

Effects of spatial and environmental factors on benthic a macroinvertebrate community

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ABSTRACT. Interactions between terrestrial and aquatic systems influence the structure of river habitats and, consequently, affect their benthic macroinvertebrate composition. The aim of this study was to evaluate the effects of spatial and environmental variables (local physical and chemical variables of water and regional landscape characteristics) on the benthic macroinvertebrate community of the Pandeiros River Basin. Biotic and abiotic variables were evaluated at 20 sampling sites distributed across the primary sub-basins of the Pandeiros River Basin. We found that the macroinvertebrates were primarily affected by environmental variables. The most important environmental variables were pebble proportion and water conductivity at the local scale (7.2% of explained variation) and elevation and non-forest areas at the regional scale (6.9% of explained variation). The spatial variables were representative only in shared explained variation with the environmental matrices (local-spatial = 0.2% and regional-spatial = 2%; all matrices combined = 4.4%). Sampling sites with higher non-forest areas, lower elevations, and steeper slopes presented low pebble fractions and higher electrical conductivities. Habitat diversity was lower when the percentage of pebbles decreased, resulting in decreased taxonomic richness and diversity in macroinvertebrate communities. High electrical conductivities and non-forest areas also had negative effects on macroinvertebrate density due to the loss of habitat diversity. We conclude that higher proportions of pebbles in the substrate and higher altitudes were likely the primary variables for positive effects on the taxonomic richness and density of macroinvertebrate communities.

KEY WORDS. Elevation; metacommunity; non-forest areas; pebbles.

Watersheds are one of the major landscape units affected by human activities (e.g., agriculture, industry, urbanization) and by natural events (e.g., native forest succession), and these activities are the key determinants of watershed quality (NESSIMIAN *et al.* 2008). In addition to natural variations (e.g., upstream-downstream gradients) in the aquatic environment (VANNOTE *et al.* 1980), understanding the effects of land use is important for predicting changes in the physical, chemical, and biological health of ecosystems (GARDINER *et al.* 2009). Different land uses (e.g., agriculture, industry, and urbanization) may generate physical changes in the habitat (PARK *et al.* 2011), which alter the diversity and function of the ecosystem. Thus, when trying to understand the processes affecting stream biodiversity, the regional landscape should be considered (TUPINAMBAS *et al.* 2007).

To assess local environmental conditions, the composition and diversity of the physical environment must be considered (BEISEL *et al.* 1998). According to HARPER *et al.* (1997), substrate composition (e.g., pebbles, gravel, and stones), detritus input, and canopy cover are three of the primary variables

that control biodiversity in lotic macroinvertebrate communities. Natural topographical characteristics may also decrease macroinvertebrate diversity if fine sedimentary particles are predominant in the substrate (VANNOTE *et al.* 1980). The physical and chemical characteristics of the water (e.g., dissolved oxygen, conductivity, alkalinity, and temperature) may also influence aquatic life by altering the environment and the community composition (ALLAN 2007, MELO 2009). Therefore, environmental characteristics are critical for understanding the distribution and diversity of the macroinvertebrate communities in aquatic systems (COSTA & MELO 2007, MELO 2009).

Benthic macroinvertebrate communities are central components of freshwater ecosystems (VANNOTE *et al.* 1980, ALLAN 2007) and are perhaps the most widely used biological indicators of aquatic health (e.g., TUPINAMBAS *et al.* 2007, MORENO *et al.* 2009, FERREIRA *et al.* 2011). Previous studies have attempted to clarify the relationship between local (ONODA *et al.* 2009) and regional habitat conditions (ALLAN 2007, JUN *et al.* 2011, PARK *et al.* 2011) because these relationships affect the structure of

benthic macroinvertebrate communities. These studies have generally been performed in temperate systems and have primarily focused on the importance of local environmental conditions. Some studies have examined the effects of local (physical and chemical variables of water) and regional (land use and landscape characteristics) habitat conditions on benthic macroinvertebrate communities in tropical regions (BOYERO & BAILEY 2001, COSTA & MELO 2007, BÜCKER *et al.* 2010). However, few studies have also investigated the influence of spatial processes on community structure (SIQUEIRA *et al.* 2012).

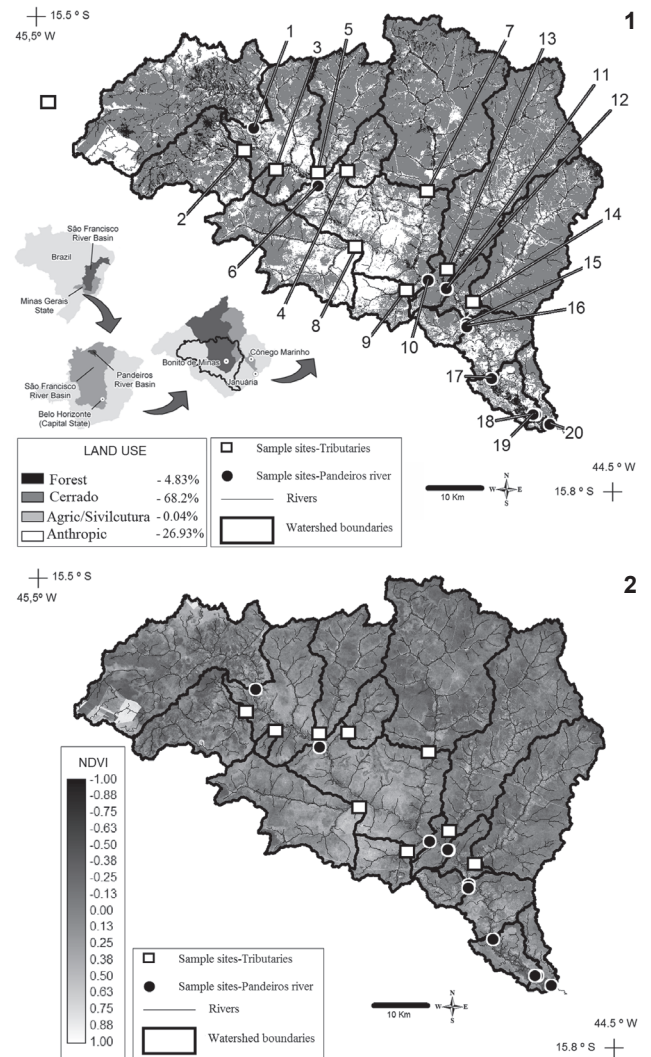
Ecological theory predicts that different processes act as filters on communities at local and regional scales, and the metacommunity framework can be useful for studying these structuring processes (LEIBOLD *et al.* 2004, COTTENIE 2005, SIQUEIRA *et al.* 2012). A metacommunity can be defined as a set of local communities linked by the dispersal of multiple potentially interacting species (LEIBOLD *et al.* 2004), and metacommunities are structured by both environmental and spatial processes (HOLYOAK *et al.* 2005). The metacommunity framework suggests that local communities are controlled by neutral processes, species sorting, patch dynamics and mass effects, depending on the relative influences of environmental and spatial processes on community structure (LEIBOLD *et al.* 2004, SIQUEIRA *et al.* 2012).

