

Biodiversity under rocks in disturbed habitats: the role of microhabitats in landscape heterogeneity and community maintenance

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Abstract. The construction of reservoirs for electric power generation is becoming a frequent action in Brazil. In these modified environments, the water level suffers seasonal and stochastic oscillations. The difference among maximum and minimum water levels forms a depletion zone, in which these oscillations represent a disturbance for the installed communities. Analyzing 30 shelters in the depletion zone of Três Marias Reservoir, we aimed to evaluate the richness and diversity of associated communities and verify the relationship between shelter's area, distance from water, concentration of organic matter and humidity and communities' traits. We collected 183 individuals distributed in 64 morfo-species of 33 families from the orders Acarina, Araneida, Scorpionida, Lithobiomorpha, Scolopendromorpha, Coleoptera, Collembola, Dermaptera, Dictyoptera, Diptera, Ensifera, Homoptera, Hymenoptera, Lepidoptera, and Zygentoma. Araneida was the richest order (40.4%), represented mainly by the families Salticidae and Theridiidae. Hymenoptera (18%) and Diptera (13.1%) were abundant. Nearly 68% of the species are predators, the others are basically scavengers. Most of the species (73%) use more than a shelter for obtaining resources. The similarity among the shelters varied between 0 and 0.5, and most presented similarity values less than 0.3. Soil moisture was significantly related to distance from water and organic matter and distance from water was also related to organic matter. No correlation was observed among physical and biological variables. Shelters seem to be important in the depletion zone of the reservoir, offering conditions and resources that make the permanence of associated communities possible in a strongly modified area subject to stochastic disturbances.

Key-words: Depletion zone, invertebrates, communities, reservoirs, neotropics

NTRODUCTION

Spatial and temporal heterogeneity have a great influence on the dynamics and structure of communities and, so, on regional biodiversity (TILMAN, 1994; DUELLI, 1997). Microhabitat availability and quality are variables that influence on the distribution pattern of organisms. Nevertheless, there are few studies on the effects that environmental disturbances caused by man may have on the distribution of organisms in a small scale (GUIDO & GIANELLE, 2001). Studies that quantify habitat use by species can be used to improve the knowledge on the biological needs of species, allowing an evaluation of the effects of habitat disturbances caused by man (ARTHUR *et al.*, 1996).

There is a strong relationship between the environment and the organisms that exploit it. Features such as organism size and mobility determine whether the use of a given habitat is possible or not (HASLETT, 1994; ROSENZWEIG, 1981). According to PARSONS (1995), habitat physical conditions can also limit organisms occurrence, sites where physical stress is relatively low being selected. Then, habitat selection allows the co-existence of different species (ROSENZWEIG, 1981), influencing diversity. Human activities generate environmental conditions very different from original ones, causing changes in species composition (BENDER *et al.*, 1998). Environmental disturbances are usually seen as causing negative impacts on affected species. Nevertheless, in any disturbance, some species may be benefited (MCKINNEV & LOCKWOOD, 1999). According to EKSCHMITT & GRIFFITHS (1998), such species are those able to maintain their activities so that they can acquire resources and reestablish their populations even during an environmental disturbance.

Considering the great hydric potential of Brazil, specially in the Southeastern region, the construction of reservoirs to generate hydroelectric energy is becoming more and more frequent (GODINHO & GODINHO, 1994). In such artificial habitats, water level suffers annual oscillations according to rainfall variations, and also stochastic variations, that depend on water use by human populations. The difference between maximum and minimum water levels form a depletion zone, where oscillations in water level represent a disturbance for established populations.

Invertebrate communities that use rock shelters (lapidicolous communities) may have their structure influenced by physical features of these shelters. So, shelters with different shapes and dimensions can offer different microhabitat conditions to these organisms (FERREIRA & SOUZA-SILVA, 2001).

Considering the rarity of researchs focusing the use of rocks as shelters and, more specifically, its importance in disturbed areas, the present work aimed to evaluate the diversity and the structure of the lapidicolous community of the depletion zone of a reservoir, as well as to verify whether physical and chemical features of shelters influence on their use by the different groups of associated invertebrates.

