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Distribution of Chironomidae in a Semiarid Intermittent River of Brazil

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Abstract

The effects of the intermittency of water flow on habitat structure and substrate composition have been reported to create a patch dynamics for the aquatic fauna, mostly for that associated with the substrate. This study aims to describe the spatial distribution of Chironomidae in an intermittent river of semiarid Brazil and to associate assemblage composition with environmental variables. Benthic invertebrates were sampled during the wet and dry seasons using a D-shaped net (40 cm wide and 250 μm mesh), and the Chironomidae were identified to genus level. The most abundant genera were *Tanytarsus*, *Polypedilum*, and *Saetheria* with important contributions of the genera *Procladius*, *Aedokritus*, and *Dicrotendipes*. Richness and density were not significantly different between the study sites, and multiple regression showed that the variation in richness and density explained by the environmental variables was significant only for substrate composition. The composition of genera showed significant spatial segregation across the study sites. Canonical Correspondence Analysis showed significant correspondence between Chironomidae composition and the environmental variables, with submerged vegetation, elevation, and leaf litter being important predictors of the Chironomidae fauna. This study showed that Chironomidae presented important spatial variation along the river and that this variation was substantially explained by environmental variables associated with the habitat structure and river hierarchy. We suggest that the observed spatial segregation in the fauna results in the high diversity of this group of organisms in intermittent streams.

Introduction

The hydrological variation has been recognized as an important agent organizing communities in river systems of tropical (Maltchik & Florin 2002) and temperate regions (Vannote *et al* 1980). In dryland river systems, the hydrological extremes proportionate high spatial variability (Sheldon *et al* 2010), since water flow magnitude varies greatly in different river reaches (Labbe & Fausch 2000) or can be absent for long periods (Maltchik & Medeiros 2006). This creates a patchy distribution of organisms, which is also determined by local environmental characteristics and morphology (Sheldon & Walker 1998, Marshall *et al* 2006). It has been proposed that the patch dynamics is more important in variable systems, where habitats become more restricted and the composition of communities is governed by abiotic factors rather than biotic ones (Peckarsky 1983, Williams 1987, Uys & O'Koeef 1997). Studies indicate that the hydrological dynamics in streams create a mosaic of environmental conditions at different spatial scales which influence the distribution and abundance of the fauna and, consequently, their spatial composition (Ward & Stanford 1995, Amoros & Bornette 2002). Thus, the water flow plays a key role in creating and connecting these diverse patches of habitat with specific morphology and physicochemical characteristics.

The intermittency in water flow is the principal characteristic of Brazilian semiarid streams (Steffan 1977). In their natural state, these streams are characterized by extremes of flood and drying (Maltchik & Medeiros 2006). These events of hydrological disturbance are the main agents structuring these ecosystems, leading to spatial fluctuations in habitat structure and biotic communities (Maltchik & Medeiros 2006). These biotic communities are thought to respond to these disturbances by structuring themselves in order to maximize survival and distribution of species throughout the river (see Resh *et al* 1988).

In this sense, aquatic macroinvertebrates have been used to determine these patterns of distribution of species since they are associated with the substrate and are highly dependent on underwater structures and substrate composition (Bennison *et al* 1989). Therefore, the macroinvertebrate composition is expected to respond to the spatial variation, typical of disturbance-dominated systems such as intermittent streams (Boulton & Lake 1992, Robinson *et al* 2004, Acuña *et al* 2005).

Among the aquatic macroinvertebrates, the Chironomidae is the most representative group in number of individuals and richness (Trivinho-Strixino & Strixino 1995, Rocha *et al* 2012). Chironomidae larvae show high resistance to the environmental variation being able to rapidly colonize new habitats (Pires *et al* 2000, Silva-Filho & Maltchik 2000, Silva-Filho *et al* 2003). Their small body size, short life cycle, and dispersion patterns by the adults contribute to the high capacity of the group to colonize and adapt to variable environments (Miller & Golladay 1996, Lake 2000). Furthermore, these organisms are generalists in habitat allowing a wide spatial distribution (Brito-Júnior *et al* 2005). The physical structure of the habitat also contributes to their patterns of distribution, the latter being associated mostly with water flow and temperature, concentration of dissolved oxygen, pH, and food availability (Cummins & Lauff 1969). Substrate composition and underwater structures have also been emphasized as important factors determining the distribution and abundance of Chironomidae populations (Minshall 1984).