According to SIQUEIRA *et al.* (2012), the community controls mentioned above can act simultaneously and should not be viewed as independent processes but rather as points along a continuum. The neutral model (driven primarily by stochastic processes and resulting in strong spatial structures) and species sorting (based on niche theory) represent the endpoints of a continuum of processes acting on communities; patch dynamics and mass effects combine both perspectives (for details, see HUBBELL 2001, LEIBOLD *et al.* 2004, COTTENIE 2005, HOLYOAK *et al.* 2005, SIQUEIRA *et al.* 2012). Therefore, one could hypothesize that some communities are conforming to environmental processes and that other communities are more influenced by spatial processes (LEIBOLD *et al.* 2004, HOLYOAK *et al.* 2005, SIQUEIRA *et al.* 2012).

Our goal was to evaluate the effects of spatial and environmental variables (local physical and chemical variables of water and regional landscape characteristics) on the benthic macroinvertebrate community in the Pandeiros River Basin, Brazil. Specifically, we addressed the following questions: 1) What are the relative importances of spatial and environmental variables (local and regional scale) on the richness and density of this benthic macroinvertebrate community? 2) Which environmental variables are the most important for structuring this benthic macroinvertebrate community?

MATERIAL AND METHODS

The present study was performed in the Pandeiros River Basin, state of Minas Gerais, southeastern Brazil (Figs 1 and 2). This river basin, which occupies 3,800 km², is populated by a small ca. 8,164 inhabitants, who are distributed in small, rural



Figures 1-2. Sampling sites and sub-basins within the Pandeiros River Basin drainage, showing their geographical location within Brazil and Minas Gerais State and the distributions of land use (1) and NDVI values (2) in the study area.

communities, and subsist on small-scale agriculture and livestock farming. The climate of this region is predominantly semi-arid, with temperatures varying from 18 to 35°C. The altitude ranges from 600 to 780 m, and the soils are predominantly red oxisols (latosols) with a sandy texture and quartz sand. Based on historical data, the average discharge of the primary river is 8 m³/s during the dry season and 24 m³/s during the rainy season. The Pandeiros River, which is the primary water body in the basin, is approximately 145 km long. The sampling sites represent 20 river reaches, with 11 sites on the Pandeiros River and 9 sites on its primary tributaries (Figs 1 and 2). We sampled each site four times in 2008: February, May, September, and

November. The sampling sites were selected based on their geographical locations within the hydrographic basin, as represented by the Otto Pfafstetter coding system-coded basin areas designated by the National Water Agency of Brazil (Agência Nacional de Águas – ANA, Appendix S1*).

Landscape analysis was performed using a geographical information system (GIS) based on a recent (2010) multispectral Landsat 5 Thematic Mapper (TM) image. The image was classified into cerrado (Brazilian savanna), forest, agriculture/silviculture, and non-forest areas (primarily characterized by roads). Land use was determined using a maximum-likelihood classification algorithm. The normalized difference vegetation index (NDVI) was used as an additional investigative tool due to its potential to detect anthropogenic or natural changes in vegetation (ROUSE *et al.* 1973) (Fig. 2). The index ranges from –1 to +1, with positive values indicating more dense vegetation (DENNISON *et al.* 2009). Vegetation indices can be used to measure the changes in leaf area (i.e., canopy openness) that result from defoliation (DENNISON *et al.* 2009). The NDVI (ROUSE *et al.* 1973) is calculated as follows: $NDVI = \rho_{NIR} - \rho_{red} / \rho_{NIR} + \rho_{red}$, where ρ_{NIR} and ρ_{red} are the reflectances of the near-infrared bands and the red band, respectively.

Elevation data supplied by the National Aeronautics and Space Administration Shuttle Radar Topography Mission (NASA/SRTM) project were used to extract the primary topographical features, including the elevation, slope, and drainage network. The georeferenced database was structured to provide secondary topographical information related to the drainage areas of individual sampling sites, including the watershed surface, sinuosity index, and slope (Figs 1 and 2).

Three sediment samples were collected from each sampling site using a plastic container to determine the granulometric composition and organic matter content of the sediment. The granulometric composition of the sediment was determined according to the methodology proposed by SUGUIO (1973) and modified by CALLISTO & ESTEVES (1996). Ten stones were collected randomly at each sampling point in the field, and their volumes were estimated using a caliper to measure their heights, widths, and thicknesses. The sediment organic matter was estimated according to the method of SUGUIO (1973) by incinerating three 0.3 g aliquots for 4 hours at 550°C. A multi-analyzer (Model 85, YSI Incorporated, Yellow Springs, OH, USA) was used to record the following water-column parameters in situ: temperature, electrical conductivity, and dissolved oxygen. The total alkalinity was determined by Gran plots as described by CARMOUZE (1994). The riparian-vegetation canopy openness was quantified using hemispheric photographs (taken with a Nikon FCE9 fisheye lens (Nikon Corp, Tokyo, Japan) and analyzed using the Gap Light Analyzer 2.0 software (Simon Fraser University, Burnaby, BC, Canada).

To examine the benthic community (Appendix S2*), three sample units were collected to represent the different

microhabitats at each sampling site using a Surber stream-bottom sampler with a sampling area of 1024 cm² and a mesh size of 0.250 mm (PÉREZ 1988). The collected material was washed on 0.50 mm sieves and screened using a stereomicroscope. Then, the aquatic macroinvertebrates were collected and identified (to the family level) using available and appropriate taxonomic keys (PÉREZ 1988, MERRIT & CUMMINS 1996, CUMMINS *et al.* 2005). Based on this inventory of the benthic macroinvertebrate communities, the average family richness and density were calculated for each sampling site. This methodology has yielded good results in studies of the São Francisco River Basin (MORENO *et al.* 2009, FERREIRA *et al.* 2011).

The importances of spatial (geographical coordinates) and environmental variables (local physical and chemical parameters of water and regional landscape variables) on the structure of benthic macroinvertebrate communities were evaluated by a partial redundancy analysis (pRDA). The local physical parameters used were granulometric fractions (silt + clay, very fine sand, fine sand, medium sand, coarse sand, very coarse sand, gravel, pebbles, and stones), the percentage of organic matter, and the percentage of canopy openness. The chemical parameters of water used were dissolved oxygen, electrical conductivity, water temperature, and alkalinity. The regional landscape variables used were the average value of non-forest areas; drainage density; drainage form; sinuosity; average elevation; slope; percentage of forest, cerrado, agriculture/silviculture, and anthropic areas; and the NDVI at each of the sampling sites.

The geographical coordinates (latitude and longitude in Universal Transverse Mercator (UTM)) of each sampling site were used in a principal coordinates of neighbor matrices (PCNM) method described by BORCARD & LEGENDRE (2002) and by DRAY *et al.* (2006). Next, redundancy analysis (RDA) was used to remove the effects of non-important variables on the spatial and environmental data matrix. One forward selection was made for each set of predictor variables (spatial, local, and regional landscape variables). A global test was also performed, including all explanatory variables and the R^2_{adj} (according to Ezekiel's correction: PERES-NETO *et al.* 2006), which was used as a second criterion (in addition to an alpha-value of 0.05) to select the variables to retain in the subsequent analyses.