METHODS

Study area

The Estação Ecológica de Pirapitinga is located at the reservoir of the Hydroelectric Power Station of Três Marias, Minas Gerais, Brazil (18°20'S -18°23'S, 4517'W - 44°20'W). The reservoir was filled in 1962, when an area of about 1000 ha became an island (ARAÚJO,1987).

The station has two different groups of rocks: the siltystone-micaceous, from the Superior Pre-Cambrian, and the coluvian-eluvionars, of dendritic-lateritic type, dating from the Pleistocenic-Holocenic age (ARAÚJO, 1997). The siltystone-micaceous are distributed mainly in the central and northern regions of the hydroelectric station, being easily observed alongside most of the island margins during the dry period or during the lowering of the reservoir water level. In the areas where these rocks appear, cambissoils and sparse vegetation can be observed.

The "cerrado senso stricto" is the vegetation type that predominates in the area, but mesophyll forests ("cerradão"), and fields also occur (GONÇALVES-ALVIM & FERNANDES 2001).

This study was conducted in the depletion margin of the reservoir, in an area of Cambissoils, where a great number of ooliths (spheroid silty exfoliations) of varied size and shapes are used as shelters by many invertebrate species.

Procedures

Thirty randomly selected shelters were numbered from the margin of the reservoir to the borders of a 150 m distant "cerrado" area, and sampled in October 2001.

The substrata under each shelter was inspected and organisms were visually searched for, collected with aid of tweezers and brushes, and fixed in 70% ethanol. The organisms were identified to the lowest taxonomic level possible in the laboratory, using a stereomicroscope, and separated in morpho-species to calculate richness and equitability according to Shannon-Wiener indexes (ZAR, 1984). For such analyses, immature individuals were considered as different morpho-species (FERREIRA & MARQUES, 1998). The specimens are deposited in the Laboratório de Ecologia e Comportamento de Insetos - Universidade Federal de Minas Gerais.

Organisms were classified according to trophic/ functional categories (predators, detritivores, omnivores, or herbivores) (BORROR & WHITE, 1970). Species were also separated in two categories, according to dispersal potential, as follows: it was

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assumed that species that modify the habitat (building channels or webs) and those with reduced size and mobility, use the same shelter during a considerable part of or the whole life cycle. These species were called "anchor species" herein. The remaining species, which potentially use more than one shelter, were called "satellite species".

The area under each of the shelters was calculated by combining the paths measured along the longitudinal axis of each shelter (FERREIRA & SOUZA-SILVA, 2001). The inclination of each shelter was measured with a clinometer, supported on the substratum under each of the shelters.

In the field, soil samples were collected from each shelter and put in plastic bags. In the laboratory, these samples were initially weighed, dried in a heater (24 hours at 100°C) and weighed again to determine water content from weight lost. The heater-dry samples were then burnt at 550°C for three hours and weighed again to quantify organic matter, that corresponds to the weight lost after burning (JACKSON, 1974).

The similarity among shelters was determined using the qualitative Sorensen index (MAGURRAN, 1988). The relationship among physical and chemical parameters (area, declivity, distance from water, soil moisture, and organic matter concentration) and biological ones (richness, diversity, and equitability) was tested using linear regression (TRIOLA, 1998). The variables that did not have normal distribution were log transformed.

RESULTS

A total of 183 individuals belonging to 64 morphospecies from at least 33 families of the orders Acarina, Araneida, Scorpionida, Lithobiomorpha, Scolopendromorpha, Coleoptera, Collembola, Dermaptera, Dictyoptera, Diptera, Ensifera, Homoptera, Hymenoptera, Lepidoptera, and Zygentoma was collected (Tab. 1). The order Araneida was the richest (40.4% of species sampled), represented mainly by the families Salticidae and Theridiidae. Other well represented orders were Hymenoptera (18%) and Diptera (13.1%). The greatest abundance was observed in Shelter 14 (30 individuals) and the greatest richness, in Shelter 8 (13 species). Only Shelter 18 had no occupants and four shelters (2, 7, 9, and 29) had a single organism.

