundance and richness of mites observed in the Lapa Nova guano deposit corroborate the data provided in several studies, in which the subclass Acari was the most representative [3,6,9,21–24]. Some guano-feeding mites are so abundant that their populations have been estimated in the millions of individuals per square meter [25]. Among the most frequently found mite taxa in guano deposits in Brazil are the orders Trobidiformes, Sarcoptiformes and Mesostigmata; the latter includes the families Macrochelidae, Phytoseiidae, Rhodacaridae and Uropodidae [6,19]. In addition to the taxa listed above, with the exception of Trombidiformes, the following were also found in the guano at Lapa Nova: Tryginaspida, Microdispidae, Stigmaeidae and Nanorchestidae. One of the species (from Tryginaspidae) had only one identified specimen. Representatives of that family have phoretic habits, and it is likely that the organism accidentally fell into the guano deposit.

The species richness of the Lapa Nova guano deposit showed high values when compared to other deposits [3,19,24,31]. Nevertheless, the collection curve generated from the 25 sampled points shows that almost 80% of the species richness was reached using the employed methodology.

4.1. Guano–soil interface

There are currently no studies in the literature on the guano–soil interface. The data of the present work suggest that the community shows a clear preference toward associating with the guano deposit. Also noteworthy is the significant increase in species richness in the guano–soil interface area. That peak in richness in the interface may be due to the preference of certain species for intermediate pH, as proposed by Ferreira et al. [3]. Moreover, the lower abundance observed for several species in that interface area can allow colonization by species with lower competitive strength, given that the site still features feeding resources in the form of guano, although in lower quantities. Finally, the interface can be considered an ecotone between the two systems, possibly hosting species from both, which would explain the higher richness in that area.

4.2. Relationships between the fauna and physicochemical parameters

Physical and chemical parameters of guano vary over time. The moisture of a deposit undergoes changes due to drying as the guano ages, resulting in noticeably different microhabitats [7]. The most recently deposited (and therefore moister) guano shows a larger number of ectoparasites and colonizing species when compared to older and drier guano, which usually shows a predominance of saprophagous species [21].

The guano/soil continuum studied herein showed two moisture peaks coinciding with the points of most recently deposited guano. However, there is a third moisture peak, coinciding with a location of high soil predominance, where there was no guano deposition. According to Ferreira et al. [3], guano deposits are not completely closed systems. As such, their physicochemical characteristics can be affected by different agents such as percolating water, dripping and sedimentation, among others. Thus, it can be inferred that this sudden increase in moisture may have occurred due to one of those processes.

Moisture influenced the richness and diversity of the communities associated with guano in the Morrinho cave, located in the state of Bahia, Brazil [19] and also at Bat Cave (Naracoorte) in southern Australia [10]. The same pattern was observed in the present work, corroborating the influence of moisture on those communities. The CCA showed that moisture is also an important factor in the distribution of the population abundances, given that seven of the 16 analyzed species were positively correlated to that parameter. Nevertheless, data in the literature is scarce regarding the preference for different moisture levels by mites associated with guano. Among the organisms that showed correlation with moisture, only Astigmata, Histiostomatidae and Oribatida have data regarding their preferences. Species from those groups often show clear preferences for high-moisture locations in epigean habitats [27,28].

Few studies have evaluated the interferences of nitrogen and phosphorus concentration in the communities associated with guano. Emerson & Roark [29] evaluated the concentrations of those elements in different types of guano (from frugivores, insectivores and hematophagous species). However, the mentioned authors do not correlate those concentrations with the "age" of guano or even the community of invertebrates associated with the deposits. Herrera [22] demonstrated that the high concentrations of nitrogen and phosphorus in the guano of oilbirds (*Steatornis caripensis*) favor the existence of arthropod communities in a Venezuelan cave. The rate of nitrogen in the guano at Lapa Nova was higher in areas where guano was fresher and more abundant, decreasing when soil was more abundant.

Guano deposits with high levels of organic matter are potential maintainers of rich and diversified communities [3,19]. The same pattern was observed in the present study, considering that the organic matter significantly explained the variation of all the community parameters evaluated. Furthermore, the level of organic matter proved to be a good indicator of the transition continuum from guano to soil, with its maximum levels coinciding with the locations where there is guano and a steep decline in the transition area from guano to soil – which was expected.

