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RESEARCH ARTICLE

Benthic invertebrate density, biomass, and instantaneous secondary production along a fifth-order human-impacted tropical river

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Abstract The aim of this study was to assess land use effects on the density, biomass, and instantaneous secondary production (IP) of benthic invertebrates in a fifth-order tropical river. Invertebrates were sampled at 11 stations along the Rio das Mortes (upper Rio Grande, Southeast Brazil) in the dry and the rainy season 2010/2011. Invertebrates were counted, determined, and measured to estimate their density, biomass, and IP. Water chemical characteristics, sediment heterogeneity, and habitat structural integrity were assessed in parallel. Total invertebrate density, biomass, and IP were higher in the dry season than those in the rainy season, but did not differ significantly among sampling stations along the river. However, taxon-specific density, biomass, and IP differed similarly among sampling stations along the river and between seasons, suggesting that these metrics had the same bioindication potential. Variability in density, biomass, and IP was mainly explained by seasonality and the percentage of sandy sediment in the riverbed, and not directly by urban or agricultural land use. Our results suggest that the consistently high degradation status of the river, observed from its headwaters to mouth, weakened the response of the invertebrate community to specific land use impacts, so that only local habitat characteristics and seasonality exerted effects.

Keywords Benthic community · Ecosystem processes · Land use impacts · Agriculture · Urbanization · Bioindication

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Introduction

The conversion of natural into agricultural and urban areas has impacted freshwater ecosystems around the globe and become one of the most important threats to ecosystem integrity (Vitousek et al. 1997; Lambin and Meyfroidt 2011). Impacts related to agriculture include bank erosion and increased sediment transport, decreased organic matter inputs due to the removal of riparian vegetation, pesticide inputs, increased eutrophication through fertilization practices in the surrounding catchment, as well as changes in channel morphology and in the availability and diversity of microhabitats (Young et al. 2008; Gücker et al. 2009; Rasmussen et al. 2012). Urbanization effects are frequently related to the deterioration of water quality, mainly due to discharge of wastewater and pollutants (Gücker et al. 2006; Boëchat et al. 2014), and to large impervious surface areas, resulting in increased runoff and changes in runoff timing, thereby affecting hydrodynamic features and sediment structure of urban running waters (Walsh et al. 2005; Chadwick et al. 2006; Gücker et al. 2006).

Together with landscape modifications, alterations of habitat features caused by agriculture and urbanization reduce the structural diversity of freshwater ecosystems (Elmore and Kaushal 2008; Brauns et al. 2011) and adversely affect both community composition and diversity (Paul and Meyer 2001; Allan 2004; Silveira et al. 2005). Along with changes in community structure and composition, important ecosystem processes, such as organic matter decomposition (Silva-Junior et al. 2014), secondary production (Shieh et al. 2002; DeBruyn et al. 2003), and ecosystem metabolism (Gücker et al. 2006; Young et al. 2008; Rosa et al. 2013), are as well affected. Thus, systematic assessments of both structural characteristics and ecosystem processes should provide a better understanding as to how local and landscape alterations result in habitat transformation, with subsequent consequences for ecosystem dynamics (Clapcott et al. 2010). However, such complementary approaches are rare, and most monitoring and impact assessment studies focus on a few, mostly structural indicators.