The diversity in shelters varied from 0 to 1.75, whereas most of them had equitability values higher than 0.57 (Tab. 2).

The morpho-species Entomobryiidae sp1, despite not abundant, was the most frequent in shelters. It was found in 9 out of 30 sampled shelters. The morpho-species Corinnidae sp1, Theridiidae sp1, and Formicidae sp1 were collected in 5 shelters each. The most abundant morpho-species, Formicidae sp4 and Salticidae sp9, were restricted to Shelters 14 and 17, respectively.

Most species found (nearly 68%) are predators, the remaining being mainly scavengers (Tab. 1). Most species (73%) use more than one shelter to get resources. The large number of "satellite" organisms is due mainly to the order Araneida. The anchor species are represented mainly by the family Theridiidae (Araneida), appearing also in the orders Acarina, Dermaptera, and Lepidoptera and in the family Theraphosidae (*Acanthoscurria* sp., Araneida) (Tab. 1). The similarity among shelters varied between 0 and 0.5, most of them having similarity lower than 0.3.

The abiotic features of each shelter (area, declivity, organic matter, moisture, and distance from water) varied considerably (Tab. 2). Soil moisture was significantly related to distance from water ($F_{1.27}$ = 15.94, R= -0.609, and P< 0.0005) (Fig.1) and to organic content ($F_{1.28}$ = 26.095, R= 0.695, and P < 0.00002) (Fig. 2) and distance from water was also related to organic content ($F_{1.27}$ = 93.05, R = -0.880, and P< 0.0000) (Fig. 3). No correlation was found among any of the abiotic and biotic parameters.

DISCUSSION

According to KOTLIAR & WIENS (1990), small organisms do not perceive an habitat mosaic as a single habitat, as larger organims do. In a macroscopic scale, the depletion zone of the Três Marias reservoir seems to be an homogeneous habitat. For invertebrates, though, shelters seems to interrupt this homogeneity, contributing for the formation of a mosaic

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Class	Order	Family	Richness	Abundance	Guild	Motility
Arachnida	Acari		2	3	P/S	А
	Aranae		1	1	S	?
		Araneidae	1	2	Р	А
		Coriniidae	2	9	Р	S
		Gnaphosidae	4	5	Р	S
		Lycosidae	1	1	Р	S
		Philodromidae	1	1	Р	S
		Titanoecidae	1	4	Р	S
		Salticidae	10	33	Р	S
		Theridiidae	6	17	Р	А
		Theraphosidae	1	1	Р	S
	Scorpiones	Buthidae	1	1	Р	S
Chilopoda	Lithobiomorpha		2	2	Р	?
	Scolopendropmorpha		1	3	Р	S
Insecta	Coleoptera		2	1	?	?
		Carabidae	2	4	Р	S
		Elateridae	1	1	H/S	S
		Pselaphidae	1	1	S	S
		Staphilinidae	2	2	P/S	S
	Collembola	Entomobryiidae	2	17	S	?
	Dermaptera	Forficulidae	1	4	S	А
	·	Labiduridae	1	2	S	?
		Labiidae	1	2	S	?
	Dictyoptera	Blattidae	1	1	0	?
	Diptera		3	4	?	?
		Cecydomiidae	2	8	S	
		Ceratopogonidae	2	12	Р	
	Ensifera	Grillidae	1	1	S	S
	Homoptera	Cixiidae	1	5	Н	A/S
	Hymenoptera		1	1	?	?
		Formicidae	4	33	S	S
	Lepidoptera	Tineidae	1	1	S	A
	Zygentoma	Lepismatidae	1	1	S	A/S

Table 1. Families and abundances of the collected organisms and relation of these in different trophic guilds.

P - predator, S - scavenger, H - Herbivorous, O - Omnivorous, A - "Anchor" species, S - "satellite" species

of environmental conditions more or less restrictive to their establishment. Besides, moisture and organic matter gradients observed to form as one gets farther from water contribute to such heterogeneity.