Nevertheless, the role of the hydrological disturbances in the spatial dynamics of the habitat and their associated communities in intermittent streams has received little attention. There is important indication that higher magnitude flooding is able to disrupt and destroy benthic communities of intermittent streams in short-term spatial and temporal scales (Silva-Filho *et al* 2003). Furthermore, at larger time scales and at the level of the catchment basin, the effects of sediment transport and the modification of the habitat structure available for colonizers by water flow are critical to produce and maintain a mosaic of pools that can be used for colonization and refugia for aquatic organisms (Labbe & Fausch 2000).

This dynamics makes intermittent streams complex and heterogeneous systems, which can be seen as highly hierarchical systems subject to the patch dynamics (see Frissell *et al* 1986 and Pringle *et al* 1988). Studies indicate a subdivision in hierarchical scales in such systems into macrohabitats, representing distinct morphological zones (Thoms *et al* 2004); mesohabitats, representing pools, runs, and riffles; and the microhabitats, representing stands of macrophytes or submerged vegetation and substrate types (Frissell *et al* 1986).

The importance of these spatial scales to the aquatic invertebrates in streams has been recognized (e.g., Downes *et al* 1993, Scarsbrook & Towsend 1993), but it is still under debate whether these scales actually generate a response from the aquatic organisms (Frissell *et al* 1986) or whether highly variable and fragmented systems such as intermittent streams will generate such responses. Therefore, to determine the patterns of spatial distribution of aquatic macroinvertebrates in dryland intermittent streams can provide the basis for the understanding of the function of these systems, the potential importance of the processes acting at these different scales, and as a consequence, the ecological interactions that maintain the diversity in such communities.

This study describes the distribution of Chironomidae genera in an intermittent stream and associates the assemblages' composition with environmental variables that represent the structure of the habitat and water quality. It is hypothesized that the Chironomidae fauna (density, richness, and species composition) is patchy with the assemblages' composition representing local characteristics of the habitat and that the environmental variables will be important elements explaining the spatial distribution of genera.

Material and Methods

Study area

The present study was carried out in the upper reaches of the Ipanema River, an affluent of the left margin of the São Francisco River. The catchment area of the Ipanema River is located in the states of Pernambuco and Alagoas (Fig 1). Average annual temperature and precipitation in the area are 25°C and 1,095.9 mm, respectively (Rodal *et al* 1998). The wet season starts in January–February, with higher precipitation between April and June. The peak of the dry season lasts from September to January (Rodal *et al* 1998). Elevation ranges from 650 to 1,000 m (CPRM 2005). Predominant vegetation in the study area is the Caatinga, an arboreal to shrubby open forest, characterized by the presence of xerophytic species (Silva & Sales 2008). This type of vegetation is sparse and does not provide strong protection to the soil, which increases the loss of water by evaporation enhancing the intermittency of the streams and rivers of the region. Climate is classified as semiarid BSh and tropical Aw according to the classification of Köeppen–Geiger modified by Peel *et al* (2007).

Sampling design and data collection

Samples were taken from three reaches of the Ipanema River on four occasions during the wet (April and July 2007) and dry (October 2007 and January 2008) periods (Fig 1). At each river reach, three subsamples of benthic macroinvertebrates 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 and preserved in 70% ethanol. A subsample of the larvae of Chironomidae was counted (Baker & Huggins 2005) and identified to the level of genus (Borror & Delong 1988, McCafferty 1988, Trivinho-Strixino & Strixino 1995, Epler 2001, Trivinho-Strixino 2011). Identification was performed after the individuals were mounted in semipermanent slides using Hoyer's medium following Trivinho-Strixino (2011), and voucher specimens were deposited in the reference collection of the Laboratório de Ecologia, UEPB.