The importance of environmental variables on the structure of the benthic macroinvertebrate communities was obtained in the RDA (forward model selection) by first selecting the explanatory variable that maximized the fit of the model and by computing an F-ratio and a p-value by permuting the residuals under the full model approach (BLANCHET *et al.* 2008). Whenever $p \leq 0.05$ was obtained, then R^2_{adj} was computed for the forward model selection. If R^2_{adj} was smaller for the forward model-selection than for the global test, then another environmental variable was added to the analysis, and the permutation test was repeated (BLANCHET *et al.* 2008). All of the

*Available as Online Supplementary Material accessed with the online version of the manuscript at <http://www.scielo.br/zool>

analyses were performed using the average values of the environmental and biological variables measured during all of the sampling periods at each site. Analyses were performed in the R environment (R DEVELOPMENT CORE TEAM 2013) using the vegan package (OKSANEN *et al.* 2013).

RESULTS

Regional and local physical and chemical characteristics of the stream

The drainage area of the sampling sites totaled 390,326 ha and was divided as follows: forest (4.83%), cerrado (Brazilian savanna; 68.2%), agriculture/silviculture (agroforestry; 0.04%), and anthropogenic areas (26.93%). The latter category primarily consisted of unpaved roads and a small amount of urban area. The average NDVI value of the entire basin was 0.339, indicating that the study area could be considered preserved (Table I). Regarding the granulometric composition, very fine sand was the most abundant fraction (average: $46 \pm 18\%$ SD; range: 16 to 83%), followed by pebbles (average: $20 \pm 19\%$ SD; range: 0 to 33%), fine sand (average: $12 \pm 8\%$ SD; range: 2 to 32%), and medium sand (average: $8 \pm 7\%$ SD; range: 2 to 33%). The silt, clay, coarse sand, very coarse sand, gravel, and stone fractions showed low percentages throughout the river system (< 2%; Table II). The sampling sites varied widely in oxygen saturation (average: $63 \pm 15\%$ SD; range: 33 to 81%),

electrical conductivity (average: $80 \pm 56 \mu\text{S cm}^{-1}$ SD; range: 27 to $277 \mu\text{S cm}^{-1}$), and alkalinity (average: $655 \pm 577 \mu\text{Eq/L}$ SD; range: 130 to $1298 \mu\text{Eq/L}$). However, the water temperature was similar between sampling sites (average: $24 \pm 2^\circ\text{C}$ SD; range: 20 to 26°C ; Table III).

Variables structuring the benthic macroinvertebrate community

The family richness (average: 9 ± 3 SD; range: 2 to 15; accumulated: 28 ± 5 SD; range: 13 to 38) and density (average: $125 \pm 85 \text{ ind/m}^2$ SD; range: 14 to 332 ind/m^2) of macroinvertebrate communities varied widely in the sampling sites (Table IV). The family richness and density values of macroinvertebrate communities were higher in tributary streams (richness average: 11 ± 2 SD; richness accumulated: 30 ± 4 SD; density average: $181 \pm 86 \text{ ind/m}^2$ SD) compared with the Pandeiros River (richness average: 6 ± 3 SD; richness accumulated: 25 ± 5 SD; density average: $78 \pm 51 \text{ ind/m}^2$ SD).

The pRDA indicated that the local physical and chemical matrix explained 7.2% of the total faunal variation (adjusted R^2 ; $p < 0.001$), whereas the regional landscape matrix explained 6.9% of the total faunal variation (adjusted R^2 ; $p < 0.001$); thus, 14.1% of the total faunal variation was explained by the environmental matrices. The shared variation between the local and regional environmental variables was near zero, indicating that their effects were independent of each other. The spatial matrix

Table I. Average values for non-forest areas (A/ha), drainage density (DD), drainage form (F), sinuosity (S), average elevation (AE), slope (SI), percentage of forest (% F), cerrado (% C), agriculture/silviculture (% A/F), anthropic areas (% A), and NDVI at each of the sampling sites along the Pandeiros River Basin.

Sites	A/ha	DD	F	S	AE	SI	% F	% C	% A/S	% A	NDVI
P1	49,146	5.466	2.224	1.266	780.0	4.918	7.774	63.646	0.000	28.580	0.336
P2	22,475	5.249	1.876	1.249	714.6	6.636	11.528	70.083	0.002	18.387	0.369
P3	1,446	4.949	1.463	1.188	666.0	4.339	0.831	88.474	0.000	10.695	0.348
P4	8,630	4.845	1.484	1.179	672.3	4.617	3.213	70.419	0.000	26.367	0.328
P5	21,517	4.654	1.877	1.223	692.9	4.826	4.821	75.791	0.000	19.388	0.352
P6	122,610	5.224	2.036	1.241	725.4	5.166	7.069	66.773	0.000	26.158	0.341
P7	57,049	4.970	1.795	1.184	715.8	4.481	5.239	82.171	0.253	12.336	0.379
P8	30,191	4.752	1.996	1.239	630.6	3.130	1.271	0.000	54.699	44.030	0.296
P9	8,123	4.806	1.588	1.172	606.7	3.729	1.802	0.000	35.914	62.284	0.264
P10	266,470	5.066	2.238	1.224	691.0	4.674	5.236	64.589	0.054	30.121	0.334
P11	318,462	5.080	2.214	1.215	690.2	4.580	4.817	67.428	0.046	27.710	0.338
P12	318,454	5.080	2.214	1.215	690.2	4.580	4.817	67.428	0.046	27.710	0.338
P13	47,661	5.072	2.063	1.170	696.9	4.163	2.615	81.832	0.001	15.552	0.362
P14	37,797	5.069	1.846	1.175	640.5	3.922	2.885	83.148	0.001	13.966	0.361
P15	362,089	5.086	2.176	1.210	682.8	4.495	4.603	69.284	0.040	26.072	0.341
P16	367,109	5.087	2.181	1.210	681.0	4.503	4.560	69.203	0.040	26.198	0.341
P17	378,930	5.103	2.207	1.212	676.3	4.488	4.523	68.871	0.039	26.567	0.340
P18	386,618	5.133	2.340	1.215	672.4	4.451	4.754	68.376	0.038	26.832	0.340
P19	386,519	5.132	2.334	1.215	672.4	4.451	4.743	68.389	0.038	26.830	0.340
P20	392,017	5.149	2.341	1.218	669.9	4.426	4.832	68.197	0.037	26.933	0.339

Table II. Average values and standard deviations of the sediment variables evaluated in 20 sites along the Pandeiros River Basin. Granulometric fractions were silt + clay (S + C), very fine sand (VFS), fine sand (FS), medium sand (MS), coarse sand (CS), very coarse sand (VCS), gravel (G), pebbles (P), stones per cubic meter (S), and the percentage of organic matter (% OM).