General patterns of richness and diversity

The word "patterns" is used herein with caution, considering that sampling was conducted for a short time period. FERREIRA & SOUZA SILVA (2001) studied the lapidicolous fauna in a granitic outcrop surrounded by a seasonal semi-deciduous forest and observed that area, declivity, moisture, and organic content had an important influence on richness and diversity in the invertebrate communities associated to those rocky shelters. In the present study, though, these same variables did not show any significant relationship with the biotic variables of the communities.

Notwithstanding, it is important to stress that, in spite of phocusing on lapidicolous communities, both studies were conducted at sites with different environmental features. FERREIRA & SOUZA-SILVA (2001) studied shelters located directly on rocks; it

Shelter	Inclination (°)	Distance from water (m)	Area (cm ²)	Moisture content (%)	Organic content (%)	Richness	H′	E
1	8	9,53	275	19,77	32	6	1.48	0.92
2	18	12,3	243,9	14.07	22.6	1	0	0
3	6,5	5,07	237,6	17.58	26.7	3	1.1	1
4	18	6,2	282,8	6.7	26.8	1	0	0
5	2	13,7	-	12.63	20.4	2	0.69	1
6	7,5	13,7	405	12.23	21.6	5	1.55	0.96
7	38	17,3	835,2	12.86	19.8	1	0	0
8	27	26,1	654,8	12.25	25.1	13	2.43	0.95
9	12	21,8	369,6	12.93	21	2	0.69	1
10	2	40,9	414.3	25.97	16.7	8	2.04	0.98
11	13	42,6	124.6	1.49	16.8	7	1.83	0.94
12	15	65	316	9.81	16.3	7	1.91	0.98
13	7	58,5	428	13.11	19.3	6	1.52	0.85
14	10,5	75,8	496	8.28	9	5	0.91	0.57
15	12	70,5	741	7.05	13.2	4	1.39	1
16	12	96,5	568.2	10.09	16.8	4	1.39	1
17	20	100,9	1063.7	5.8	11.8	3	0.63	0.58
18	8	105	172,2	5,41	11,9	0	0	0
19	11	?	680	4,54	9,3	3	1,10	1,00
20	7	108,7	439,2	8,73	14,6	2	0,69	1,00
21	3	122,17	608,4	4,52	10,6	2	0,45	0,65
22	5	116,37	864,4	6,13	11,5	6	1,75	0,98
23	11	123,67	271	8,44	14,5	2	0,64	0,92
24	7	131,87	672,92	2,15	6,1	3	0,95	0,86
25	6	131,87	890,5	7,09	12,3	2	0,69	1,00
26	3	137,23	423,1	3,37	5,9	6	1,67	0,93
27	9	139	303,88	6,66	12,8	2	0,69	1,00
28	8	139,87	478,47	5,90	12,6	1	0	0
29	5	141,1	342,7	7,94	14,6	1	0	0
30	4	141,1	120	3,83	6	4	1,28	0,92

Table 2: Relative physical and biological parameters of each shelter

is possible that, in such habitats, shelters are more important for moisture maintenance in a microhabitat scale than in the cambissoils of the depletion zone. Considering that insects are prone to dessication, and that susceptibility to water loss can limit the distribution of some groups (PARSONS, 1995), the possibility of moisture maintenance by shelters assumes a great importance in a substratum with low water retention capability.

Besides, FERREIRA & SOUZA-SILVA (2001) worked in a system where colonization occurred alongside the border of the rocky outcrop, that contacts the preserved vegetation directly. Such situation is very different from the depletion margin, where colonization occurred mainly from the vegetation border, parallel to water level at the

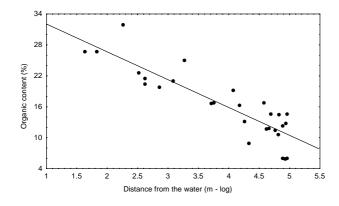


Figure 1. Regression between organic content under each shelter and distance from the water (log).

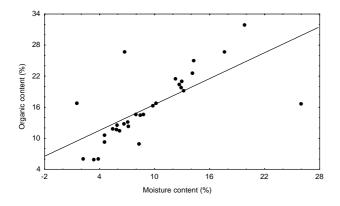


Figure 3: Regression between organic content under each shelter and moisture content.

reservoir. This vegetation was prone to the same seasonal impacts suffered by the depletion zone.

