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Benthic invertebrates and the habitat structure in an intermittent river of the semi-arid region of Brazil

Macroinvertebrados bentônicos e a estrutura do habitat em um rio intermitente do semiárido brasileiro

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Abstract

Interactions between the habitat structure and physical and chemical parameters generate environmental conditions that influence the distribution and abundance of macroinvertebrate species and their assemblages. This study describes the habitat structure and its effects on macroinvertebrate composition in an intermittent stream in the Brazilian semi-arid. Collections of benthic invertebrates were performed in three reaches along the Ipanema River during the dry and wet seasons using a "D" shaped net (40 cm wide and 250 µm mesh). A total of 23 taxa was recorded, Insecta being the most representative with 12 families and an average density of 168.1 ind/m². Correlations between environmental variables and CCA axes showed that substrate composition (sand and mud), macrophytes, litter and altitude were the main variables explaining benthic macroinvertebrate composition in the study stream. Canonical correlations between macroinvertebrate and physical and chemical variables were not significant. This study shows that the habitat structure contributes to the persistence and stability of macroinvertebrate communities in a Brazilian semi-arid stream, by creating refugia for organisms and contributing to the physical structures available for colonization.

Key words: hydrological disturbances, patch dynamics, drylands.

Resumo

As interações entre a dinâmica do habitat e os parâmetros químicos e físicos criam condições ambientais que influenciam fortemente a distribuição e a abundância de macroinvertebrados. Este estudo descreve a estrutura do habitat ao longo de um rio intermitente do semiárido brasileiro, quantifica variações na composição da fauna bentônica e avalia associações de variáveis físicas e químicas e da estrutura física do habitat com a fauna de macroinvertebrados. Foram realizadas coletas em três trechos ao longo do rio Ipanema, durante os períodos seco e chuvoso. Macroinvertebrados bentônicos foram amostrados usando uma rede tipo "D" com 40 cm de abertura e malha de 250 µm. Foram registrados 23 táxons, sendo a classe Insecta a mais representativa com 12 famílias e uma densidade média de 168.1 ind/m². As correlações entre as variáveis ambientais e os eixos da CCA mostraram a composição do substrato (areia e lama), percentual de macrófitas e folhiço, e altitude como variáveis explicativas para a composição da fauna de macroinvertebrados. A associação entre as variáveis físicas e químicas e a composição de macroinvertebrados não foi significativa. Este trabalho mostra que a estrutura do habitat tem o potencial de contribuir para a persistência e a estabilidade das comunidades de macroinvertebrados nos rios do semiárido por criar refúgios para a diversidade e contribuir para a estrutura física disponível para colonização destes organismos.

Palavras-chave: perturbação hidrológica, distribuição em manchas.

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Introduction

Drylands are usually associated with high and variable degrees of aridity, which are a reflection of low precipitation and high evapotranspiration. These areas also show unevenly distributed (frequently sparse) and temporally variable vegetation cover (Tooth, 2000). Drylands include deserts, arid and semi-arid lands and dry sub-humid regions; the semi-arid regions alone comprise almost 18% of the drylands (Kassas, 1999).

The hydrological regime plays a major role on the organization of aquatic systems and their communities in drylands, by structuring the spatial distribution of organisms (Sheldon *et al*., 2002), enhancing diversity of species (Maltchik and Medeiros, 2006) and creating habitat variability (Mugodo *et al*., 2006). This is achieved as a result of flooding events that connect habitats previously isolated during the dry season and dry periods that spatially segregate the physical characteristics of the environment (Marshall *et al*., 2006). In such a patchy environmental framework, it is expected that the aquatic fauna becomes extremely variable, differing significantly among spatial scales (rivers, reaches and habitats) (Blanchette and Pearson 2012).

In Brazil, the extremes of drought and flooding are regarded as the main agents structuring the physical and biological systems in semi-arid streams, conditioning the river morphology, physical and chemical characteristics of the water and enhancing habitat heterogeneity (Maltchik and Florin, 2002; Medeiros *et al*., 2008). The interaction of these factors creates and maintains heterogeneous systems that segregate the abundance and distribution of species at different spatial scales and thus the community composition (see Medeiros *et al*., 2011; Maddock, 1999). Therefore, the characteristics of the habitat and their spatial variation are thought to have important effects on the structure and organization of biological communities in semi-arid streams.

Some groups of the macroinvertebrate fauna show high resistance to the environmental variation, whereas others are able to rapidly colonize new habitats created from flooding (Pires *et al.,* 2000; Silva-Filho and Maltchik, 2000; Silva-Filho *et al.,* 2003). The small body size, the short life cycle and the dispersion patterns of aquatic insects associated with the benthos, as well as their susceptibility to water flow, make them a dynamic group well adapted to colonize variable environments such as intermittent streams (Miller and Golladay, 1996; Lake, 2000). Most of the benthic macroinvertebrates are generalists in habitat and feeding habits, allowing a wide spatial distribution (Brito-Júnior *et al*., 2005). Nonetheless, benthic macroinvertebrates are particularly subject to the effects of water flow (Stenert *et al.,* 2008) given their close association with the substrate and the physical structure of the habitat. Some studies show that the main factors that affect the macroinvertebrate community distribution are associated with the stability, heterogeneity and granulometry of sediment, dissolved oxygen concentrations, pH, water velocity and temperature and food availability (Palmer *et al*., 1994; Hynes, 2001), besides water flow and hydroperiod. Other studies mention that the riparian vegetation can affect macroinvertebrate assemblages by increasing the availability of underwater structures for colonization, resulting in greater densities and diversity of organisms (Trivinho-Strixino and Strixino, 1993; Beltrão *et al*., 2009).