Sites	S + C	VFS	FS	MS	CS	VCS	G	P	S	OM
P1	0.59 ± 0.55	16.26 ± 6.70	5.84 ± 11.24	1.93 ± 1.68	0.19 ± 0.12	0.78 ± 0.18	9.94 ± 2.55	64.48 ± 15.50	0.029 ± 0.001	2.28 ± 0.71
P2	0.82 ± 0.89	32.04 ± 17.73	11.65 ± 11.57	4.30 ± 3.52	1.30 ± 1.46	1.73 ± 1.62	13.56 ± 21.06	34.60 ± 25.46	0.033 ± 0.002	1.47 ± 0.99
P3	0.57 ± 0.65	39.88 ± 30.97	28.37 ± 14.68	25.62 ± 20.77	4.89 ± 7.90	0.66 ± 0.44	0.00 ± 0.00	–	–	0.50 ± 0.41
P4	1.21 ± 2.06	37.40 ± 17.32	8.37 ± 7.48	6.51 ± 9.36	0.79 ± 1.09	1.26 ± 1.28	3.55 ± 4.99	40.90 ± 15.54	0.037 ± 0.004	1.59 ± 0.99
P5	1.00 ± 1.25	43.39 ± 32.37	9.01 ± 7.34	1.86 ± 1.51	0.71 ± 1.08	0.22 ± 0.31	2.18 ± 2.92	41.64 ± 28.49	0.049 ± 0.002	0.80 ± 0.93
P6	1.37 ± 1.36	76.70 ± 32.30	15.04 ± 29.36	6.45 ± 7.43	0.29 ± 0.22	0.16 ± 0.22	–	–	–	2.56 ± 3.07
P7	0.35 ± 0.36	20.05 ± 18.86	8.66 ± 8.65	2.58 ± 2.21	1.29 ± 1.54	3.96 ± 3.86	24.97 ± 12.38	38.14 ± 18.1	0.037 ± 0.003	1.01 ± 0.53
P8	1.18 ± 1.22	63.30 ± 16.94	28.17 ± 5.91	4.79 ± 7.09	1.28 ± 1.61	0.68 ± 1.21	0.00 ± 0.52	0.00 ± 14.18	–	2.06 ± 0.69
P9	1.19 ± 2.02	25.88 ± 28.10	8.67 ± 9.73	3.46 ± 3.60	4.07 ± 4.70	4.26 ± 5.62	14.4 ± 14.33	38.07 ± 16.82	–	2.42 ± 1.51
P10	0.52 ± 1.00	56.33 ± 42.83	6.76 ± 7.50	8.74 ± 9.76	1.14 ± 1.22	0.76 ± 1.10	0.37 ± 0.50	24.87 ± 33.62	0.037 ± 0.005	1.73 ± 0.97
P11	1.18 ± 0.39	42.96 ± 25.70	8.89 ± 9.67	1.61 ± 1.40	0.39 ± 0.46	0.88 ± 1.31	5.55 ± 5.71	38.55 ± 31.12	0.041 ± 0.007	1.29 ± 0.48
P12	1.38 ± 0.89	52.38 ± 26.04	4.89 ± 3.89	9.11 ± 14.08	3.96 ± 6.84	3.84 ± 6.25	7.01 ± 8.23	17.43 ± 19.21	0.033 ± 0.009	0.97 ± 0.51
P13	0.43 ± 0.34	35.42 ± 13.19	21.53 ± 7.59	7.06 ± 5.64	0.66 ± 0.26	0.63 ± 0.38	3.01 ± 2.08	31.27 ± 19.00	0.037 ± 0.009	1.41 ± 0.40
P14	4.12 ± 4.01	60.78 ± 39.49	5.36 ± 1.81	5.00 ± 4.91	6.31 ± 6.66	7.87 ± 12.61	10.57 ± 11.95	–	–	1.52 ± 0.57
P15	2.26 ± 0.38	47.10 ± 9.08	8.58 ± 4.44	2.04 ± 1.90	1.87 ± 0.13	1.81 ± 0.03	0.88 ± 1.75	35.46 ± 8.79	0.037 ± 0.008	1.03 ± 0.03
P16	1.42 ± 1.61	51.90 ± 38.05	29.58 ± 32.21	12.19 ± 11.78	1.69 ± 2.99	1.66 ± 3.09	1.57 ± 3.15	–	–	2.08 ± 1.77
P17	1.89 ± 1.91	66.60 ± 38.80	8.33 ± 9.63	11.65 ± 14.79	0.23 ± 0.24	0.02 ± 0.03	–	11.28 ± 22.57	–	1.48 ± 0.85
P18	15.26 ± 17.63	23.01 ± 15.62	10.4 ± 5.09	20.94 ± 8.87	22.92 ± 17.87	7.47 ± 6.38	–	–	–	31.47 ± 3.86
P19	1.71 ± 1.06	83.94 ± 21.02	2.02 ± 1.76	1.69 ± 1.80	1.79 ± 1.99	2.48 ± 2.88	6.37 ± 12.73	–	–	2.69 ± 0.91
P20	2.27 ± 1.84	55.86 ± 42.40	15.55 ± 23.71	25.45 ± 33.46	0.64 ± 0.79	0.24 ± 0.47	–	–	–	1.05 ± 0.76

Table III. Average values and the standard deviation of the percentage of dissolved oxygen in the water (O₂% St), electrical conductivity (µS/cm²), water temperature (Temp), alkalinity (µEq/L), and the percentage of canopy openness (% CO) in 20 sites along the Pandeiros River Basin.

Sites	O ₂ % St	Conductivity	Temp (°C)	Alkalinity	% CO
P1	73.33 ± 24.82	65.28 ± 5.02	24.13 ± 1.21	394.90 ± 253.61	68.04
P2	79.90 ± 4.35	181.63 ± 17.14	23.13 ± 0.95	756.53 ± 513.93	5.28
P3	63.38 ± 20.91	64.08 ± 0.61	26.78 ± 0.10	236.15 ± 184.30	33.35
P4	73.43 ± 13.39	93.25 ± 57.37	21.40 ± 2.04	204.24 ± 295.62	9.48
P5	69.63 ± 18.50	41.63 ± 22.74	22.53 ± 2.41	179.48 ± 136.57	21.14
P6	66.45 ± 25.23	76.00 ± 7.29	25.03 ± 1.01	458.03 ± 206.43	16.13
P7	67.38 ± 26.64	37.75 ± 49.62	21.85 ± 1.87	734.22 ± 915.14	90.45
P8	39.58 ± 26.88	27.05 ± 19.50	24.83 ± 1.58	164.29 ± 295.20	54.64
P9	40.33 ± 3.90	28.30 ± 37.81	23.28 ± 1.94	130.19 ± 186.11	54.86
P10	71.93 ± 24.86	60.13 ± 1.89	23.70 ± 1.44	468.55 ± 196.75	16.13
P11	73.48 ± 23.10	60.17 ± 1.88	23.30 ± 1.41	373.76 ± 214.67	92.85
P12	73.48 ± 25.31	60.13 ± 2.63	23.25 ± 1.67	493.83 ± 156.01	22.46
P13	48.90 ± 30.26	77.27 ± 17.81	19.80 ± 2.21	526.20 ± 361.75	85.67
P14	33.99 ± 24.87	277.43 ± 5.55	21.80 ± 1.51	2590.33 ± 1340.11	37.99
P15	70.35 ± 29.13	104.73 ± 5.16	25.58 ± 0.07	1178.18 ± 219.20	85.38
P16	81.48 ± 15.23	70.50 ± 3.84	25.05 ± 2.37	1323.58 ± 1679.62	15.57
P17	71.13 ± 23.87	71.76 ± 2.12	25.93 ± 2.36	485.58 ± 119.64	14.14
P18	47.95 ± 40.55	81.53 ± 10.81	29.08 ± 5.90	510.35 ± 272.98	100.00
P19	71.10 ± 24.25	69.95 ± 4.70	24.98 ± 1.94	604.93 ± 284.47	100.00
P20	44.56 ± 27.84	71.38 ± 4.87	26.15 ± 2.20	1298.33 ± 1226.16	100.00

Table IV. Average family richness (AvR), accumulated family richness (AcR), and density (ind/m²) of macroinvertebrates in 20 sites along the Pandeiros River Basin.