The pH variations can be extreme, resulting in a strong differentiation between fresher and older guano [6,9,22]. The values obtained at Lapa Nova corroborate the observations of Hutchinson [28] that fresher guano is alkaline, and acidifies with age due to ammoniacal fermentation. The points farthest from the deposition areas showed high acidity, corresponding to the locations where the resource becomes ever scarcer, with the higher soil concentration.

The lack of linear relationships between pH and abiotic factors has already been observed in many works [3,9,19,26]. But in this study pH showed a significant relation with the Simpson's diversity index. This could be explained by the fact that high pH values could favor the dominance of few species, reflecting in low diversity [10]. Furthermore, intermediary pH values could enable the existence of many different species, reflecting in high diversity values [3].

4.3. Interspecies interactions

Several authors have established trophic webs in communities of invertebrates associated with guano deposits, based on their knowledge of the biology of each group [5,6,24,30,31]. Unfortunately, in trophic webs in the Neotropics the recognition of decomposers and predators is not easy, as Gibert and Deharveng [32] considered for large communities of guano piles in the old world. Accordingly, the web proposed in this work, in addition to compiling literature data on the feeding preferences of each group, was also based on statistical data (significant correlations between groups) and preference for substrates, in order to structure those relationships. Species that occurred closer in the CCA analyses are influenced by the same abiotic factors and, thus, are more likely to interact to each other. Furthermore, microhabitat preferences shown by some organisms, indicates the existence of succession communities on guano deposits, resulting from the physical–chemical alterations that occur over time [18]. Those relationships are speculative and more detailed knowledge about the behavioral biology of each group is needed to confirm the data proposed by this work.

5. Conclusions

Studies on invertebrate communities associated with guano deposits provide a wide variety of new data, given the few existing studies in this field. Populations associated with this resource reveal a strong association with some physical–chemical parameters of the guano. The pattern found in this work suggests a possible change in the components of the trophic web according to the guano age. Such communities reveal a complex arrangement of interspecific relations, still considered simple, when compared to epigean communities. Hence, those communities are important models for ecological studies, which aim to understand the functioning of small communities.

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Appendix I

List from Acari morphospecies found at the bat guano.

TAXA				
Order	Suborder	Family	Species	Abundance
Mesostigmata	Monogynaspida	Ameroseiidae	*Ameroseius* sp.	34
Mesostigmata	Monogynaspida	Ascidae	Ascidae sp.	1
Mesostigmata	Monogynaspida	Digamasellidae	Digamasellidae sp.	634
Mesostigmata	Monogynaspida	Laelapidae	*Androlaelaps* sp.	1045
Mesostigmata	Monogynaspida	Laelapidae	*Stratiolaelaps* sp.	798
Mesostigmata	Monogynaspida	Macrochelidae	*Macrocheles* sp.	7
Mesostigmata	Monogynaspida	Melicharidae	*Proctolaelaps* sp.	1607
Mesostigmata	Monogynaspida	Rhodacaridae	Rhodacaridae sp.1	1017
Mesostigmata	Monogynaspida	Rhodacaridae	Rhodacaridae sp.2	2
Mesostigmata	Monogynaspida	Trachytidae	Trachytidae sp.	1413
Mesostigmata	Monogynaspida	Trematuridae	Trematuridae sp.	410
Mesostigmata	Monogynaspida	–	Uropodina sp.2	5434

(*continued*)