The role of the extreme variations in water flow in the spatial dynamics of the macroinvertebrate assemblages and their association with habitat structure in semi-arid intermittent streams has received little attention. Flooding magnitude has been indicated as playing a major role in macroinvertebrate assemblages in semi-arid rivers of Brazil by disrupting and destroying benthic communities in short-term spatial and temporal scales (Silva-Filho *et al*., 2003).

This study describes the structure of the habitat and physical and chemical variables along an intermittent river of the semi-arid region of Brazil. We aim to (i) quantify the variation in the composition of macroinvertebrates and (ii) analyze the association between physical and chemical variables and habitat structure with the macroinvertebrate composition. The hypothesis that the environmental variables will be correlated with the spatial segregation in assemblage composition of macroinvertebrate is tested.

Material and methods

Study area

The present study was performed in the upper reaches of the Ipanema River, a 4^{th} order (Strahler, 1964) intermittent river affluent of the São Francisco River (Figure 1). The Ipanema River flows south for 139 km through the states of Pernambuco and Alagoas and presents a catchment basin area of approximately 6209 km^2 (Moreira-Filho, 2011). Average annual discharges are 7.17m^3/s reflecting the low and irregular precipitation in the area and leading to the intermittent hydrological regime (Silva *et al*., 2004). This is aggravated by the semi-arid climate (BSh, Köppen-Geiger climate classification updated by Peel *et al*., 2007). Precipitation is higher between April and June, with an annual average of 1095.9 mm (Rodal *et al*., 1998). Maximum altitudes in the area range between 650 and 1000 m (Beltrão *et al*., 2005) and average annual temperatures are 25 ºC. The vegetation in the area is the Caatinga/Agreste, a mostly deciduous open forest (Beltrão *et al*., 2005).

Macroinvertebrate collections

Collections were performed on three 100-500 m reaches of the Ipanema River during four occasions, two during the wet (April and July 2007) and two during the dry (October 2007 and January 2008) periods (Figure 1).

At each river reach, three subsamples of 40 x 40 x 2.5 cm of sediment were randomly taken using a D-shaped net (40 cm wide and 250 µm mesh). Samples were fixed in 4% formalin in the field and taken to the laboratory where they were wet sieved (250 µm) and preserved in 70% alcohol. Macroinvertebrate individuals were sorted, identified to the lowest possible level (usually family) and counted. Identification followed standard literature (Mugnai *et al*., 2010; McCafferty, 1998; Williams and Feltmate, 1992; Borror and Delong, 1988).

Habitat analysis

The environmental characteristics measured consisted of (i) habitat structure and substrate composition, (ii) reach morphology and (iii) physical and chemical water variables. The substrate composition and habitat structure were averaged from 9 to 12 survey points of 1 square meter measured in the margins (see Medeiros *et al*., 2008; Farias *et al*., 2012 for further details). In each survey point the proportion of the sediment composition (mud, sand, gravel and cobbles) and littoral and underwater structures (e.g. macrophytes, littoral grass, submerged terrestrial vegetation, overhanging terrestrial vegetation, leaf litter, algae and woody debris) were estimated visually (adapted from Pusey *et al*., 2004). River reach morphology was evaluated by the average width (m) and depth (cm) taken from three transects randomly placed in the river reach or pool (during the dry phase). Water velocity (m/s) was estimated using the float method (Maitland, 1990). Altitude was estimated using a Garmin GPS receiver. Physical and chemical variables were measured in the water surface using portable equipment for pH (TECNOPON MPA-210), conductivity (µS/cm) (TECNOPON MCS-150), dissolved oxygen (mg/L) and temperature (°C) (Lutron DO-5510). Transparency (cm) was measured using a Sechi disc.

Data analyses

Statistical analyses were performed using mean invertebrate density (ind/m²), calculated as the number of individuals divided by the total sampled area of the D-shaped net for each stream reach. Density and richness of taxa were used to describe patterns of distribution of the assemblages and life stages (larval, pupae and adult) were treated as separate taxa given their differences in resource and habitat use. Significance of differences for density and richness between sites and seasons were measured using two-way ANOVA (Sokal and Rohlf, 1969; Maltchik *et al*., 2010).