Sites	AvR	AcR	Density
P1	11.9	29	140.9
P2	10.5	34	73.1
P3	12.7	30	245.4
P4	15.3	38	215.9
P5	12.7	29	237.5
P6	4.3	25	13.9
P7	13.9	33	331.8
P8	8.8	34	175.5
P9	10.5	23	172.4
P10	8.3	32	94.3
P11	8.8	27	55.0
P12	6.9	27	143.5
P13	9.0	31	101.2
P14	8.6	26	82.1
P15	9.0	35	146.2
P16	8.7	27	117.7
P17	5.8	26	33.8
P18	2.3	13	26.1
P19	4.3	20	27.1
P20	6.3	22	61.2

did not explain the variation in the community structure, and the shared correlations of the spatial variables with local (0.2%) and regional environmental variables (2%) were extremely low, indicating that space was primarily unimportant in this study. The percentage of explained variation shared among all three matrices was 4.4%. Most of the variation in the macroinvertebrate communities (81%) remained unexplained (Fig. 3). A single spatial variable was selected (PCNM 2, adjusted $R^2 = 0.081$, $F = 2.68$, $p < 0.001$). Two local environmental matrix variables were selected: the electrical conductivity (adjusted $R^2 = 0.117$, $F = 1.91$, $p = 0.042$) and the pebble fraction (adjusted $R^2 = 0.072$, $F = 2.49$, $p = 0.002$). Additionally, two regional environmental matrix variables were selected: non-forest areas (adjusted $R^2 = 0.073$, $F = 2.49$, $p = 0.001$) and average elevation (adjusted $R^2 = 0.132$, $F = 2.24$, $p = 0.005$) (Fig. 3).

DISCUSSION

Effects of spatial and environmental patterns on benthic macroinvertebrate communities

Our results demonstrate that the environmental variables at the local and regional scales (which explained 14.1% of the total variation) were responsible for structuring the composition (the community composition and relative abundance) of aquatic macroinvertebrate communities. Local-scale

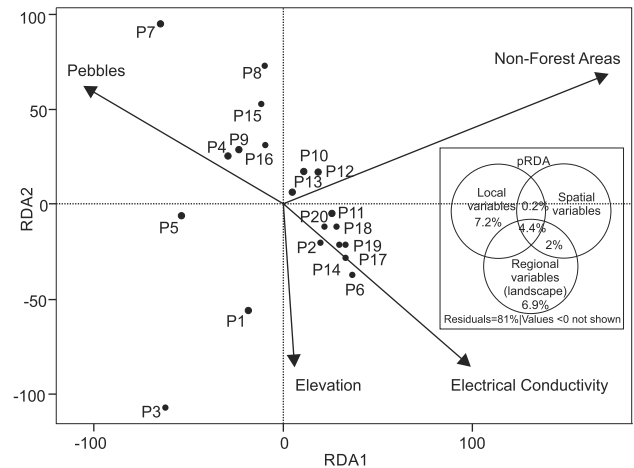


Figure 3. Partial redundancy analysis (pRDA) of the invertebrate communities based on the spatial and local and regional environmental matrices. Percentages of explained variation are shown in the inset Venn diagram.

studies investigating environmental and spatial effects on community variation in Central European (FELD & HERING 2007) and southern Brazilian streams (HEPP *et al.* 2012) have obtained similar results. Despite the increased effort to assess the effect of local environmental conditions (7.2% of explained variation), we found that regional variables (6.9% of explained variation) can also modify the macroinvertebrate communities. According to COTTENIE (2005), most studies that assessed the importance of environmental and spatial variables found that the former, specifically habitat heterogeneity, was the most important. This pattern was also observed for macroinvertebrate communities, which were primarily influenced by niche changes along an environmental gradient (LEIBOLD *et al.* 2004, SIQUEIRA *et al.* 2012).

The percentage of explained variation shared by the environmental matrices (local and regional scales) was nearly zero, indicating that the effects of these two groups of variables were independent. The percentages of explained variation shared by spatial and environmental variables (spatial-local = 0.2% and spatial-regional = 2%) were low, indicating that environmental effects are uncorrelated in space. COTTENIE (2005) found that the relative importance of local and regional processes showed the prevalence of three (neutral model, species-sorting, and mass-effect) theoretical metacommunity types for real systems in a unified framework, although we found only an environmental pattern influencing the macroinvertebrate communities (see also LEIBOLD *et al.* 2004). Although the total percentage of explained variation was low, this pattern is common in ecological studies and is due (at least in part) to important variables that were missing from the analysis or to communities that are not controlled by environmental variables (GENNER *et al.* 2004, HEPP *et al.* 2012).

Effects of environmental variables on benthic macroinvertebrate communities

The sampling sites with higher family richness and densities of macroinvertebrate communities were associated with the coarse fractions of the substrate, particularly pebbles, in the pRDA ordination. The occurrence of pebbles creates high habitat diversity in the sediment (DOMINGUEZ-GRANDA *et al.* 2011, JUN *et al.* 2011), increasing the availability of shelter for aquatic organisms (TUPINAMBAS *et al.* 2007, BÜCKER *et al.* 2010). Furthermore, high elevations and steep slopes within the landscape provide the streams, which are primarily small, with great strength, increasing their capacity to carry fine sedimentary particles and leaving behind a greater percentage of pebbles (ROSGEN 1996, CHURCH 2002). Thus, the flat plains at the bottom of the basin are prime areas for the deposition of fine particles (VANNOTE *et al.* 1980). This finding corroborates the proposition of VINSON & HAWKINS (2003) that aquatic communities are structured by natural fluvial processes and helps to explain the higher richness and densities of macroinvertebrates in tributary streams (upstream) compared with the Pandeiros River. These natural fluvial processes cause the local habitat characteristics (e.g., water velocity, water depth, river width, and substrate) to vary spatially along the drainage basin (River Continuum Concept; VANNOTE *et al.* 1980, BÜCKER *et al.* 2010).

The sampling sites with low taxonomic richness and densities of macroinvertebrate communities were associated with the electrical conductivity and non-forest areas in the pRDA ordination. These variables are associated with effluent discharge and deforestation (MYKRA *et al.* 2008). Compared with those water bodies in preserved areas, the water bodies in anthropogenic areas have more diffuse sources of organic and inorganic matter, particularly those bodies without vegetative protection, resulting in higher electrical conductivity (GARDINER *et al.* 2009, JUN *et al.* 2011). In anthropogenic areas, inadequately treated effluents may flow into adjacent water bodies, increasing the nutrient concentrations of the water and altering the electrical conductivity (MYKRA *et al.* 2008). In spite of the low percentage of anthropogenic areas within the Pandeiros River Basin, our results suggest negative effects of higher electrical conductivity and non-forest areas on the richnesses and densities of macroinvertebrate communities. Anthropogenic areas (particularly urbanized areas) strongly influence biological communities, and their effects are disproportionate to the size of the area used (PAUL & MEYER 2001), thus enhancing their real effect on macroinvertebrate communities (JOHNSON *et al.* 2012).