The environmental characteristics consisted of (1) physical and chemical variables, (2) reach morphology, (3) substrate composition, and (4) habitat structure. Physical and chemical variables were measured using portable equipment for pH (TECNOPON MPA-210), conductivity (in microsiemens per centimeter) (TECNOPON MCS-150), dissolved oxygen (in milligrams per liter), and temperature (in degrees Celsius) (Lutron DO-5510). Transparency (in centimeters) was measured using a Secchi disk, and water velocity (in meters per second) was estimated using the float method (Maitland 1990). Stream reach morphology was evaluated by the average width (in centimeters) and depth (in centimeters) taken from three transects randomly placed in the stream reach or pool (during the dry phase). The substrate composition and habitat structure were estimated in 9 to 12 survey points of 1 m^2 measured in the margins (see Medeiros *et al* 2008). In each survey point, the proportion of the sediment composition (classified as mud, sand, gravel, and cobbles) and littoral and underwater structures (e.g., macrophytes, grass, submerged vegetation, overhanging vegetation, leaf litter, algae, and woody debris) were estimated visually.

Data analyses

All statistical analyses were performed on density [individuals (ind) per square meter], 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 genera are used to describe patterns of distribution of the assemblages.

Fig 1 Study area with the location of the Ipanema River in the states of Pernambuco and Alagoas and the study reaches during the hydrological cycle of 2007/2008. *1* upper reach, *2* middle reach, and *3* lower reach.

The correlation between density and richness (dependent variables) with the environmental characteristics (independent variables) was evaluated using hierarchical multiple regression (HMR) (Sheridan & Lyndall 2001). The independent variables for each environmental characteristic were incorporated into the regression model based on their expected order of importance in describing the assemblages studied: (1) physical and chemical variables: dissolved oxygen, temperature, transparency, conductivity, and pH; (2) morphometrical variables: water velocity, depth, width, and elevation; (3) substrate composition: mud, sand, gravel, and cobbles; and (4) habitat structure: macrophytes, submerged vegetation, leaf litter, algae, woody debris, overhanging vegetation, and grass. Density and richness were square root transformed, and the environmental variables were $\log_{10}(x+1)$ transformed to enhance normality and homogeneity of variances (Sokal & Rohlf 1969, Maltchik *et al* 2010).

In order to identify the spatial patterns of variation in the Chironomidae assemblage composition, a Detrended Correspondence Analysis (DCA) was performed on the $\log_{10}(x+1)$-transformed density data. The significance of differences between stream reaches was tested using the Multiresponse Permutation Procedure (MRPP) (Biondini *et al* 1985, McCune & Grace 2002). To all MRPP analyses, the value of *A* is presented as a measure of the degree of homogeneity between groups compared to random expectation. When MRPP showed significant differences in fauna between stream reaches, the Analysis of Indicator Species (ISA) was performed to determine which Chironomidae genera contributed significantly as the source of difference. The indicator value (IV) for each genus was calculated using the method of Dufrene & Legendre (1997). This value is tested for significance using the Monte Carlo test with 1,000 runs.

The Canonical Correspondence Analysis (CCA) was performed to establish possible multivariate correlations between Chironomidae composition and the environmental variables (McCune & Grace 2002). The data matrix was centered and normalized and the correlations tested by the Monte Carlo test with 999 runs. The environmental variables used in the CCA were: water velocity, elevation, mud, sand, macrophytes, submerged vegetation, leaf litter, and woody debris. Density data and environmental variables were $\log_{10}(x+1)$ transformed (Sokal & Rohlf 1969, Maltchik *et al* 2010). Statistical analyses were performed on SPSS 13.0 (Sheridan & Lyndall 2001) and PC-ORD 4.27 (McCune & Mefford 1999).

Results

Environmental variables

The Ipanema River showed surface water flow during the sampling occasions of April and July. Values of pH and dissolved oxygen indicated neutral to slightly alkaline (pH range, 7.8 to 8.7) and well-oxygenated water (3.7 to 7.7 mg/L). Conductivity was higher than 600 μS/cm during the study period (reaching 1,268.9 μS/cm), and water temperature ranged between 23.3 and 30.8°C. Transparency ranged between 19.0 and 79.5 cm throughout the sampling occasions. River width was higher during the flooding phase, whereas the average depth tended to be greater during the period with absence of water flow, when pool formation was intensified. Substrate was composed mostly of sand and mud, with gravel being observed in higher proportion in the middle and lower study reaches. The littoral habitat was diverse with woody debris, aquatic macrophytes, algae, grass, and leaf litter. Overhanging and submerged vegetation were scarcely present (Table 1).