Patterns of variation in assemblage composition (based on Bray-Curtis distance) among reaches and sampling occasions were evaluated using Nonmetric Multidimensional Scaling (NMDS). Variance explained in the ordination axes was calculated based on the coefficient of determination (r^2) between distances in the ordination space and distances in the original space (McCune and Grace, 2002). This is an after-the-fact analysis to verify how well the distances in the ordination space represent the distances in the original space. The Multiresponse Permutation Procedure (MRPP) was used to test for significances of differences in composition across river reaches (Biondini *et al*., 1985; McCune and Grace, 2002). The value of "A" is presented as a measure of the degree of homogeneity between groups compared to random expectation. The Indicator Species Analysis (ISA) was used to determine which taxa were significant indicators of each river reach. The indicator values (IV) for each taxon was calculated using the method of Dufrene and

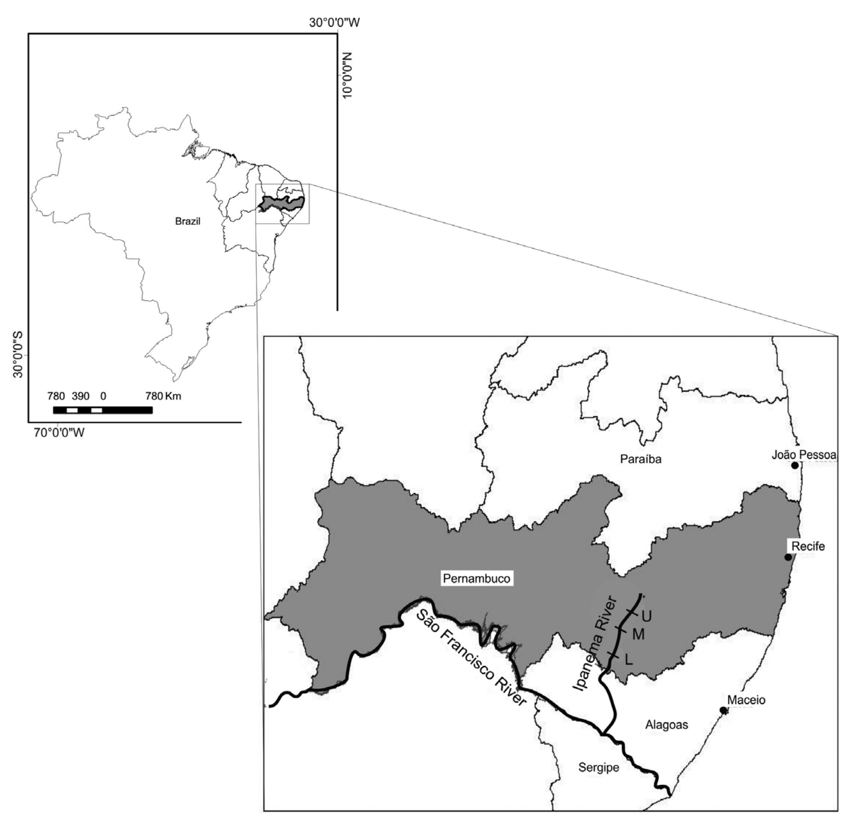

Figure 1. Study area with the location of the Ipanema River in the states of Pernambuco and Alagoas, Brazil, with the study reaches during the hydrological cycle of 2007/2008. U = Upper reach, M = Middle reach and L = Lower reach.

Legendre (1997). This value is tested for significance using the Monte Carlo test (1000 permutations).

To establish the effect of the environmental variables on the benthic fauna, a Canonical Correspondence Analysis (CCA) was performed (McCune and Grace, 2002). The data matrix was centered and normalized and the correlations tested by the Monte Carlo test with 999 permutations. The environmental variables used in the CCA were: percentage of macrophytes, submerged vegetation, leaf litter, algae, woody debris, mud, sand, water velocity, elevation, dissolved oxygen, pH, conductivity, turbidity and temperature. Density data, richness and environmental variables were $log_{10}(x+1)$ transformed (Sokal and Rohlf, 1969). Statistical analyses (α=0.05) were performed on PC-ORD 4.27 (McCune and Mefford, 1999).

Results

During the study period, the Ipanema River showed an intermittent hydrological regime characterized by a wet phase with surface water flow in April and June and a dry phase in October and January, when flow was absent and pools were formed in the river bed (Figure 2). Two study reaches dried out before the end of the study (lower and middle). Width followed the effect of water velocity, being higher during the wet phase, whereas depths were more variable with no clear trend in regard with water velocity (Figure 2). Waters were alkaline with pH ranging from 7.8 to 8.7 and well oxygenated (3.7 to 7.7 mg/L). Temperature ranged from 23.3 to 30.8 °C and the conductivity and transparency did not show clear pattern of variation across reaches and sampling occasions (Figure 2). The structure of the littoral habitat was diverse, composed mostly of woody debris (8.8% ±7.9), aquatic macrophytes (8.0% ±13.3), algae (5.4% ±9.3), littoral grass (3.3% ±4.1) and leaf litter (3.1% ±5.5) (Table 1). Woody debris and macrophytes were abundant in the upper (14.9% ±8.0 and 14.5% ±19.6, respectively) and middle (6.4% ±6.6 and 7.3% ±6.7, respectively) reaches, whereas leaf litter was present, mostly in April, in the lower study reaches (Figure 2). Substrate composition was mainly composed of mud (44.9% ±37.1) and sand (45.7% ±30.2), and to a lesser extent gravel (9.1% ±11.9) and cobbles (0.3% ±0.6) (Table 1, Figure 2).