We found that the environmental variables (local and regional) have greater effects on the macroinvertebrate community than do spatial variables. We also identified the most important local (pebble fraction and conductivity) and regional variables (higher altitude and non-forest areas) structuring the macroinvertebrate community. Sampling sites with higher non-forest areas can allow higher inputs of allochthonous soil sediment. Downstream areas (primarily lower altitude) can present

higher depositions of fine particles, resulting in low pebble fractions and higher electrical conductivities (contribution by upstream areas). Another aspect is that the pebble fraction can increase habitat diversity and result in a positive effect on the richness and densities of macroinvertebrate communities. Therefore, we conclude that higher percentages of coarse particles (pebbles) in substrates and topographic variation are likely to be responsible for positive effects on family richness and densities of macroinvertebrate communities.

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Appendix S1. Base watershed Otto-coded and geographical location of the river (UTM). Bold-faced code indicates the level of otto-bacia (Otto5) used in segregation of the regions.

Sites	Otto1	Otto2	Otto3	Otto4	Otto5	Otto6	Lat_Sad69	Long-Sad69	Geographical location - UTM
P1	7	74	747	7472	74729	747291	-15.185	-45.124	23 L 487078 8321388
P2	7	74	747	7472	74728	747281	-15.222	-45.139	23 L 485084 8317123
P3	7	74	747	7472	74727	747279	-15.255	-45.087	23 L 490766 8313432
P4	7	74	747	7472	74727	747274	-15.257	-44.963	23 L 505376 8312902
P5	7	74	747	7472	74727	747276	-15.262	-45.014	23 L 498526 8312719
P6	7	74	747	7472	74727	747275	-15.282	-45.013	23 L 498679 8310507
P7	7	74	747	7472	74726	747263	-15.290	-44.822	23 L 519132 8309678
P8	7	74	747	7472	74726	747262	-15.384	-44.945	23 L 505963 8299244
P9	7	74	747	7472	74725	747252	-15.457	-44.859	23 L 515210 8291122
P10	7	74	747	7472	74725	747251	-15.441	-44.822	23 L 519165 8292960
P11	7	74	747	7472	74723	747231	-15.456	-44.789	23 L 522615 8291137
P12	7	74	747	7472	74723	747232	-15.455	-44.790	23 L 5226798291483
P13	7	74	747	7472	74724	747241	-15.423	-44.789	23 L 522734 8294876
P14	7	74	747	7472	74722	747221	-15.477	-44.744	23 L 527480 8288900
P15	7	74	747	7472	74721	747212	-15.514	-44.754	23 L 526443 8284887
P16	7	74	747	7472	74721	747212	-15.519	-44.754	23 L 526523 8284205
P17	7	74	747	7472	74721	747211	-15.606	-44.711	23 L 531023 8274679
P18	7	74	747	7472	74721	747211	-15.667	-44.635	23 L 539212 8267918
P19	7	74	747	7472	74721	747211	-15.667	-44.639	23 L 538754 8267922
P20	7	74	747	7472	74721	747211	-15.683	-44.610	23 L 541841 8266150

Appendix S2. Average values of the density of benthic macroinvertebrates (individuals per m²) and the standard deviation at 20 sampling sites in the Pandeiros River Basin, Brazil. Samples were obtained during February, May, September and November of 2008.

Taxa	P1		P2		P3		P4		P5		P6		P7		P8		P9		P10													
Nematoda																																
Nematomorpha	0	±	0	0	±	0	0	±	0	9	±	32	0	±	0	0	±	0	±	37	±	128	0	±	0	0	±	0				
Annelida																																
Hyrundinae	0	±	0	0	±	0	19	±	43	0	±	0	0	±	0	0	±	0	±	102	±	266	0	±	0	9	±	32				
Oligochaeta	74	±	128	176	±	575	111	±	288	176	±	316	194	±	345	28	±	96	±	231	±	330	±	426	±	734	296	±	482	83	±	126
Mollusca																																
Bivalvia	0	±	0	56	±	89	0	±	0	148	±	261	324	±	286	19	±	64	±	0	±	0	±	19	±	64	0	±	0	120	±	383
Gastropoda																																
Ampullariidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Planorbidae	0	±	0	0	±	0	19	±	43	9	±	32	0	±	0	0	±	0	±	0	±	0	±	9	±	32	0	±	0	0	±	0
Lymnaeidae	0	±	0	120	±	326	0	±	0	37	±	99	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Thiaridae	0	±	0	37	±	128	9	±	32	194	±	339	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Pomacea	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Arthropoda																																
Chelicerata																																
Arachnida																																
Hydracarina	37	±	99	120	±	350	9	±	32	148	±	513	9	±	32	28	±	69	±	37	±	128	±	0	±	0	28	±	69	19	±	64
Crustacea																																
Malacostracoda																																
Decapoda																																
Palaemonidae	0	±	0	19	±	43	361	±	1183	19	±	64	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Amphipoda																																
Hyalidae	0	±	0	0	±	0	398	±	414	0	±	0	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Branchiopoda																																
Cladocera	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	±	278	±	895	±	0	±	0	0	±	0	0	±	0
Ostracoda	37	±	128	0	±	0	0	±	0	28	±	96	0	±	0	9	±	32	±	0	±	0	±	19	±	64	0	±	0	0	±	0
Maxillopoda																																
Copepoda	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	9	±	32	±	111	±	385	±	0	±	0	0	±	0	0	±	0
Atelocerata																																
Hexapoda																																
Collembola	0	±	0	0	±	0	9	±	32	0	±	0	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Insecta																																
Ephemeroptera																																
Leptophlebiidae	306	±	432	111	±	251	2315	±	3120	1102	±	697	491	±	640	9	±	32	±	1343	±	2056	±	83	±	256	259	±	467	231	±	606
Leptohyphidae	343	±	305	648	±	995	676	±	598	2102	±	2768	1713	±	2072	28	±	69	±	3620	±	4313	±	3370	±	4266	1370	±	1772	1426	±	3029
Baetidae	935	±	1033	306	±	421	389	±	687	435	±	500	1241	±	1062	148	±	191	±	4056	±	5626	±	1222	±	1867	1537	±	1927	176	±	274
Caenidae	0	±	0	19	±	43	0	±	0	0	±	0	0	±	0	9	±	32	±	0	±	0	±	111	±	385	185	±	435	19	±	64
Oligoneuridae	56	±	101	9	±	32	0	±	0	0	±	0	46	±	129	9	±	32	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Polymitarcyidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	±	0	±	0	±	0	±	0	9	±	32	0	±	0
Euthyplociidae	0	±	0	9	±	32	0	±	0	0	±	0	0	±	0	0	±	0	±	9	±	32	±	9	±	32	213	±	186	37	±	99
Odonata																																
Zygoptera																																
Coenagrionidae	19	±	43	46	±	74	139	±	143	194	±	300	37	±	72	0	±	0	±	46	±	88	±	435	±	541	46	±	88	28	±	96
Calopterygidae	0	±	0	0	±	0	0	±	0	9	±	32	9	±	32	37	±	128	±	0	±	0	±	0	±	0	0	±	0	9	±	32
Anisoptera																																
Libellulidae	389	±	611	9	±	32	65	±	88	380	±	507	167	±	353	19	±	43	±	361	±	207	±	722	±	765	685	±	726	102	±	253
Gomphidae	37	±	99	46	±	100	83	±	126	389	±	350	259	±	269	37	±	72	±	93	±	156	±	28	±	69	352	±	288	130	±	288
Aeshnidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	±	0	±	0	±	0	±	0	0	±	0	0	±	0
Plecoptera																																
Perlidae	213	±	353	28	±	50	0	±	0	287	±	386	9	±	32	19	±	64	±	111	±	222	±	0	±	0	0	±	0	19	±	64
Hemiptera																																
Pleidae	0	±	0	0	±	0	19	±	43	9	±	32	444	±	506	0	±	0	±	167	±	443	±	0	±	0	0	±	0	0	±	0
Naucoridae	130	±	182	130	±	141	324	±	270	231	±	386	426	±	516	0	±	0	±	37	±	72	±	65	±	120	0	±	0	37	±	128
Notonectidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	9	±	32	±	0	±	0	±	37	±	128	0	±	0	0	±	0
Gerridae	0	±	0	0	±	0	0	±	0	0	±	0	9	±	32	28	±	69	±	0	±	0	±	19	±	64	0	±	0	139	±	332