Chironomidae assemblages

A total of 18 genera of Chironomidae was registered, distributed in the Chironominae and Tanypodinae subfamilies. The Chironominae subfamily showed 13 genera and a total average density (±SD) of 183.6 (±350.6) ind/m². Tanypodinae presented five genera and an overall 22.7 (±16.2) ind/m². The densest genera were *Tanytarsus* (116.3±90.76 ind/m²), *Polypedilum* (64.2±55.5 ind/m²), and *Saetheria* (36.9±50.6 ind/m²) that represented 86.9% of the overall density of Chironomidae. These genera and *Dicrotendipes* were the most commonly observed, being present in 9 out of the 10 sampling occasions (Table 2).

In the upper study reach, *Tanytarsus* (119.8±147.6 ind/m²), *Polypedilum* (84.4±77.8 ind/m²), *Saetheria* (13.5±9.7 ind/m²), and *Procladius* (9.4±14.7 ind/m²) were the densest genera. In the middle reach, the densest genera were *Tanytarsus* (88.2±38.5 ind/m²), *Polypedilum* (25.7±17.3 ind/m²), and *Aedokritus* (18.1±14.6 ind/m²) followed by *Saetheria* and *Dicrotendipes*, both with average densities of 13.2 ind/m² (±15.6 and ±5.2, respectively). In the lower study reach, *Tanytarsus* (139.8±29.5 ind/m²), *Saetheria* (91.8±68.5 ind/m²), and *Polypedilum* (75.9±35.2 ind/m²) were the densest genera followed by *Dicrotendipes* with an average density of 8 ind/m² (±7.5) (Table 2). ANOVA showed no significant difference in richness (ANOVA, $F=0.23$; $df=2, 7$; $P=0.798$) and density (ANOVA, $F=0.79$; $df=2, 7$; $P=0.489$) between the study reaches. The lower reach of the study river presented 13 of the 18 observed genera; the upper reach showed 12 genera, and the middle reach showed 10 genera (Table 2).

Tanytarsus, *Polypedilum*, and *Saetheria* were the densest across the study period, followed by *Dicrotendipes* in April (6.6±3.0 ind/m²) and October (11.8±5.2 ind/m²) and *Aedokritus* (11.8±18.7 ind/m²) in July. October (14 genera) and July (13 genera) showed greater richness, followed by April (11 genera) and January (3 genera). It is important to

Table 1 Environmental variables surveyed in the Ipanema River during the 2007/2008 hydrological cycle.

Habitat elements	Upper reach				Middle reach			Lower reach				
	April	July	October	January	April	July	October	April	July	October	Average	±SD
Water quality												
pH	7.9	8.0	8.3	8.7	7.9	8.3	8.5	7.8	8.2	8.6	8.2	±0.3
Dissolved oxygen (mg/L)	7.2	4.8	3.7	5.0	5.8	6.6	4.2	6.2	7.7	4.1	5.5	±1.4
Conductivity (µS/cm)	1,000.0	1,101.3	1,000.0	1,000.0	645.7	1,056.7	700.0	1,268.9	972.5	970.0	917.5	±181.0
Temperature (°C)	30.8	23.8	24.2	30.1	26.8	24.4	25.8	26.1	23.3	24.8	26.0	±2.6
Transparency (cm)	66.5	79.5	38.7	19.0	39.8	66.7	31.8	74.0	51.7	41.0	50.9	±20.0
Morphology												
Water velocity (m/s)	0.1	0.1	0	0	0.9	0.1	0	0.2	0.1	0	0.2	±0.3
Elevation (m)	466.0	466.0	466.0	466.0	440.7	440.7	440.7	386.7	386.7	386.7	431.1	±40.5
Average depth (cm)	46.9	49.2	67.3	21.7	74.8	91.1	105.5	24.3	38.6	30.6	55.0	±28.7
Width (cm)	1,550.0	1,635.0	760.0	332.0	1,790.0	2,227.5	1,650.0	1,110.0	1,545.0	816.7	1,341.6	±517.4
Substrate composition												
Mud	68.3	70.0	55.0	96.7	34.4	93.8	1.0	3.3	1.5	25.0	44.9	±37.1
Sand	31.7	30.0	43.8	3.3	38.3	3.8	85.2	63.3	86.0	71.3	45.7	±30.2
Gravel	0	0	1.3	0	27.2	2.5	13.8	31.7	12.5	2.5	9.1	±11.9
Cobbles	0	0	0	0	0	0	0	1.7	0	1.3	0.3	±0.6
Habitat structure												
Macrophytes	8.3	43.3	6.3	0	3.9	15.0	2.9	0	0	0	8.0	±13.3
Grass	11.7	5.0	3.3	0	0	5.5	0	0	7.8	0	3.3	±4.1
Submerged vegetation	0	0	0	0	0	0.8	0	0	4.6	0	0.5	±1.4
Overhanging vegetation	0	0	1.3	0	0	0	0	5.0	0.4	0	0.7	±1.6
Leaf litter	3.3	0.3	2.5	0.3	0.8	0.5	0.3	18.3	0.5	4.0	3.1	±5.5
Algae	30.0	0	0	3.3	0.4	0	1.8	0	6.3	9.0	5.1	±9.3
Woody debris	23.3	19.3	11.5	5.3	13.9	3.8	1.5	5.0	0	4.5	8.8	±7.9