A total of 28,986 macroinvertebrate individuals were collected, distributed across 26 taxa and life stages (Table 2). Insecta was the most important class with 12 families and an average den-

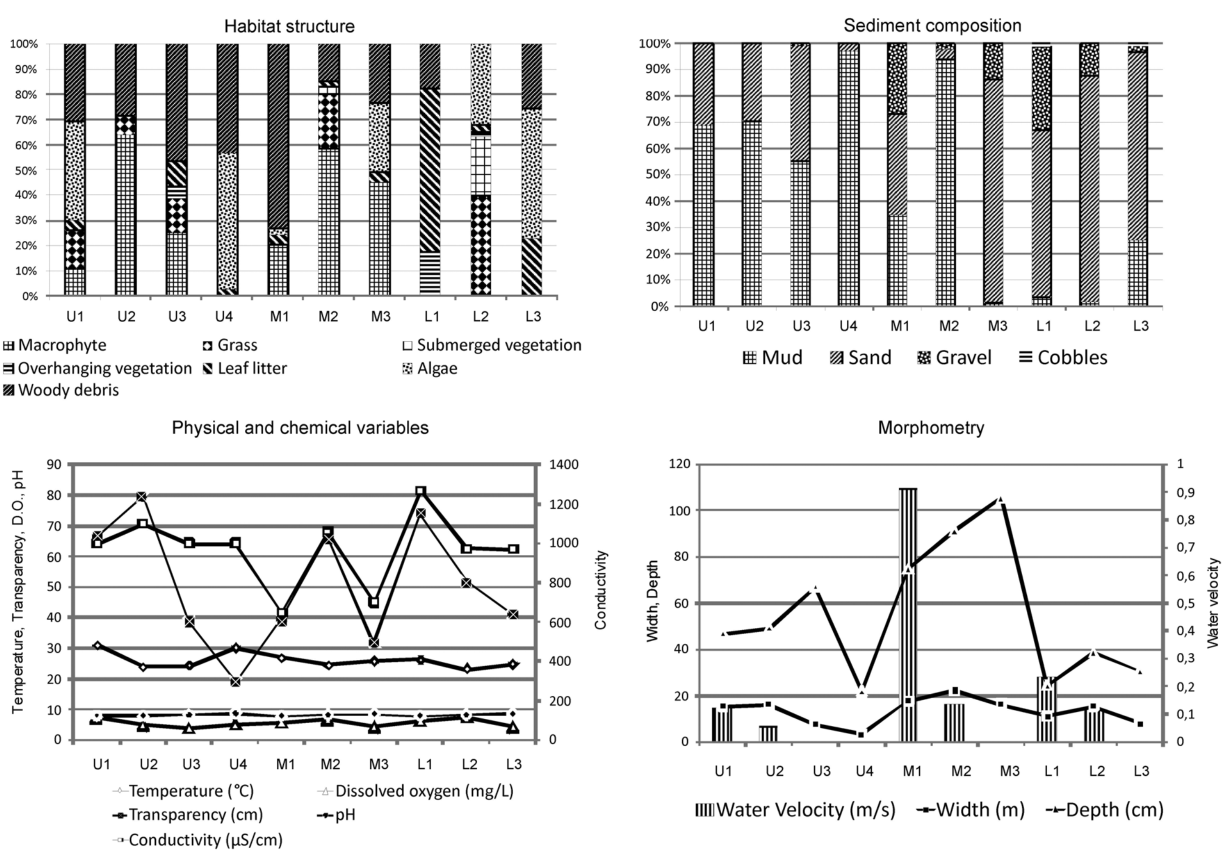

Figure 2. Environmental variables surveyed in the Ipanema River, Northeastern Brazil, during the 2007/2008 hydrological cycle. Codes indicate river reach (U=upper, M=middle and L=lower) and sampling occasion (1,2,3,4).

Table 1. Average proportional cover of habitat elements, morphometry, and physical and chemical variables (±SD) in the Ipanema River, Northeastern Brazil, during the 2007/2008 hydrological cycle. Max: maximum; Min: minimum; SD: standard deviation.