Taxa	P1		P2		P3		P4		P5		P6		P7		P8		P9		P10	
Velidae	0	± 0	19	± 64	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0	296	± 549
Mesovelidae	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	9	± 32	9	± 32
Hebridae	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	9	± 32	0	± 0	9	± 32	0	± 0	0	± 0
Corixidae	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	46	± 100	0	± 0	0	± 0
Belostomatidae	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	9	± 32	28	± 69	0	± 0	0	± 0
Megaloptera																				
Corydalidae	139	± 247	9	± 32	0	± 0	9	± 32	9	± 32	0	± 0	46	± 74	0	± 0	0	± 0	9	± 32
Trichoptera																				
Hydropsychidae	1546	± 1884	204	± 466	454	± 569	250	± 335	148	± 224	9	± 32	1000	± 1225	139	± 269	157	± 244	139	± 213
Glossosomatidae	0	± 0	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0	37	± 128	0	± 0	46	± 160	0	± 0
Leptoceridae	19	± 43	9	± 32	28	± 50	463	± 523	333	± 462	37	± 72	287	± 482	0	± 0	65	± 120	19	± 64
Helicopsychidae	9	± 32	37	± 99	28	± 69	28	± 50	0	± 0	56	± 161	37	± 55	9	± 32	0	± 0	28	± 69
Philopotamidae	19	± 43	65	± 100	0	± 0	389	± 631	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	19	± 43
Odontoceidae	65	± 138	0	± 0	74	± 137	120	± 319	0	± 0	0	± 0	0	± 0	0	± 0	9	± 32	0	± 0
Hydroptilidae	74	± 197	0	± 0	0	± 0	9	± 32	148	± 238	0	± 0	917	± 1039	74	± 179	111	± 164	28	± 69
Polycentropodidae	0	± 0	0	± 0	0	± 0	324	± 278	9	± 32	9	± 32	19	± 64	102	± 234	56	± 130	0	± 0
Lepidoptera																				
Pyralidae	0	± 0	9	± 32	204	± 280	213	± 294	315	± 720	0	± 0	130	± 163	65	± 192	102	± 120	9	± 32
Orthoptera	37	± 64	0	± 0	0	± 0	0	± 0	37	± 64	0	± 0	74	± 64	0	± 0	0	± 0	37	± 64
Coleoptera																				
Hydrophilidae	9	± 32	19	± 43	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	204	± 295	0	± 0	0	± 0
Elmidae	2574	± 2843	583	± 465	5917	± 4183	1981	± 1726	4231	± 4606	102	± 192	2278	± 2130	426	± 1123	1944	± 1156	444	± 519
Psephenidae	389	± 543	83	± 135	0	± 0	0	± 0	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0	0	± 0
Curculionidae	0	± 0	0	± 0	0	± 0	28	± 96	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Lutrochidae	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Scirtidae	0	± 0	0	± 0	37	± 128	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Gyrinidae	0	± 0	0	± 0	0	± 0	19	± 64	0	± 0	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0
Noteridae	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Dytiscidae	0	± 0	28	± 96	0	± 0	46	± 129	0	± 0	0	± 0	19	± 43	130	± 245	0	± 0	9	± 32
Diptera																				
Chironomidae	1463	± 2338	1213	± 1076	3287	± 3641	4250	± 6231	4435	± 3263	213	± 234	5704	± 4750	3204	± 5197	3824	± 3593	2389	± 3633
Ceratopogonidae	46	± 100	222	± 444	796	± 1037	37	± 86	37	± 55	28	± 69	204	± 284	65	± 111	56	± 75	176	± 234
Simuliidae	194	± 269	65	± 129	28	± 50	46	± 74	556	± 732	0	± 0	528	± 826	259	± 898	19	± 64	46	± 100
Empididae	102	± 225	19	± 64	176	± 274	28	± 69	28	± 50	9	± 32	56	± 111	19	± 64	0	± 0	19	± 43
Tabanidae	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	9	± 32	0	± 0	0	± 0	0	± 0
Tipulidae	65	± 153	343	± 441	204	± 314	93	± 156	37	± 72	0	± 0	111	± 157	0	± 0	0	± 0	0	± 0
Stratiomyidae	0	± 0	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Muscidae	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Culicidae	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	83	± 207	0	± 0	0	± 0
Nematoda																				
Nematomorpha	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Annelida																				
Hyrundinae	0	± 0	0	± 0	12	± 37	0	± 0	0	± 0	9	± 32	9	± 32	0	± 0	19	± 64	0	± 0
Oligochaeta	148	± 173	583	± 1619	333	± 799	136	± 287	231	± 374	370	± 380	287	± 417	9	± 32	46	± 74	278	± 248
Mollusca																				
Bivalvia	19	± 43	1296	± 3551	259	± 497	222	± 229	204	± 639	194	± 373	259	± 731	9	± 32	9	± 32	787	± 1431
Gastropoda																				
Ampullariidae	0	± 0	0	± 0	49	± 113	1914	± 5617	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Planorbidae	0	± 0	0	± 0	99	± 218	12	± 37	28	± 96	9	± 32	0	± 0	0	± 0	0	± 0	28	± 69
Lymnaeidae	0	± 0	120	± 290	0	± 0	0	± 0	9	± 32	9	± 32	0	± 0	0	± 0	0	± 0	19	± 64
Thiaridae	0	± 0	93	± 321	0	± 0	407	± 692	9	± 32	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0
Pomacea	0	± 0	0	± 0	0	± 0	12	± 37	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	19	± 64
Arthropoda																				
Chelicerata																				
Arachnida																				
Hydracarina	9	± 32	9	± 32	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0	0	± 0
Crustacea																				
Malacostracoda																				
Decapoda																				