For tropical running waters, the effects of land use on ecosystem processes include increased nutrient uptake (Bott and Newbold 2013), slower leaf decomposition (Silva-Junior et al. 2014), and increased primary productivity and/or ecosystem metabolism (Gücker et al. 2009; Boëchat et al. 2011; Rosa et al. 2013; Bott and Newbold 2013). In the last decades, secondary production of benthic invertebrates has also been described as a promising ecosystem process revealing degradation of aquatic ecosystems (Cross et al. 2006; Benke and Huryn 2006, 2010). This is expected because secondary production combines compositional information (density and biomass) with process information such as growth and mortality and is thus affected by changes in ecosystem carbon and energy fluxes, as well as nutrient cycling (Fisher and Gray 1983; Buffagni and Comin 2000). Structural variables such as density and biomass, on the other hand, may not always properly indicate changes in ecosystem functioning (Benke et al. 1984; Wohl et al. 1995). For example, changes in invertebrate density and biomass may not necessarily result in changes secondary production and vice versa (Lugthart and Wallace 1992; Buffagni and Comin 2000). Thus, assessments of secondary production can provide important complementary information, e.g., regarding human impacts on matter fluxes through benthic communities. However, secondary production has only rarely been used as a tool for understanding impacts on tropical aquatic systems, partly because metrics based on changes in species composition and functional feeding groups dominate bioindication studies using benthic invertebrates (Baptista et al. 2007; Buss and Vitorino 2010). Moreover, accurate estimates of annual secondary production are often difficult to obtain, as they require detailed knowledge on population dynamics, including growth and mortality for each population present, only possible through frequent and intensive sampling effort (Dolbeth et al. 2012). Such high sampling effort is often difficult to justify for monitoring and impact assessment purposes if dealing with larger rivers, whose dimensions necessitate extensive sampling periods. In such cases, secondary production can be quantified based on shortcut approaches such as empirical models (Benke and Huryn 2010). Especially, the instantaneous production method (Morin and Dumont 1994, Morin 1997)—that estimates a taxon's production based on the taxon's mean individual weight, density, and instantaneous growth rate, with the latter estimated from empirical relationships between growth rate and mean taxon individual weight and temperature—has received considerable attention, because its cost-saving approaches enable a functional assessment of anthropogenic impacts (DeBruyn et al. 2003; Gücker et al. 2011).

In this study, we assessed the effects of land use alteration on a larger tropical river using both structural (density and biomass) and process-based characteristics (instantaneous secondary production, IP) of benthic invertebrate communities. In parallel, we assessed catchment and riparian corridor land use, sediment structure, river habitat integrity, and water quality in order to provide a detailed analysis of the effects of land use alteration on a larger tropical river. We hypothesized that land use-related impacts on local sediment structure and habitat integrity adversely affected both structural and process-based invertebrate variables. Further, we hypothesized that an approach combining structural and process-based variables should provide complementary information to traditional structural community assessment, and therefore prove useful to access local and catchment-wide land use impacts.

Materials and methods

Study site

The present study was conducted at the Rio das Mortes (Fig. S1), a tributary to the Rio Grande in the upper Paraná basin (Federal State of Minas Gerais, SE Brazil). The Rio das Mortes catchment area of 6619 km^2 covers two mesoregions, with 27 cities (IBGE 2007). Land use in the Rio das Mortes catchment is dominated by native vegetation (52 % of total catchment area), followed by agriculture (30 % pasture, 6 % crop plantation, 7 % open soil and burnt areas, and 1 % eucalyptus plantation), and 4 % urban areas, such as roads, railways, and mining areas. Accordingly, impacts related to agriculture, such as riparian clearcutting, channelization, erosion, and sedimentation, are common from the river's headwaters to its mouth, and a natural river continuum is accordingly absent (Vannote et al. 1980). Additionally, the river's water quality is affected by massive raw sewage discharge from several municipalities in close proximity to the river, which accommodate 85 % of the total population of the catchment of about 550,000 habitants (IBGE 2007). In order to understand the drivers of density, biomass, and instantaneous secondary production of the benthic invertebrate community in the river, we selected 11 sampling stations, from the river's headwater (first-order stream) to its mouth (fifth-order river), including sites located upstream and downstream of urban centers and agricultural areas (Fig. S1). All sites were sampled in triplicate during two campaigns carried out in the dry (May 2010) and the rainy season (March 2011). In parallel to invertebrate sampling, water chemical and habitat characteristics, as well as subcatchment and riparian corridor land use were characterized. Data for habitat characteristics (i.e., structural integrity scores and sediment characteristics) were taken from the datasets described in Boëchat et al. (2013, 2014).

Land use characterization

Land use of the entire Rio das Mortes catchment was categorized into three land cover types, i.e., natural, agricultural, and urban land cover, in a previous study (Silva-Junior et al. 2014). Riparian corridors of 60-, 120-, 180-, 240-, and 300-m width and 500-m length upstream of each sampling site were delimited based on hypsometric maps using ArcGIS 2 (version 10.1, ESRI, Redlands, USA). Subsequently, land cover distributions for entire subcatchments upstream of each sampling station, as well as the riparian corridors, were calculated from the previously compiled land use map (Silva-Junior et al. 2014). As the relative contributions of each land cover type to the total areas of riparian corridors of different widths were highly correlated among each other, and with subcatchment land cover (all $R^2 > 0.99$), only total subcatchment land cover data were used in further analyses.