Table 2 Density (ind per square meter) of Chironomidae genera along the Ipanema River during the 2007/2008 hydrological cycle.

	Upper reach				Middle reach			Lower reach				
	April	July	October	January	April	July	October	April	July	October	Average	±SD
Chironominae												
Aedokritus	0	2.08	0	0	16.67	33.33	4.17	0	0	2.08	5.83	±10.93
Asheum	0	0	0	0	0	4.17	4.17	1.56	0	0	0.99	±1.74
Apedilum	0	0	0	0	0	0	0	0	2.08	4.17	0.63	±1.41
Cladopelma	0	0	2.08	0	0	0	0	0	0	0	0.21	±0.66
Chironomus	4.17	14.58	2.08	4.17	2.08	0	2.08	4.69	0	4.17	3.80	±4.15
Dicrotendipes	8.33	8.33	6.25	0	8.33	18.75	12.50	3.13	4.17	16.67	8.65	±5.89
Fissimentum	0	0	2.08	0	0	0	0	0	0	0	0.21	±0.66
Goeldichironomus	0	0	0	0	2.08	0	2.08	1.56	0	0	0.57	±0.93
Lauterborniella	0	2.08	0	0	0	0	0	0	0	0	0.21	±0.66
Paratendipes	0	0	0	0	0	0	0	0	2.08	0	0.21	±0.66
Polypedilum	181.25	50.0	106.25	0	31.25	39.58	6.25	67.19	45.83	114.58	64.22	±55.50
Saetheria	22.92	14.58	16.67	0	31.25	4.17	4.17	167.19	33.33	75.0	36.93	±50.64
Tanytarsus	41.67	106.25	331.25	0	112.50	108.33	43.75	173.44	118.75	127.08	116.30	±90.76
Tanypodinae												
Ablabesmyia	0	0	0	0	0	0	0	0	2.08	0	0.21	±0.66
Coelotanypus	4.17	6.25	2.08	6.25	4.17	0	6.25	0	0	0	2.92	±2.81
Procladius	2.08	4.17	31.25	0	0	0	0	7.81	0	0	4.53	±9.74
Tanypus	0	0	0	18.75	0	0	4.17	0	0	0	2.29	±5.93
Larsia	0	0	0	0	0	0	0	14.06	0	0	1.41	±4.45

note that the data for the January sampling occasion refer only to the upper reach, where *Tanypus* (18.7 ind/m²) and *Coelotanypus* (6.2 ind/m²) dominated, since the other reaches dried out.

HMR showed that the variations in richness and density explained by the environmental variables were not significant for the models incorporating the physical and chemical (Fchange richness=0.28; *df*=1, 4; *P*=0.620 and Fchange density=0.92; *df*=1, 4; *P*=0.390, respectively) and morphological (Fchange richness=0.003; *df*=1, 5; *P*=0.957 and Fchange density=0.001; *df*=1, 5; *P*=0.985, respectively) variables. On the other hand, HMR showed that for the substrate composition, the model incorporating mud and sand explained 61.4% (Fchange=6.9; *df*=1, 7; *P*=0.034) of the variation in richness and 44.8% (Fchange=5.6; *df*=1, 7; *P*=0.049) of the variation in density. For the habitat structure, the model incorporating macrophytes, submerged vegetation, and leaf litter explained 72.3% (Fchange=15.4; *df*=1, 6; *P*=0.008) of the variation in density, whereas the variation in richness explained by the structure of the habitat was not significant (Fchange=7.08; *df*=1, 2; *P*=0.117).