	Average (±SD)	Min-Max
Habitat structure (%)		
Macrophytes	8.0 (± 13.3)	0-43.3
Grass	3.3 (± 4.1)	0-11.7
Submerged vegetation	0.5 (± 1.4)	0-4.6
Overhanging vegetation	0.7 (± 1.6)	0-5
Leaf litter	3.1 (± 5.5)	0.3-18.3
Algae	5.4 (± 9.3)	0-30
Woody debris	8.8 (± 7.9)	0-23.3
Substrate composition (%)		
Mud	44.9 (± 37.1)	1-96.7
Sand	45.7 (± 30.2)	3.3-86
Gravel	9.1 (± 11.9)	0-31.7
Cobbles	0.3 (± 0.6)	0-1.7
Morphometry		
Elevation (m)	434.5 (± 34.7)	387-466
Average depth (cm)	55.0 (± 28.7)	21.8-105.5
Width (m)	13.4 (± 5.7)	3.3-22.2
Water velocity (m/s)	0.2 (± 0.3)	0-0.9
Water quality		
Temperature (°C)	26.0 (± 2.6)	23.3-30.8
Conductivity (μS/cm)	971.5 (± 181.0)	645.7-1268.9
Dissolved oxygen (mg/L)	5.5 (± 1.4)	3.7-7.7
Transparency (cm)	50.9 (± 19.0)	19.0-79.5
pH	8.2 (± 0.3)	7.8-8.7

sity of 168.1 ind/m² ± 669.7 compared to the overall macroinvertebrate average density of 226.3 ind/m² ± 1087. Density and richness values of macroinvertebrates were variable across river reaches, 301.3 ± 1692.4 ind/m² and 8-12 taxa in the middle reach, compared to the lower (209.8 ± 718.3 ind/m² and 8-21 taxa) and upper (182.6 ±665.2 ind/m² and 8-20 taxa) reaches. Density of macroinvertebrates was greater during the dry phase (300.9 ± 1552.9 ind/m² and 8-21 taxa) compared to the wet phase (176.7 ± 607.2 ind/m² and 8-19 taxa). Nevertheless, two-way ANOVA showed no interaction for density or richness between river reaches and seasons ($F_{density}$ =1.3; d.f.=2,4; p=0.365 and $F_{richness}$ =0.6; d.f.=2,4; p=0.582). In addition, the differences observed are not significant for river reaches ($F_{density}$ =0.7; d.f.=2,4; p=0.544 and $F_{richness}$ =0.8; d.f.=2,4; p=0.496) and seasons ($F_{density}$ =0.3; d.f.=1,4; p=0.614 and $F_{richness}$ =0.6; d.f.=1,4; p=0.483).

The most representative taxa were Chironomidae (1156.1 ± 1592.2 ind/m²) among the insects, with high average density during the wet phase (1172.2 ± 1394.2 ind/m²), mostly in the upper and lower reaches. Among the gastropods, Thiaridae (2238.4 ±4460.6 ind/m²) showed higher density during the dry phase (4417.2 ± 6841.5 ind/m²), representing 64.8% of all the macroinvertebrate counts and Planorbidae (650.2 ± 1017.8 ind/m²) showed high average densities during the wet phase (788.8 ± 1285.7 ind/m²) (Table 2).These families were present in all sampling occasions. Other less dense taxa such as Baetidae, Gomphidae and Hydrophilidae were representative during the wet phase, mostly in the lower study reach (128.2 ± 185.7 ind/m²). During the wet phase in the middle reach Atyidae amounted 147.9 ind/m² of a total average of 158.3 ind/m². Dytiscidae and Hydrophilidae, as well as Hemiptera, were present mostly in the lower study reach with densities reaching 408.3 ind/m² (Table 2).

The NMDS explained 93% of the variation in the dataset, having a stress of 3.5. The first axis accounted for 36.4% of the variance explained and the second axis explained 25.3% of the variation. The study reaches were spatially distant in regard to their macroinvertebrate composition (Figure 3). Nevertheless, significant differences were observed only between the upper and middle reaches (MRPP; A = 0.34; p = 0.009) and the upper and lower reaches (MRPP; A = 0.1; p = 0.04). Differences between the middle and lower reaches were not significant (MRPP; A = 0.20; p = 0.09). Significant differences in assemblage composition between the dry and wet phases were not detected (MRPP; A = -0.04; p = 0.67).

Taxa correlated ($r^2 \geq 0.3$) with the first and second NMDS axes were Physidae, Lymnaeidae, Planorbidae, Ceratopogonidae (upper reach), Gerridae (middle reach), Chironomidae, Hydrophilidae, Corixidae, Baetidae and Dytiscidae (lower reach) (Figure 3).

Table 2. Density (ind/m²) and frequency of occurrence (F.O.) (%) of macroinvertebrates in the Ipanema River, Northeastern Brazil, during the 2007/2008 hydrological cycle. * Family not identified.