Water quality, sediment structure, and habitat structural integrity

We measured physical and chemical variables, such as pH, specific conductance (SC), temperature (T), dissolved oxygen concentration (DO), and saturation (%DO) in situ using a multiparameter probe (556MPS, Yellow Springs Instruments, OH, USA). Water samples for nutrient analyses were taken in triplicate at each site using a 5-L horizontal Van Dorn bottle (Limnotec, Brazil). Concentration of ammonium-nitrogen (NH_4-N), nitrate + nitrite-nitrogen (NO_3 + NO_2-N), and soluble reactive phosphorus (SRP) was measured by flow injection analysis (FIALab 2500, FIALab, Bellevue, WA, USA) according to standard analytical procedures (APHA 2003), after filtering samples through preflushed fiber glass filters (Macherey-Nagel, GF-3, 0.45-μm nominal pore size). At each station, we collected sediment samples in triplicate using an Ekman bottom grab sampler (150-cm^2 sampled surface area). In the laboratory, sediment samples were dried, and the percentage of silt, sand, and pebbles was quantified by dry sieving and granulometry analysis (Boëchat et al. 2014).

River habitat structural integrity of study sites was analyzed using the German river habitat on-site survey methodology (Kamp et al. 2007; Boëchat et al. 2013). Following this methodology, each sampling station received a score, representing the structural integrity of the riverbed, banks, and a 100-m-wide and 500-m-long floodplain corridor upstream of each sampling station. This habitat survey method considers six main parameters (channel morphometry, longitudinal and transversal profile, sediment and bank structures, and surrounding landscape features) defined by 14 functional units (sinuosity, constructions, presence of native riparian zone, prevalent land use type, among others). The final survey score value varies from 1 (undisturbed condition) to 7 (totally disturbed).

Benthic invertebrate sampling and calculation of instantaneous secondary production (IP)

Benthic invertebrates were sampled from surface sediments (sampled area 300 cm^2) in triplicate at each sampling station, considering the prevailing habitat types. Depending on sediment type and water depth, samples were taken with a Surber sampler (250-μm mesh size) or an Ekman bottom grab sampler. Animals were separated from the sediment in the field by elutriation and preserved in 70 % ethanol. In the laboratory, organisms were identified to the lowest possible taxonomic level using binocular and stereo microscopes and appropriate identification keys (e.g., Flint 1983; Merrit and Cummins 1996; Pes et al. 2005; Domínguez et al. 2006; Passos et al. 2007; Pimpão and Mansur 2009; Mugnai et al. 2010). We calculated densities (D, individuals m^{-2}) for each sample and season.

To estimate instantaneous secondary production (IP), micrographs of the first 100 randomly chosen individuals of each taxon, if present in such high numbers, in each sample were imported into the Digimizer Image Analysis Software (v. 4.1.2, MedCalc Software, Belgium), and body length measures were obtained. Subsequently, individual weight (IW in mg dry weight [DW]) was mainly estimated using taxon-specific length body mass relationships (e.g., Towers et al. 1994; Benke et al. 1999; Miserendino 2001). For some groups (e.g., Bivalvia, Turbellaria), we did not find reliable or taxon-specific length body mass relationships in the literature. Individuals of those taxa were dried at 60 °C until constant weight was reached and directly weighed. The mean IW for each taxon in each sample was then calculated as the arithmetic mean of the estimated IWs, and multiplied with taxon density to estimate total taxon biomass (BM) for each sample. Biomasses of all encountered taxa were then summed up for each sample to estimate total biomass of the respective sample.