Detrended Correspondence Analysis showed segregation in the composition of Chironomidae genera across the study reaches (total variance "inertia" of 1.09) (Fig 2a), and the MRPP showed that this segregation was significant between all study reaches (upper and middle: *A*=0.14, *P*=0.02; upper and lower: *A*=0.13, *P*=0.01; middle and lower: *A*=0.26, *P*=0.02). Grouping by DCA, defined as the genera with correlation greater than 20% with the ordination axes, showed that *Procladius*, *Fissimentum*, *Cladopelma*, *Coelotanypus*, and *Tanypus* were important in segregating the upper reach; *Asheum*, *Aedokritus*, and *Dicrotendipes* segregated the middle reach; and *Tanytarsus* and *Polypedilum* segregated the lower reach (Fig 2b). However, ISA showed that only *Aedokritus* (IV=80.3, *P*=0.03) and *Saetheria* (IV=49.3, *P*=0.02) were significant indicators of the middle and lower reaches, respectively.

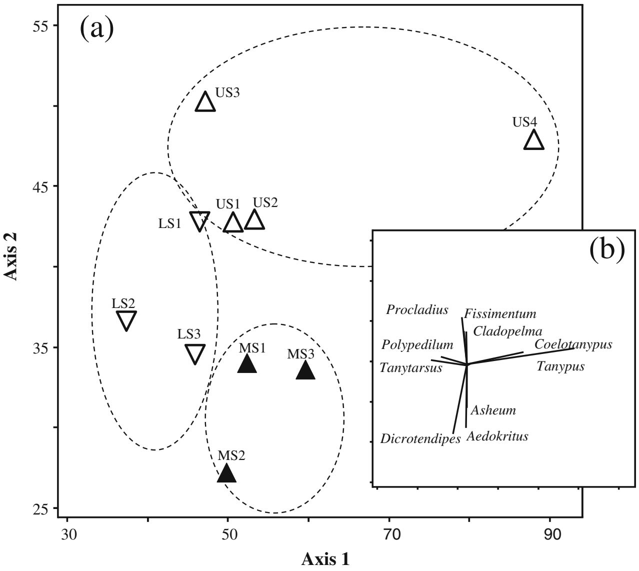

Fig 2 DCA for the study river reaches in the 2007/2008 hydrological cycle (**a**) and the Pearson correlations (r^2>0.2) between the recorded genera and the axes of the ordination (**b**). The direction and size of the vectors indicate the direction and strength of the correlation. Codes indicate river reach (*U* upper, *M* middle, and *L* lower) and sampling occasion (*S*).

The first three axes of CCA explained 66.8% of the variation in Chironomidae composition across river reaches, with a total variance ("inertia") of 0.79. Most of the explained variation (based on the correlation between the environmental variables and the CCA axes) were explained by the first axis (26.2%), even though axes 2 and 3 have also been important, explaining a substantial part of the variation in the data matrix. The correlation between the Chironomidae composition and the environmental variables was significant as shown by the Monte Carlo test for the eigenvalues (*P*=0.007) and the genera–environment correlations (*P*=0.033) (Table 3). According to the intragroup correlations between the environmental variables and the CCA axes (see Table 3 and Fig 3), the most important variables explaining the Chironomidae composition were the presence of submerged vegetation, elevation, and leaf litter.

Discussion

Chironomidae is a highly diverse group considered ecologically important with a key role in the decomposition of

Table 3 Axes summary for the Canonical Correspondence Analysis of the Chironomidae fauna and the environmental variables in the Ipanema River during the 2007/2008 hydrological cycle.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.209	0.193	0.131
Monte Carlo test	0.007		
% Variance explained	26.2	24.1	16.5
Pearson correlations	1.000	1.000	1.000
Group correlations (inter-set)			
Macrophytes	−0.333	0.354	−0.621
Submerged vegetation	0.411	−0.753	0.020
Leaf litter	0.371	0.431	0.707
Woody debris	−0.038	0.702	−0.340
Mud	0.015	0.344	−0.607
Sand	0.320	−0.039	0.238
Water velocity	0.177	−0.118	0.116
Elevation	−0.381	0.459	−0.692
Genera–environment correlations	1.000	1.000	1.000
Monte Carlo test	0.033		