	Upper reach				Middle reach			Lower reach			F.O.
	April	July	October	January	April	July	October	April	July	October	
Diptera											
Ceratopogonidae	104.2	220.8	322.9	58.3	0.0	10.4	70.8	1.6	200.0	22.9	90.0
Chironomidae (larvae)	2654.2	1606.3	5004.2	75.0	1864.6	1456.3	237.5	4409.4	1781.3	3447.9	100.0
Chironomidae (pupa)	8.3	58.3	145.8	0.0	45.8	16.7	12.5	4.7	160.4	131.3	90.0
Coleoptera											
Dytiscidae (larvae)	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	8.3	156.3	30.0
Dytiscidae (adult)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	408.3	20.0
Hydrophilidae (larvae)	8.3	16.7	2.1	0.0	0.0	0.0	0.0	0.0	335.4	8.3	50.0
Hydrophilidae (adult)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.6	62.5	20.0
Hemiptera											
Corixidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.8	2.1	20.0
Gerridae	0.0	0.0	0.0	0.0	35.4	0.0	0.0	0.0	4.2	6.3	30.0
Notonectidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	10.0
Odonata											
Libellulidae	20.8	45.8	8.3	0.0	0.0	0.0	0.0	0.0	0.0	10.4	40.0
Gomphidae	6.3	6.3	18.8	12.5	0.0	0.0	8.3	145.3	39.6	41.7	80.0
Ephemeroptera											
Ephemeroptera*	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0
Baetidae	27.1	37.5	70.8	0.0	0.0	0.0	0.0	3.1	487.5	25.0	60.0
Caenidae	0.0	50.0	337.5	0.0	0.0	0.0	6.3	0.0	41.7	104.2	50.0
Trichoptera											
Leptoceridae	0.0	35.4	12.5	0.0	0.0	0.0	0.0	0.0	6.3	14.6	40.0
Gastropoda											
Ampularidae	0.0	54.2	33.3	0.0	0.0	0.0	0.0	0.0	2.1	0.0	30.0
Planorbidae	1454.2	3141.7	1175.0	350.0	8.3	4.2	22.9	7.8	116.7	220.8	100.0
Lymnaeidae	0.0	22.9	25.0	22.9	0.0	0.0	0.0	0.0	0.0	0.0	30.0
Physidae	4.2	2.1	2.1	6.3	0.0	2.1	2.1	0.0	0.0	2.1	70.0
Thiaridae	52.1	37.5	391.7	43.8	2862.5	1577.1	14525.0	21.9	164.6	2708.3	100.0
Bivalvia											
Sphaeridae	8.3	545.8	87.5	8.3	2.1	0.0	2.1	0.0	8.3	177.1	80.0
Crustacea											
Atyidae	0.0	0.0	2.1	0.0	6.3	141.7	8.3	0.0	0.0	0.0	40.0
Conchostraca	45.8	31.3	6.3	0.0	0.0	0.0	0.0	0.0	2.1	4.2	50.0
Oligochaeta*	235.4	193.8	8.3	0.0	8.3	18.8	527.1	7.8	727.1	54.2	90.0
Hirudinea*	0.0	10.4	2.1	0.0	0.0	0.0	14.6	0.0	0.0	0.0	30.0

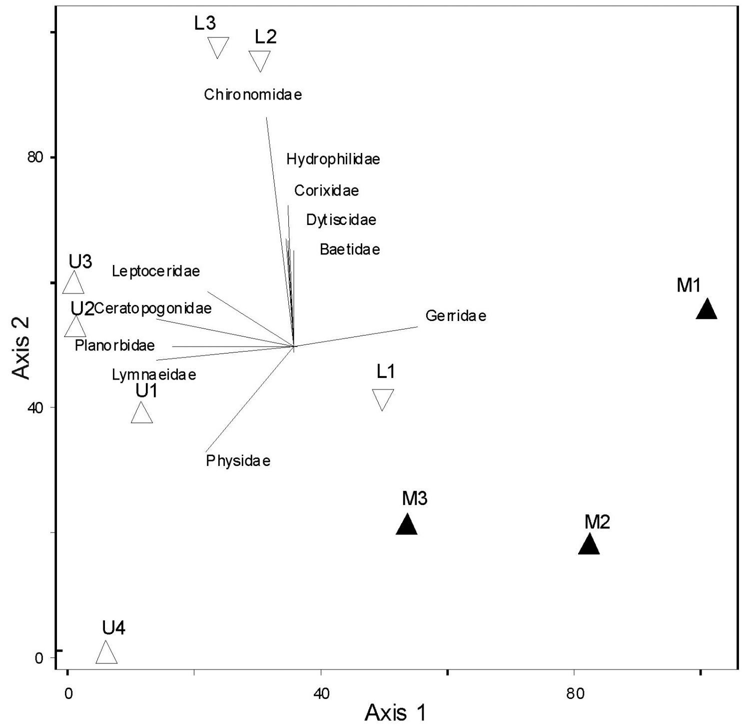

Figure 3. Bi-dimensional solution of the NMDS (stress = 3.5) for the composition of the macroinvertebrate assemblages across the study reaches in the Ipanema River, Northeastern Brazil. Vectors indicate direction and strength of correlation between the macroinvertebrate taxa and the NMDS axes (r^2 > 0.3). Codes indicate river reach (U=upper, M=middle and L=lower) and sampling occasion (1,2,3,4).

Indicator Species Analysis showed Planorbidae (IV=75.3, p=0.008) and Physidae (IV=56.7, p=0.03) as significant indicators of the upper reach, Atyidae (IV=95.1, p=0.01) as indicator taxa for the middle reach and Gomphidae (IV=67.8, p=0.001) as the indicator taxa for the lower reach.