Instantaneous secondary production (IP, mg DW m^{-2} day^{-1}) was estimated for each taxon and sample as the product of taxon

D, mean IW, and instantaneous growth rate (GR, day^{-1}; Plante and Downing 1989; Edgar 1990; Morin and Dumont 1994; Morin 1997). Instantaneous growth rate was estimated for each taxon and sample based on mean IW, water temperature (T, °C), and specific coefficients (*a*, *b*, and *c*) of empirical models for insects (Morin and Dumont 1994; Eq. 1), Oligochaeta (Plante and Downing 1989; Eq. 2), and mollusks and platyhelminthes (Edgar 1990; Eq. 3). Taxa IPs were then summed up to estimate total IP for each sample.

$$\log_{10}(\mathrm{GR}) = a + b\log_{10}(\mathrm{IW}) + c(\mathrm{T}) \tag{1}$$

$$\log_{10}(\mathrm{GR}) = 0.06 + 0.79\log_{10}(\mathrm{IW}) - 0.16\log_{10}(\mathrm{IW}) + 0.05\log_{10}(\mathrm{T}) \tag{2}$$

$$\log_{10}(\mathrm{GR}) = a + b\log_{10}(\mathrm{IW}) + c\log_{10}(\mathrm{T}) \tag{3}$$

Statistical analyses

Relationships of land cover of subcatchments upstream of sampling sites with water chemistry variables, sediment structure, and structural integrity of sampling stations were tested using Spearman rank correlations separately for seasons. Student's *t* tests were used to test for differences in water quality and Mann-Whitney *U* tests tested for differences in benthic invertebrate density, biomass, and IP, respectively, between seasons. One-way ANOVA followed by the Tukey HSD test was used to test for differences in water quality variables, as well as benthic invertebrate total density, biomass, and IP among sampling stations within each season. A principal component analysis was carried out for each season in order to identify spatial patterns in abiotic river ecosystem structure, i.e., water physical and chemical characteristics, sediment composition, and structural habitat integrity, and to explore whether potential patterns correspond to land use patterns. Analyses of similarity (two-way nested ANOSIM) based on Bray-Curtis similarity of invertebrate density, biomass, and IP data were carried out in order to test for differences in the invertebrate community between seasons and among sampling sites (with site nested in season). Subsequent analyses of indicator taxa were performed to identify the invertebrate taxa responsible for the found differences. To analyze relationships between the invertebrate community and both abiotic ecosystem structure and land use, we carried out distance-based redundancy analyses (dbRDA) separately for density, biomass, and IP data. Two-way nested ANOSIM, indicator taxa analyses, and dbRDA were performed using the PRIMER software package (version 6, PRIMER-E Ltd., UK). All other statistical procedures were conducted using Statistica for Windows (v. 10.0, Statsoft, USA), and test assumptions, such as normality and homoscedasticity, were verified prior to analyses.

Results

Catchment land cover, sediment structure, structural integrity, and water quality

Natural and agricultural land cover (41.6 to 53.7 % and 41.3 to 56.9 %, respectively, of the subcatchment area upstream of each sampling station) dominated the subcatchments of the

Table 1 Total subcatchment land cover upstream of the sampling stations at the Rio das Mortes, and sediment structure, and river habitat structural integrity score

Sampling	Land cover			Sediment structure			Integrity Score
Station	% Natural	% Urban	% Agricultural	% Sand	% Silt	% Pebble	
1 (Headwater)	41.6	1.5	56.9	32.2	0.4	67.4	3
2 (CAM)	49.0	4.7	46.3	97.9	1.8	0.3	4
3 (BAR)	52.6	5.6	41.8	85.3	14.2	0.5	6
4 (PR)	53.5	5.1	41.3	81.0	19.0	0	5
5 (BPT)	53.6	5.0	41.4	81.0	19.0	0	7
6 (UT)	53.6	5.0	41.4	69.0	31.0	0	7
7 (TIR)	53.7	5.0	41.3	0	0	100.0	6
8 (ER)	53.7	4.1	42.2	62.2	37.7	0.1	6
9 (FLONA)	52.5	4.5	42.9	87.0	9.0	4.0	4
10 (RIT)	52.6	4.4	43.0	83.5	16.5	0	5
11 (Mouth)	53.4	3.8	42.8	93.5	6.4	0.1	5

Table 2 Water chemistry mean values at the 11 sampling stations in the Rio das Mortes during the dry season