Taxa	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Paleomonidae	0 ± 0	9 ± 32	0 ± 0	12 ± 37	0 ± 0	28 ± 50	9 ± 32	0 ± 0	0 ± 0	0 ± 0
Amphipoda										
Hyalidae	19 ± 64	0 ± 0	12 ± 37	0 ± 0	0 ± 0	0 ± 0	19 ± 43	0 ± 0	0 ± 0	0 ± 0
Branchiopoda										
Cladocera	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Ostracoda	0 ± 0	0 ± 0	0 ± 0	12 ± 37	0 ± 0	56 ± 138	9 ± 32	0 ± 0	19 ± 64	9 ± 32
Maxillopoda										
Copepoda	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Atelocerata										
Hexapoda										
Collembola	0 ± 0	0 ± 0	0 ± 0	0 ± 0	9 ± 32	0 ± 0	0 ± 0	9 ± 32	0 ± 0	0 ± 0
Insecta										
Ephemeroptera										
Leptophlebiidae	28 ± 69	102 ± 286	198 ± 271	99 ± 152	46 ± 74	0 ± 0	0 ± 0	0 ± 0	9 ± 32	19 ± 64
Leptohyphidae	907 ± 566	630 ± 804	543 ± 798	383 ± 516	1852 ± 2679	37 ± 99	28 ± 50	37 ± 99	56 ± 161	602 ± 1446
Baetidae	250 ± 285	778 ± 1670	247 ± 368	99 ± 141	963 ± 1391	306 ± 397	167 ± 305	19 ± 43	120 ± 316	231 ± 425
Caenidae	0 ± 0	0 ± 0	0 ± 0	235 ± 466	111 ± 385	0 ± 0	9 ± 32	0 ± 0	9 ± 32	0 ± 0
Oligoneuridae	19 ± 43	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Polymitarcyidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	28 ± 69	0 ± 0	0 ± 0
Euthyplociidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	28 ± 96	0 ± 0	0 ± 0
Odonata										
Zygoptera										
Coenagrionidae	9 ± 32	56 ± 89	25 ± 49	173 ± 168	9 ± 32	380 ± 798	102 ± 153	0 ± 0	65 ± 225	0 ± 0
Calopterygidae	0 ± 0	0 ± 0	25 ± 74	0 ± 0	9 ± 32	0 ± 0	19 ± 64	0 ± 0	0 ± 0	0 ± 0
Anisoptera										
Libellulidae	83 ± 96	111 ± 164	37 ± 111	99 ± 103	222 ± 255	833 ± 1783	46 ± 88	9 ± 32	9 ± 32	46 ± 74
Gomphidae	9 ± 32	139 ± 218	432 ± 661	74 ± 79	19 ± 64	167 ± 253	139 ± 228	0 ± 0	28 ± 50	148 ± 159
Aeshnidae	0 ± 0	0 ± 0	12 ± 37	12 ± 37	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Plecoptera										
Perlidae	37 ± 72	9 ± 32	0 ± 0	0 ± 0	19 ± 43	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hemiptera										
Pleidae	0 ± 0	9 ± 32	160 ± 324	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Naucoridae	56 ± 130	102 ± 198	37 ± 111	0 ± 0	65 ± 88	0 ± 0	9 ± 32	9 ± 32	0 ± 0	9 ± 32
Notonectidae	0 ± 0	0 ± 0	0 ± 0	12 ± 37	0 ± 0	9 ± 32	0 ± 0	9 ± 32	0 ± 0	0 ± 0
Gerridae	9 ± 32	28 ± 96	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Veliidae	0 ± 0	9 ± 32	12 ± 37	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Mesoveliidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hebridae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Corixidae	0 ± 0	0 ± 0	0 ± 0	12 ± 37	0 ± 0	9 ± 32	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Belostomatidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Megaloptera										
Corydalidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Trichoptera										
Hydropsychidae	167 ± 192	102 ± 248	49 ± 113	12 ± 37	306 ± 540	37 ± 128	65 ± 192	0 ± 0	28 ± 96	37 ± 128
Glossosomatidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	37 ± 86	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Leptoceridae	28 ± 50	28 ± 96	99 ± 130	12 ± 37	46 ± 74	37 ± 72	37 ± 72	0 ± 0	28 ± 50	37 ± 99
Helicopsychidae	139 ± 143	83 ± 151	0 ± 0	0 ± 0	46 ± 57	0 ± 0	9 ± 32	0 ± 0	0 ± 0	9 ± 32
Philopotamidae	9 ± 32	0 ± 0	25 ± 74	0 ± 0	9 ± 32	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Odontoceidae	0 ± 0	0 ± 0	62 ± 113	0 ± 0	19 ± 64	0 ± 0	9 ± 32	0 ± 0	0 ± 0	0 ± 0
Hydroptilidae	19 ± 64	19 ± 64	25 ± 74	37 ± 79	83 ± 256	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Polycentropodidae	0 ± 0	19 ± 64	49 ± 98	62 ± 148	9 ± 32	102 ± 174	0 ± 0	0 ± 0	28 ± 96	0 ± 0
Lepidoptera										
Pyrallidae	37 ± 55	19 ± 43	12 ± 37	25 ± 49	167 ± 477	37 ± 86	83 ± 207	0 ± 0	0 ± 0	0 ± 0
Orthoptera										
Coleoptera										
Hydrophilidae	0 ± 0	0 ± 0	12 ± 37	0 ± 0	9 ± 32	74 ± 152	0 ± 0	0 ± 0	19 ± 64	0 ± 0
Elmidae	370 ± 333	333 ± 452	840 ± 1053	62 ± 148	833 ± 1324	796 ± 1211	148 ± 173	19 ± 43	28 ± 50	111 ± 134
Psephenidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Curculionidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	9 ± 32	0 ± 0	9 ± 32	0 ± 0	0 ± 0

Taxa	P1		P2		P3		P4		P5		P6		P7		P8		P9		P10											
Lutrochidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0									
Scirtidae	0	±	0	0	±	0	0	±	0	9	±	32	0	±	0	0	±	0	0	±	0									
Gyrinidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0									
Noteridae	0	±	0	0	±	0	0	±	0	93	±	321	0	±	0	0	±	0	0	±	0									
Dytiscidae	9	±	32	0	±	0	12	±	37	0	±	0	9	±	32	19	±	43	0	±	0									
Diptera																														
Chironomidae	1139	±	1385	2148	±	5914	2877	±	3072	1272	±	1056	3944	±	9942	3926	±	4933	685	±	777	1556	±	3017	1009	±	1221	1361	±	1110
Ceratopogonidae	56	±	101	296	±	957	12	±	37	12	±	37	176	±	446	176	±	278	9	±	32	19	±	64	222	±	364	46	±	74
Simuliidae	19	±	43	0	±	0	62	±	185	0	±	0	9	±	32	46	±	160	9	±	32	0	±	0	28	±	96	213	±	671
Empididae	9	±	32	0	±	0	49	±	148	0	±	0	28	±	69	0	±	0	0	±	0	0	±	0	0	±	0	19	±	64
Tabanidae	0	±	0	9	±	32	0	±	0	0	±	0	0	±	0	83	±	135	0	±	0	0	±	0	0	±	0	0	±	0
Tipulidae	28	±	69	0	±	0	0	±	0	0	±	0	0	±	0	9	±	32	0	±	0	9	±	32	0	±	0	0	±	0
Stratiomyidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0
Muscidae	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0	9	±	32
Culicidae	0	±	0	0	±	0	0	±	0	0	±	0	9	±	32	0	±	0	0	±	0	0	±	0	0	±	0	0	±	0