TAXA				
Order	Suborder	Family	Species	Abundance
Mesostigmata	Monogynaspida	–	Uropodina sp.3	202
Mesostigmata	Monogynaspida	–	Uropodina sp.5	439
Mesostigmata	Tryginaspida	–	Tryginaspida sp.	1
Sarcoptiformes	Endeostigmata	Nanorchestidae	Nanorchestidae sp.	65
Sarcoptiformes	Oribatida	Acaridae	*Tyrophagus* sp.	3906
Sarcoptiformes	Oribatida	Histostomatidae	Histiostomatidae sp.	4060
Sarcoptiformes	Oribatida	Acaridae	Acaridae sp.	368
Sarcoptiformes	Oribatida	–	Astigmata sp.1	120
Sarcoptiformes	Oribatida	–	Astigmata sp.2	2
Sarcoptiformes	Oribatida	–	Astigmata sp.3	160
Sarcoptiformes	Oribatida	Cosmochthoniidae	*Cosmochthonius* sp.	3
Sarcoptiformes	Oribatida	Sphaerochthoniidae	*Sphaerochthonius* sp.	159
Sarcoptiformes	Oribatida	–	Oribatida jovem	239
Sarcoptiformes	Oribatida	–	Oribatida sp.1	2712
Sarcoptiformes	Oribatida	–	Oribatida sp.2	17,932
Sarcoptiformes	Oribatida	–	Oribatida sp.3	499
Sarcoptiformes	Oribatida	–	Oribatida sp.4	636
Trombidiformes	Prostigmata	Microdispidae	Microdispidae sp.	186
Trombidiformes	Prostigmata	Scutacharidae	*Imparipes* sp.	2638
Trombidiformes	Prostigmata	Tarsonemidae	*Tarsonemus* sp.	64,817
Trombidiformes	Prostigmata	Cheyletidae	*Cheyletus cacahuamilpensis*	6782
Trombidiformes	Prostigmata	Stigmaeidae	Stigmaeidae sp.	1132
Trombidiformes	Prostigmata	Eupodidae	Eupodidae sp.	1792
Trombidiformes	Prostigmata	Tydeidae	*Lorryia* sp.	35,065

Appendix II

List from arthropoda morphospecies found at the bat guano, except for the subclass Acari.

TAXA			
Class/order	Family	Species	Abundance
Araneae	Sicariidae	*Loxosceles variegata*	1
Araneae	Sicariidae	Sciariidae sp.	2
Psocoptera	–	Psocoptera sp.	126
Pseudoscorpiones	Chernetidae	Chernetidae sp.1	61
Pseudoscorpiones	Chernetidae	Chernetidae sp.3	4
Pseudoscorpiones	Chernetidae	Chernetidae sp.2	2
Pseudoscorpiones	Chernetidae	Chernetidae sp.4	1
Oligochaeta	–	Oligochaeta sp.	146
Miriapoda	–	Geophilomorpha sp.	1
Lepdoptera	–	Larva lepidoptera sp.	203
Lepdoptera	–	Larva tineidae sp.	190
Hymenoptera	–	Hymenoptera sp.1	1
Hymenoptera	–	Hymenoptera sp.2	1
Diptera	Cecidomyiidae	Cecidomyiidae sp.	1
Diptera	–	Drosophila sp.1	1
Diptera	–	Larva diptera sp.1	18
Diptera	–	Larva diptera sp.2	4
Collembola	Entomobryidae	Entomobryidae sp.1	2
Collembola	Entomobryidae	Entomobryidae sp.2	35
Coleoptera	–	Coleoptera sp.2	1
Coleoptera	Histeridae	Histeridae sp.	126
Coleoptera	–	Larva coleoptera sp.1	20
Coleoptera	–	Larva coleoptera sp.2	1
Coleoptera	–	Larva tenebrionoidea sp.1	4
Coleoptera	–	Larva tenebrionoidea sp.2	2