Sampling station	T (°C)	pH	SC (μS cm^{-1})	DO (mg L^{-1})	Sat. DO (%)	SRP (μg L^{-1})	NH_4-N (μg L^{-1})	$NO_3 + NO_2$-N (μg L^{-1})
1	17.2^{A}	6.5	17^{A}	8.3	86^{A}	6.7^{A}	300^{A}	109^{A}
2	17.2^{A}	6.6	36^{B}	8.4	87^{A}	14.6^{B}	400^{B}	362^{B}
3	17.3^{A}	7.3	41^{B}	8.2	86^{A}	13.8^{C}	366^{B}	633^{C}
4	17.6^{A}	7.4	46^{C}	8.5	89^{A}	10.2^{C}	202^{C}	550^{D}
5	18.2^{B}	7.5	47^{C}	8.3	89^{A}	12.3^{C}	220^{C}	533^{D}
6	18.5^{B}	7.5	50^{C}	8.3	88^{A}	9.8^{C}	255^{C}	555^{D}
7	17.8^{B}	7.3	61^{D}	8.3	97^{B}	12.3^{C}	473^{D}	651^{C}
8	17.9^{B}	7.4	42^{B}	8.4	88^{A}	13.1^{C}	118^{E}	404^{B}
9	18.3^{B}	7.5	44^{C}	8.2	88^{A}	15.9^{D}	261^{C}	430^{B}
10	18.7^{B}	7.6	45^{C}	8.6	92^{B}	13.3^{C}	288^{C}	433^{B}
11	19.7^{C}	6.9	39^{B}	8.6	93^{B}	12.3^{C}	117^{E}	415^{B}

T temperature, *SC* specific conductance, *DO* dissolved oxygen, *Sat. DO* saturation of dissolved oxygen, *SRP* soluble reactive phosphorus

Differences tested by one-way ANOVA followed by the Tukey HSD tests (similar letters indicate no statistical difference at $p<0.05$). ANOVAs for pH and DO were not significant ($p>0.05$)

sampling sites, followed by urban land cover (1.5 to 5.6 %; Table 1). According to granulometry analysis, sand was the major sediment fraction at all sampling stations, except for the headwater station (station 1), where pebble had the highest percentage (Table 1), and station 7, which was dominated by boulders and pebble (Table 1; boulders were not included in particle size analyses). The river habitat integrity survey attributed the lowest scores (i.e., the highest structural integrity) to stations 1, 2, and 9 (Table 1), which were located either in the river's headwaters (station 1), had an apparently intact riparian corridor (station 2), or were near a protected forest reserve (station 9). Stations in the river's middle reaches, such as 5, 6, 7, and 8, exhibited the highest scores (Table 1, one-way ANOVA followed by Tukey HSD test, $p<0.05$) and were thus classified as the structurally most impacted stations in our study. None of the investigated sampling stations received score 1 or 2, which correspond to pristine or minimally impacted conditions in the investigated catchment. Further details on habitat characteristics of the investigated sampling sites are given in Boëchat et al. (2013, 2014).

Mean water temperature was higher and DO concentrations and saturation values were lower in the rainy season than in the dry season (Student's *t* test, $p<0.05$). Mean concentrations of SRP, NH_4-N, and $NO_3 + NO_2$-N were lower in the rainy season than in the dry season (Student's *t* test, $p<0.05$). Significant differences in water quality variables were found among sampling stations within seasons (Tables 2 and 3; one-way ANOVA followed by Tukey HSD test, $p<0.05$). In the dry season, significant differences in water temperature and SC were detected among sampling stations (temperature increased

Table 3 Water chemistry mean values at the 11 sampling stations in the Rio das Mortes during the rainy season