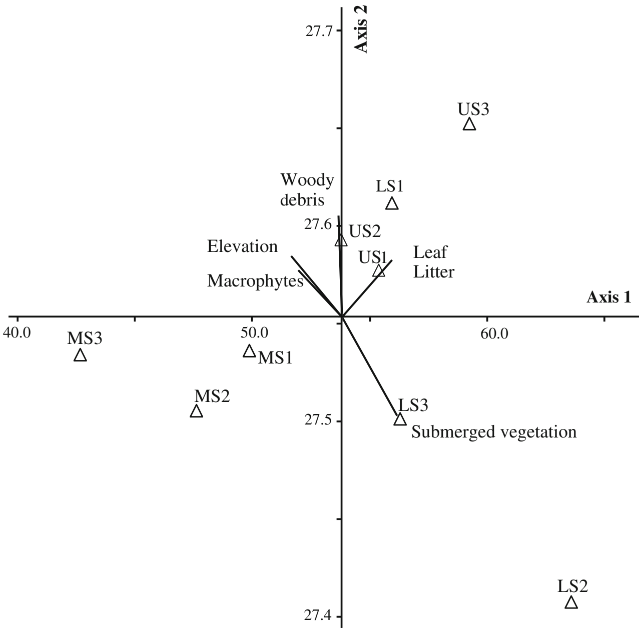

Fig 3 Biplot of CCA showing the composition of Chironomidae genera in the sampling sites and occasions (*triangles*) and the explanatory environmental variables defined by CCA. Codes indicate river reach (*U* upper, *M* middle, and *L* lower) and sampling occasion (*S*).

organic matter in aquatic systems (Trivinho-Strixino & Strixino 1995, Nessimian & Sanseverino 1998). Despite that, studies on their patterns of diversity and distribution in dryland river systems, in particular in the Brazilian semiarid, are recent (Rocha *et al* 2012) and/or limited to lentic systems (Abílio *et al* 2005, Brito-Júnior *et al* 2005, Silva-Filho 2004). The present study shows a high richness of genera (18) and abundance of individuals compared to lakes and reservoirs in the Brazilian semiarid (Abílio *et al* 2005, Brito-Júnior *et al* 2005). Richness in the present study was in accordance with other studies in Brazilian semiarid streams (Rocha *et al* 2012).

Among the genera recorded, the subfamily Chironominae showed greater richness and density. This taxon is frequently reported as being dominant in tropical and subtropical regions (Ashe *et al* 1987). In the tropics, Chironominae success has been associated with its tolerance to high temperatures (Serrano *et al* 1998) and feeding plasticity (Merritt & Cummins 1996). Predaceous taxa have been reported as showing elevated richness and low density (Callisto *et al* 2001). In the present study, the mostly predaceous subfamily, Tanypodinae, showed reduced richness when compared to the other taxa registered. Genera of the subfamily Orthocladiinae were not recorded in the present study as observed by Silva-Filho (2004) in intermittent shallow lakes in the Brazilian semiarid.

The hydrological regime has been pointed out as one of the most important factors creating spatially variable environmental conditions in dryland rivers (Sheldon & Walker 1998), and such conditions have the potential to spatially structure aquatic communities, creating segregated assemblages of species (Marshal *et al* 2006). In the present study, ordination showed that the composition of Chironomidae larvae was different across river reaches and that, despite this spatial segregation, the genera *Tanytarsus* and *Polypedilum* dominated. Dominance of specific groups within segregated assemblages has been previously reported for Brazilian semiarid aquatic systems (Medeiros *et al* 2011) and seems to be the result of species responses to the hydrological disturbances. In other dry regions, *Tanytarsus* and *Polypedilum* have also been recorded in high densities, this being associated to their opportunistic characteristics, such as the capability to colonize different types of habitat and resistance to variable environmental conditions (Pinder & Reiss 1983, Epler 2001).