Another factor that should be taken into account is the disturbance level suffered by both systems: it seems that important disturbances affect the outcrop in a seasonal frequency, whereas the reservoir depletion zone is prone to stochastic disturbances, besides seasonal ones. Considering that, the lack of relationships between community features and environmental parameters may indicate that environmental conditions are not stable long enough to allow this community to become structured in time.

Microhabitat selection and distribution patterns

PARSONS (1995) suggests that stress keeps an organism in disadvantage, so that it needs to have a

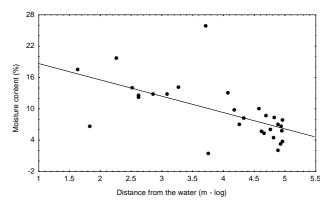


Figure 2. Regression between moisture content under each shelter and distance from the water (log).

great energy expenditure to remain alive, and an inverse relationship occurs between the suitability of an habitat and the ecological costs for its occupancy. Establishment cost for individuals in shelters results from processes that tend to reduce fitness, and such costs increase in unstable environments (GREENE, 2001). In the studied area, populations may not respond to environmental variability at the same speed and intensity in which they occur, and the drastic drought and inundation cycles may function as an important selection agent (PARSONS, 1995).

In a stressing scenery, organisms' habitats are defined as the product of the interaction between stress intensity, magnitude of environmental fluctuations, and energy from resources (PARSONS, 1995). The inverse relationship between organic matter concentration and distance from water suggests the importance of water as a transporting agent of resources to shelters. The shelters closest to water offer a greater amount of organic matter and could so shelter a more robust detritivore chain, but they are prone to more frequent disturbances, and are also available for colonization for a shorter period.

If one considers shelters as islands and the vegetation as a colonization source sending species to the depletion zone (MCARTHUR & WILSON, 1967), the distance from the "cerrado" area may be also influencing the distribution of organisms among shelters. So, the apparently random shelter occupancy may represent a balance between distance from

vegetation and the kinder and resource richer conditions in the shelters closest to water.

According to HOLT (1997), the maintenance of species richness within a trophic level may be related to stochastic temporal dynamics. Then, habitat heterogeneity, variability, and spatial dimension may allow different species to exploit it to escape in space and time. In this context, the predominance of spiders, mainly predator and wandering ones, is an importante feature of this system, representing an answer to environment heterogeneity.

Community dynamics and species flux

The word metacommunity was first suggested by GILPIN & HANSKI (1991) as representing a set of local communities from different sites connected by dispersion of one or more of its components. According to these authors, a metacommunity follows the same dynamics of a metapopulation, being subject to local extinctions and recolonizations.

There is some evidence that the system studied can constitute a metacommunity. The lack or low abundance of organisms in some shelters may represent local extinctions and possible recolonizations from other shelters or adjacent vegetation, that function as species sources (FERREIRA & SOUZA-SILVA, 2001). The shelters closest to water would be prone to suffer seasonal extinctions with the rise of water level, period when the farthest shelters would be more important for the maintenance of the system biodiversity. Recolonization would occur during the dry season, when they are exposed again. However, the dynamics of between-shelters movement remain largely unknown and merit further research.

The similarity found may be an indicative of the change of individuals among the communities from different shelters, feature typical of the metacommunity systems. A high similarity would indicate frequent individual flux, suggesting a single community whose component populations would use many shelters to get resources and protection against predation and adverse environmental conditions. By the other side, if the observed similarity was equal or very close to zero, such a system would be, probably, composed by small isolated communities, each one restricted to one or a few close shelters.

The present work reinforces, once more, the importance of spatial heterogeneity in community structure, mainly in altered habitats prone to disturbances. In this context, the rock shelters seem to play an important role in the depletion zone of the Três Marias reservoir, offering conditions and resources that make it possible for the communities to establish themselves in a highly impacted area prone to stochastic disturbances.

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