Sampling station	T (°C)	pH	SC (μS cm^{-1})	DO (mg L^{-1})	Sat. DO (%)	SRP (μg L^{-1})	NH_4-N (μg L^{-1})	$NO_3 + NO_2$-N (μg L^{-1})
1	19.3^{A}	6.5	17^{A}	7.5	82^{A}	1.3^{A}	29^{A}	46^{A}
2	20.2^{A}	7.2	38^{B}	6.7	74^{B}	7.1^{B}	37^{A}	212^{B}
3	21.4^{B}	7.7	42^{B}	7.9	90^{C}	1.4^{A}	123^{B}	52^{A}
4	21.1^{B}	7.5	50^{C}	7.3	82^{A}	3.2^{C}	70^{C}	317^{C}
5	21.7^{B}	7.9	47^{C}	7.2	81^{A}	3.9^{C}	87^{C}	439^{D}
6	21.2^{B}	7.7	48^{C}	7.3	84^{A}	4.3^{C}	118^{B}	343^{C}
7	22.2^{C}	7.1	47^{C}	7.4	83^{A}	3.8^{C}	205^{D}	362^{C}
8	21.0^{B}	7.7	42^{B}	7.3	84^{A}	4.0^{C}	135^{B}	252^{BC}
9	18.3^{A}	7.5	37^{B}	7.5	84^{A}	2.6^{AC}	116^{B}	223^{B}
10	21.0^{B}	6.8	35^{B}	7.9	89^{C}	5.3^{BC}	80^{C}	215^{B}
11	21.9^{C}	7.8	37^{B}	7.5	86^{BC}	4.3^{C}	38^{A}	256^{BC}

T temperature, *SC* specific conductance, *DO* dissolved oxygen, *Sat. DO* saturation of dissolved oxygen, *SRP* soluble reactive phosphorus

Differences tested by one-way ANOVA followed by the Tukey HSD tests (similar letters indicate no statistical difference at $p<0.05$). ANOVAs for pH and DO were not significant ($p>0.05$)

toward river mouth whereas SC values were highest between stations 4 and 7), as well as in DO saturation (highest values at stations 7, 10, and 11; Table 2; one-way ANOVA followed by Tukey HSD test, $p<0.05$). Concentrations of DO as well as pH values showed no significant differences among stations during the dry season (Table 2; one-way ANOVA followed by Tukey HSD test, $p>0.05$). During the dry season, NO_3 + NO_2-N showed higher concentrations in midcatchment stations (stations 3 to 7) than in headwater or river mouth stations (Table 2; one-way ANOVA followed by Tukey HSD test, $p<0.05$). Ammonium concentration was highest at stations located downstream of urban centers, such as stations 2, 3, and 7 (Table 2; one-way ANOVA followed by Tukey HSD test, $p<0.05$). Concentration of SRP was highest at stations 2 and 9 (Table 2; one-way ANOVA followed by Tukey HSD test, $p<0.05$). Similarly to the patterns observed in the dry season, temperature values increased toward river mouth, and saturation of DO was highest at stations 2, 3, 10, and 11 in the rainy season (Table 3; one-way ANOVA followed by Tukey HSD test, $p<0.05$). Midcatchment river stations (stations 4 to 7) had generally higher SC values than the headwater station or the river mouth (Table 3; one-way ANOVA followed by Tukey HSD test, $p<0.05$). During the rainy season, no significant differences in pH and DO were found among stations. In general, nutrient concentrations were highest at midcatchment stations of the river (e.g., stations 4 to 7 for NO_3 + NO_2-N and stations 3 to 9 for NH_4-N) and decreased toward the river mouth during the rainy season (Table 3; one-way ANOVA followed by Tukey HSD test, $p<0.05$).

Despite its small contribution to total catchment land cover (Table 1), urban land use was positively correlated to NO_3 + NO_2-N concentrations (Spearman rank correlation, $r=0.53$, $p<0.05$), dissolved inorganic nitrogen (DIN; $r=0.59$, $p<0.05$), the percentage of silt in sediments ($r=0.55$, $p<0.05$) and the structural integrity score ($r=0.51$, $p<0.05$), and negatively correlated to the percentage of pebble in sediments ($r=-0.38$, $p<0.05$) during the dry season. During the rainy season, urban land use was correlated to pH ($r=0.45$, $p<0.05$), specific conductance ($r=0.39$, $p<0.05$), and the structural integrity score ($r=0.51$, $p<0.05$). In the PCA run for the dry season,