References

[1] D.C. Culver, Cave Life. Evolution and Ecology, Harvard University Press Cambridge, 1982.
[2] R.L. Ferreira, R.P. Martins, Diversity of spiders associated with bat guano piles in Morrinho cave (Bahia state, Brazil), Diversity and Distributions 4 (1998) 235–241.
[3] R.L. Ferreira, R.P. Martins, D. Yanega, Ecology of bat guano arthropod communities in a Brazilian dry cave, Ecotropica 6 (2) (2000) 105–116.
[4] J.A. Harris, Bat-guano cave environment, Science 90 (1970) 160–162.
[5] R.F. Bernarth, T.H. Kunz, Structure and dynamics of arthropod communities in bat guano deposits in buildings, Canadian Journal of Zoology 59 (1981) 260–270.
[6] R.L. Ferreira, R.P. Martins, Guano de morcegos: fonte de vida em cavernas, Ciência Hoje 25 (146) (1999) 34–40.
[7] V. Decu, Some considerations on the bat guano synusia, Travail du Institut de Spéologie, Emile Racovitza 25 (1986) 41–51.
[8] E. Hamilton-Smith, The arthropoda of australian caves, Journal of the Australian Entomological Society 6 (1967) 103–118.
[9] T.A. Moulds, Review of australian cave guano ecosystems with a checklist of guano invertebrates, Proceedings of the Linnean Society of New South Wales 125 (2004) 1–42.
[10] T. Moulds, The Seasonality, Diversity and Ecology of Cavernicolous Guano Dependent Arthropod in Southern Australia. Thesis (Ph.D.), University of Adelaid, School of Earth and Environmental Sciences, 2006. (Electronic source), http://thesis.library.adelaide.edu.au/public/adt-SUA20060720.155455.
[11] A.S. Auler, E. Rubbioli, R. Brandi, As grandes cavernas do Brasil, first ed., Grupo Bambuí de Pesquisas Espelológicas, Belo Horizonte, 2001.
[12] A. Magurran, Ecological Diversity and Its Measurement, British Library, Cambridge, 1988.
[13] J.M. Bremmer, Determination of nitrogen in soil by the Kjeldahl method, The Journal of Agricultural Science 55 (1960) 11–30.
[14] B.V. Raij, J.A. Quaggio, N.M. Silva, Extraction of phosphorous, potassium, calcium and magnesium from soils by an ion exchange procedure, Communications in Soil Science and Plant Analysis 16 (1985) 245–260.
[15] H. Cantarella, J.A. Quaggio, Determinação da matéria orgânica, in: B.V. Raij (Ed.), Análise química para avaliação da fertilidade de solos tropicais, Instituto Agronômico, Campinas, 2001, pp. 173–180. (Chapter 9).
[16] G.O. Evans, Principles of Acarology. New York, CAB International, Cambridge, 1992.
[17] G.W. Krantz, D.E.A. Walter, Manual of Acarology, third ed., Texas Tech University Press, Lubbock, 2009.
[18] P. Gnaspini, E. Trajano, Guano Communities in Tropical Caves. Case Study: Brazilian Caves, in: H. Wilkens, et al. (Eds.), Ecosystems of the World: Subterranean Ecosystems, Elsevier Science, Amsterdam, 2001, pp. 251–268.
[19] R.L. Ferreira, X. Prous, R.P. Martins, Structure of bat guano communities in a dry Brazilian cave, Tropical Zoology 20 (2007) 55–74.
[20] D.C. Culver, T. Pipan, The Biology of Caves and Other Habitats, first ed., Oxford University Press, USA, 2009.
[21] T.L. Poulson, Bat guano ecosystems, Bulletin of the National Speleological Society 34 (1972) 55–59.
[22] F.F. Herrera, Las comunidades de artropodos Del guano de guacharos en la Cueva del Guacharo, Boletín de la Sociedad Venezolana de Espeleología 29 (1995) 39–46.
[23] R.L. Ferreira, P.S. Pompeu, Fatores que influenciam a riqueza e a diversidade da fauna associada a depósitos de guano na gruta Taboa, Sete Lagoas, Minas Gerais, Brasil, O Carste 9 (2) (1997) 30–33.
[24] J.M. Webster, J.O. Whitaker Jr., Study of guano communities of big brown bat colonies in Indiana and neighboring Illinois counties, Northeastern Naturalist 12 (2) (2005) 221–232.
[25] A. Romero, Cave Biology, Cambridge University Press, New York, 2009.
[26] G.R. Bahia, R.L. Ferreira, Influência das características físico-químicas e da matéria orgânica de depósitos recentes de guano de morcegos na riqueza e diversidade de invertebrados de uma caverna calcária, Revista Brasileira de Zoociências 7 (1) (2005) 165–180.

[27] M. Manu, V. Honciuc, Rank correlations at the level of soil mites (Acari: Gamasida; Oribatida) from central parks of Bucharest City, Romania, Acta Entomologica Serbica 15 (1) (2010) 129–140.
[28] B.M. O'Connor, Evolutionary ecology of Astigmatid mites, Annual Review of Entomology 27 (1982) 385–409.
[29] P. Hutchinson, Vertebrate excretion (cave guano), Bulletin of the American Museum of Natural History 96 (1950) 381–485.
[30] J.O. Whitaker Jr., P. Clem, J.R. Munsee, Trophic structure of the community in the guano of the evening bat nycticeius humeralis in Indiana, The American Midland Naturalist 126 (1991) 392–398.
[31] L.E.O. Braack, Arthropod inhabitants of a tropical cave 'Island' environment provisioned by bats, Biological Conservation 48 (1989) 77–84.
[32] J. Gibert, L. Deharveng, Subterranean ecosystems: a truncated functional biodiversity, BioScience 52 (6) (2002) 473–481.