The variance explained by the first three axes of CCA for the association between the environmental variables and the macroinvertebrate composition was 54.6%. The first and second axes explained most of this variation (21.1 and 20.1%, respectively). The Monte Carlo test was significant for the CCA eigenvalues (p=0.001) and for the species-environment correlations for the macroinvertebrate composition and the structure of the habitat and reach morphology (p=0.002) (Table 3). Correlations between these environmental variables and the CCA axes showed sand, mud, macrophytes (correlated with the first axis), leaf litter and elevation (correlated with the second axis) as important variables explaining the macroinvertebrate composition (Table 3 and Figure 4). Canonical Correspondence Analysis for the association between physical and chemical variables and the macroinvertebrate composition explained 41.6% of the variation in the dataset, but the Monte Carlo test showed no significance for the eigenvalues (p=0.2953) and for the species-environment correlations (p=0.5285) (Table 3).

Discussion

In the present study and in other studies undertaken in streams of semi-arid Brazil (Silva-Filho and Maltchik, 2000; Abílio *et al.*, 2007; Andrade *et al.*, 2008; Rocha *et al.*, 2012), the most abundant macroinvertebrate taxa was the class Insecta. According to Wallace and Anderson (1996) the insects are highly successful in freshwaters, presenting wide distribution and high abundance due to their ability to colonize and exploit a diverse range of habitats. This group is favored in the study stream given its variable nature, which can select rapid colonizers and taxa with the potential to become widely distributed.

Despite the tendency for the greater density of insects, and of macroinvertebrates as a whole which was observed in the lower study site, and during the dry phase, statistical analysis revealed that these differences were not significant. Similar results have also been reported for high densities of Chironomidae in the same river (Farias *et al.*, 2012). These results indicate the potential of spatial and temporal factors as agents, creating different ranges in physical and chemical variables that support a number of individuals and species. Even though these numbers did not show significant spatial and temporal variation in richness and density, differences in assemblage composition (as shown by multivariate analysis) indicates spatial segregation of the overall pool of species. This is supported by ordination tests that show significant differences in assemblages among reaches. Nevertheless, the significant indicator values for only one or two taxa per river reach, indicates that very few taxa are associated with specific reaches. These results are somewhat contrasting (see also Rocha *et al.*, 2012), seeing that the taxonomic resolution and scale of temporal sampling may be playing a role in this ambiguity. More importantly, responses to local variables and local hydrological dynamics are likely to be creating specific sets of conditions in segregating the macrobenthic assemblages (e.g. Pinder and Reiss, 1983; Epler, 2001).

The distribution and abundance of Chironomidae were studied in the Ipanema River, and it has been shown

Table 3. Axes summary of CCA for the environmental variables and macroinvertebrate composition in the Ipanema River, Northeastern Brazil, during the hydrological cycle of 2007/2008.

	Axis 1	Axis 2	Axis 3
Habitat structure			
Eigenvalues	0.464	0.441	0.296
Monte Carlo test	0.001		
Variance in species data			
% variance explained	21.1	20.1	13.5
Intra-set correlations			
Macrophytes	0.330	-0.388	0.636
Submerged vegetation	0.037	0.343	-0.043
Leaf litter	0.087	0.433	0.344
Algae	0.174	0.318	-0.537
Woody debris	-0.086	-0.264	0.301
Mud	-0.425	-0.503	0.094
Sand	0.0451	0.745	0.336
Water velocity	0.243	0.334	-0.083
Elevation	-0.228	-0.762	0.113
Species-environment correlations	1.000	1.000	1.000
Monte Carlo test	0.002		
Physical and chemical variables			
Eigenvalues	0.410	0.301	0.203
Monte Carlo test	0.2953		
Variance in species data			
% variance explained	18.6	13.7	9.2
Species-environment correlations	0.967	0.958	0.974
Monte Carlo test	0.5285		

to be spatially segregated across river reaches, even though some genera occurred throughout the river system (Farias *et al*., 2012). It has been suggested that this spatial segregation represents an strategy to maintain a high diversity of Chironomidae and benthic macroinvertebrates as a whole in intermittent streams (see Rocha *et al*., 2012), by enhancing community stability and persistence through the local hydrological disturbances (Farias *et al*., 2012). Chironomidae has been reported as highly abundant in riverine systems, being able to rapidly colonize a wide range of aquatic habitats (Callisto *et al*., 2001; Ribeiro and Uieda, 2005; Sanseverino and Nessimian, 2008). This is enhanced in temporary habitats given that some Chironomidae present strategies to resist desiccation and survive in variable environmental conditions (Suemoto *et al*., 2004). Thiaridae was another abundant taxa recorded in the present study, mostly during the dry phase. This is an exotic taxon of Asian origin, resistant to desiccation and widespread through several tropical countries (Fernandez *et al*., 2001). Besides the absence of a natural predator or other factor controlling their populations, the slightly alkaline pH and warm water temperatures may have favored the Gastropoda, such as the Thiaridae and Planorbidae, since they have been reported in high densities in warm and alkaline environments (Abílio *et al*., 2006; Santos and Eskinazi-Sant'Anna, 2010).