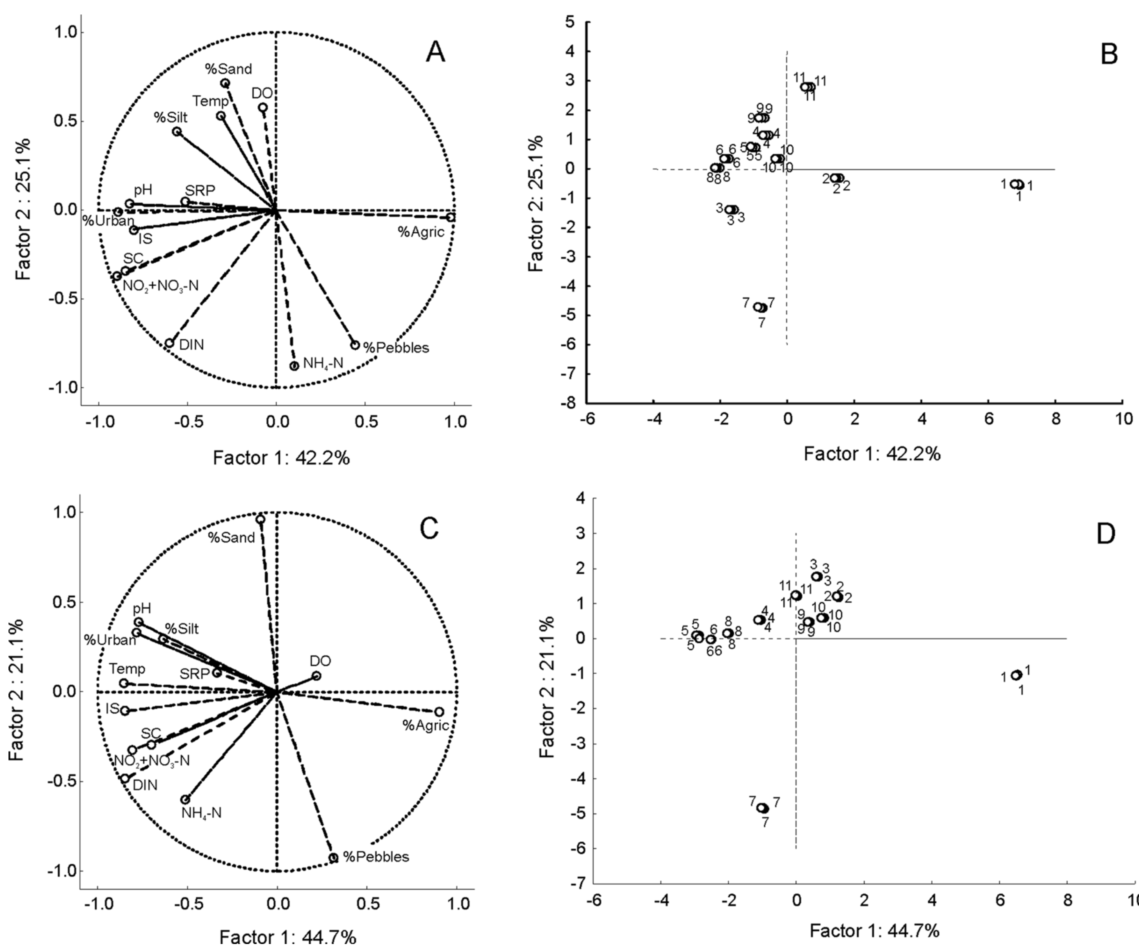

Fig. 1 PCAs identifying longitudinal distribution of environmental variables, including total subcatchment land cover upstream of each sampling station (% Agric., % Urban), water quality (temperature, pH, SC, DO, concentration of SRP, and nitrogen nutrients), sediment structure (% sand, peebles, and silt) and habitat structural integrity (IS) during the dry (**a**) and the rainy season (**c**), as well as the distribution of the 11 sampling stations along the PCA axes during the dry (**b**) and the rainy season (**d**)

percentages of urban area as well as NO_2 + NO_3-N, habitat integrity score (IS), and specific conductance (SC) were negatively correlated to the first axis, whereas the percentage of agricultural area was positively correlated to this axis (Fig. 1a, Table 4). The concentration of NH_4-N and the percentage of pebble in sediments were negatively, and the percentage of sand was positively correlated to the second axis (Fig. 1a, Table 4). According to the PCA, the headwater station was separated from the other stations on the first PCA axis, and station 7 was separated on the second PCA axis (Fig. 1b). The PCA run for the rainy season showed a pattern very similar to that observed for the dry season, with minor differences in the axis associations of DO and NH_4-N (Fig. 1d).