Environmental conditions associated with water temperature, dissolved oxygen, pH, and food availability (Cummins & Lauff 1969), as well as others associated with habitat structure and complexity and the nature and composition of the substrate, have also been reported as determinants of the composition and distribution of Chironomidae in streams (Rossaro 1991, Sanseverino & Nessimian 2001). In the present study, some environmental variables showed a greater range of variation, such as the water velocity, which was absent in most of the hydrological cycle studied. River width and length also showed wide variation. Other variables showed lower variability and values in the range expected from other studies in the Brazilian semiarid region (Medeiros *et al* 2008). Substrate composition (mostly sand and mud) and the presence of aquatic macrophytes, leaf litter, and underwater woody debris dominated in the study reaches being also relatively variable across sites and through time. According to Medeiros *et al* (2008), these elements contribute to the spatial heterogeneity in aquatic systems in semiarid Brazil and are affected by factors associated to different scales in the catchment basin, such as hierarchical level and elevation (in a larger regional scale), and the presence of water flow, width, and depth (in a local scale). Despite that, richness and density of Chironomidae did not show significant difference across study reaches. Nevertheless, the fact that the model incorporating substrate composition variables, associated with the significance of macrophytes, submerged vegetation, and leaf litter, in explaining density corroborates the importance of these elements in the structure of communities in intermittent streams and highlights the need for further studies on the role of the structure of the habitat on Chironomidae in these systems.

The substrate composition has been reported as highly associated with water flow, with sandy bottoms being easily altered by flow and poorer in organic matter (Henriques-Oliveira *et al* 2003). Therefore, a greater density of gatherer and predatory Chironomidae is expected, such as the ones recorded in greater density in the study river: *Tanytarsus*, *Polypedilum*, *Saetheria*, *Aedokritus*, *Dicrotendipes* (gatherers), *Procladius*, *Coelotanypus*, and *Larsia* (predators). Furthermore, predaceous taxa such as the genera of the Tanypodinae family prefer muddy substrate (Fittkau & Roback 1983). The predominance of sand and mud in the substrate composition in association with the extreme hydrological conditions can explain the higher densities of the more opportunistic taxa of gatherers and predators.

Among the elements of the structure of the habitat that had important effect on the Chironomidae fauna, the leaf litter has been recognized as an important source of food, acting as a trap for organic detritus and fine particulate organic matter (Short *et al* 1980, Medeiros *et al* 2010) and enhancing resource availability (food and protection) and substrate heterogeneity (Henriques-Oliveira *et al* 2003). Aquatic macrophytes may also act as filters retaining organic matter and assimilating nutrients and therefore stimulating the growth and abundance of gatherer Chironomidae (Dornfeld & Fonseca-Gessner 2005). Predator guilds are also favored by the presence of aquatic macrophytes, serving as hiding places and facilitating capture of prey organisms (McLachlan 1969).

CCA revealed that elevation was an important factor explaining the distribution and composition of Chironomidae. Recent evidence indicates that Brazilian semiarid intermittent streams may be organized as a nested hierarchy (Medeiros *et al* 2008, 2011), where large-scale process associated with geomorphology and flow patterns, and consequently elevation, determines higher levels of organization of the physical environment, which in turn affect lower-level biological processes (Poff & Ward 1990). In the present study, the influence of elevation is represented by its associated variables such as river morphology and level of hierarchy, which affect the local variables and the local pool of species. As opposed to local scale variables, such as resource availability and habitat structure, elevation reflects the catchment basin and acts at the macrodistribution of the species in the river system (see Cummins & Lauff 1969).

This study showed that the fauna of Chironomidae is spatially segregated across river reaches, even though some genera occur throughout the river system. Associated to, and as result of, the hydrological variation, the spatial heterogeneity throughout the study river has the potential to structure the wider pool of Chironomidae genera into assemblages, a consequence of the influence of the habitat structure and substrate composition on genera distribution. We suggest that this spatial segregation is an important strategy to maintain the high diversity observed in intermittent streams, compared to less variable environments such as lakes and reservoirs (see also Rocha *et al* 2012), enhancing community stability and persistence through the local hydrological disturbances. Therefore, this study contributes to the view that intermittent streams are highly complex and heterogeneous systems, subject to a spatially hierarchical structure, where benthic communities are segregated into specific groups of species resulting from specific packages of environmental conditions created by flow variability. This variability creates a wider and more segregated range of microhabitats to be colonized by the benthic organisms and the Chironomidae leading to the spatial variability.

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