Previous studies report the importance of the extreme hydrological conditions in the maintenance of the diversity in Brazilian semi-arid streams (Medeiros and Maltchik, 1999; Silva-Filho *et al*., 2003; Maltchik and Medeiros, 2006). The frequency, magnitude and duration of these extreme events are also affected by local environmental characteristics at the stream reach level, such as local river morphology (see Medeiros *et al*., 2008). In the present study, local physical and chemical water variables had low explanatory power with regard to the macroinvertebrate fauna. The high spatial and temporal variability in conductivity, transparency, and dissolved oxygen and lower variability in temperature and pH, associated with the lack of clear spatial and temporal patterns are the most likely explanation for their low multivariate correlations with the macroinvertebrate composition. The importance and the effects of physical and chemical water variables on fauna composition has yet to be better understood in the Brazilian semi-arid streams. Most of the variables measured in the present study can be affected by agents operating at different scales, such as the geological nature of the drainage basin (which affects conductivity and pH) (Oliveira, 2005) or more local agents such as land use and riparian vegetation, which may affect dissolved oxygen and transparency (Medeiros *et al*., 2008; Medeiros and Arthington, 2011).

Among the variables associated with the structure of the habitat, sediment type (sand and mud), the presence

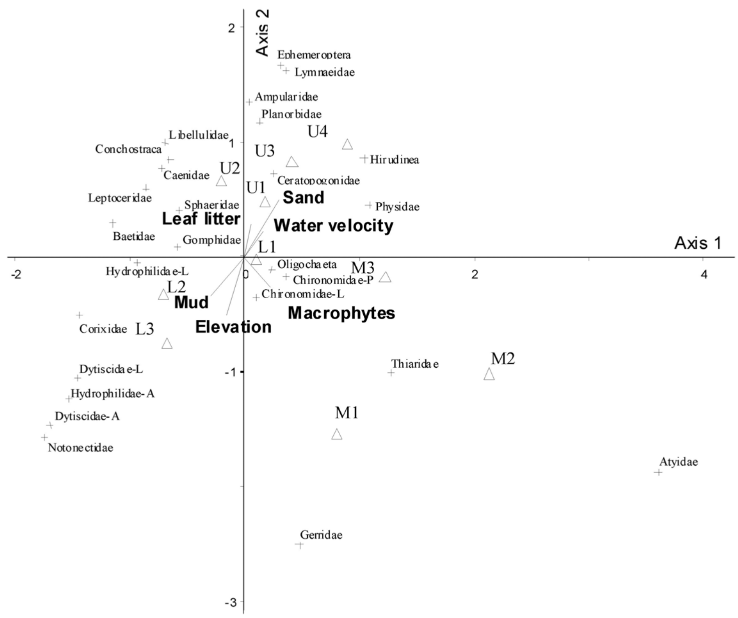

Figure 4. Biplot of CCA showing the composition of macroinvertebrate assemblages in the sampling reaches and occasions (△) and the explanatory environmental variables defined by CCA. Codes indicate river reach (U=upper, M=middle and L=lower) and sampling occasion (1,2,3,4). (+) indicates the position of a given taxa in the ordination.

of aquatic macrophytes and leaf litter were the main factors explaining the variation in macroinvertebrate composition. In association with the substrate composition, the aquatic vegetation creates microhabitats that increase richness and abundance of macroinvertebrates, mainly aquatic insects (Stenert *et al*., 2008; Nessimian and De Lima, 1997). The presence of aquatic macrophytes creates refugia for organisms and minimizes the effects of low magnitude flooding (Maltchik and Pedro, 2001) by maintaining the structure of the sediment, providing species for colonization after flooding events and producing organic matter for benthic invertebrates (see Medeiros *et al*., 2010). Associated with the local production of organic matter, leaf litter deposits contribute to invertebrate richness and abundance by increasing the diversity of sediments available for colonization and providing shelter and food for the benthic fauna (Rezende, 2007; Sanseverino and Nessimian, 2008).

Another important variable explaining the variation in macroinvertebrate composition was elevation. The effects of elevation on macroinvertebrates are known; it is expected that richness increases from higher to lower areas (Jacobsen, 2004). In the present study elevation should be seen more as an indication of stream hierarchy, given the relatively low differences between sites. Nonetheless, its effects can be observed in the variety of functional groups across stream reaches, mostly in the lower study reach, where ordination revealed the Chironomidae, Hydrophilidae (gatherers), Gomphidae, Dytiscidae (predators) and Baetidae (scraper) as correlated taxa.

In conclusion, the dynamics between flooding and drying at the stream reach level creates new areas for the colonization of macroinvertebrate and modifies the existing ones, creating a mosaic of environmental conditions with different degrees of recolonization (see Bilby, 1977; Dawson *et al*., 1978). Therefore, we propose that the structure of the habitat has the potential to contribute for the persistence and stability of macroinvertebrate communities in the Brazilian semi-arid streams by creating refugia for the diversity and increasing the dynamics of the physical structures available for colonization.

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