Temporal and spatial patterns in benthic invertebrate D, BM, and IP

The benthic invertebrate community exhibited a similar taxa composition in both sampling seasons. Thirty-one taxa were identified in the dry season, and 29 taxa were identified in the rainy season. Twenty-three taxa were found in both seasons (Table S1). Thus, a total of 37 taxa were identified in the Rio das Mortes. In terms of density (D) and instantaneous production (IP), Chironomidae were most important in both seasons, followed by Oligochaeta (Table S1). As for biomass (BM), Chironomidae had the highest values in the dry season, followed by Oligochaeta (Table S1). In the rainy season, the highest biomass values were found for Oligochaeta, followed by Chironomidae (Table S1). Other taxa had sporadically high maximum values, in one or only a few stations, generally at the headwater station, or at midcatchment stations 7 to 9 (e.g., Hydropsychidae, Gomphidae, and Bivalvia; Table S1).

Total mean D and IP values, but not BM, differed significantly between the dry and the rainy season (Mann-Whitney U test, $p<0.05$), with higher values in the dry season (Fig. 2). During the dry season, D ranged from 844 to 22,044 ind. m^{-2} and BM ranged from 115 to 2140 mg DM m^{-2} (Fig. 2a). During the dry season, mean site IP ranged from 9 to 150 mg DM m^{-2} day^{-1} (Fig. 2a). During the rainy season, D ranged from 0 to 7467 ind. m^{-2} and BM ranged from 0 to 1515 mg DM m^{-2} (Fig. 2b). During the rainy season, IP ranged from 0 to 68.4 mg DM m^{-2} day^{-1} (Fig. 2b). No significant differences in total D, BM, and IP could be detected among sampling stations in both seasons (Fig. 2a, b; one-way ANOVA, $p>0.05$).

There were significant differences in the invertebrate community among sites (two-way nested ANOSIM, global $R=0.37$, 0.35, and 0.36 for density, biomass, and IP, respectively, all $p<0.001$) and between seasons (global $R=0.20$ $p<0.011$, $R=0.22$ $p<0.003$, and $R=0.21$ $p<0.004$ for density, biomass, and IP, respectively). According to indicator taxa analysis, stations 1 and 7 were significantly different from all other stations mainly because of higher D, B, and IP of Elmidae (Xenelmis) at the station 1, and Perlidae, Glossosomatidae, Leptophlebiidae (Thraulodes), and Bivalvia at station 7 (Table 5). Stations 1 and 7 also had higher D of Empididae and higher B and IP of Simuliidae. Seasonal differences were due to higher D, B, and IP of Progomphus and Leptohyphidae (Tricorythopsis) in the rainy season, and Baetidae (Apobaetis) and Phyllocycla in the dry season (Table 5). High densities of Chironomidae were also typical for the dry season (Table 5).

According to stepwise distance-based RDA, only temperature and the percentage of sand in sediments were positively correlated to the observed differences in benthic community density ($R^2=0.28$), biomass ($R^2=0.27$), and IP ($R^2=0.29$) (Fig. 3, all $p<0.05$). All three invertebrate community variables showed similar tendencies according to the dbRDA and were similarly correlated to the same environmental variables, i.e., temperature and percentage of sandy sediment (Fig. 3).

Table 4 Results of the PCAs on habitat characteristics run separately for the dry and the rainy season (only scores >0.7 shown)

	Dry season		Rainy season	
	first axis	second axis	first axis	second axis
Variables contribution (scores-correlation matrix)	%Agric. (0.99)	NH_4-N (−0.88)	%Agric. (0.90)	%Sand (0.96)
	% Urban (-0.87)	% Pebbles (-0.76)	Temp (-0.85)	% Pebbles (-0.93)
	IS (-0.80)	% Sand (0.71)	IS (-0.84)	
	NO_3+NO_2-N (-0.89)		DIN (-0.84)	
	SC (-0.85)		% Urban (-0.78)	
Eigenvalue	5.91	3.52	6.26	2.96
Extracted variation (%)	42.2	25.1	44.7	21.1
Cumulative extracted variation (%)	42.2	67.3	44.7	65.8

IS river habitat integrity score, *SC* specific conductance, *Temp* temperature, *DIN* dissolved inorganic nitrogen

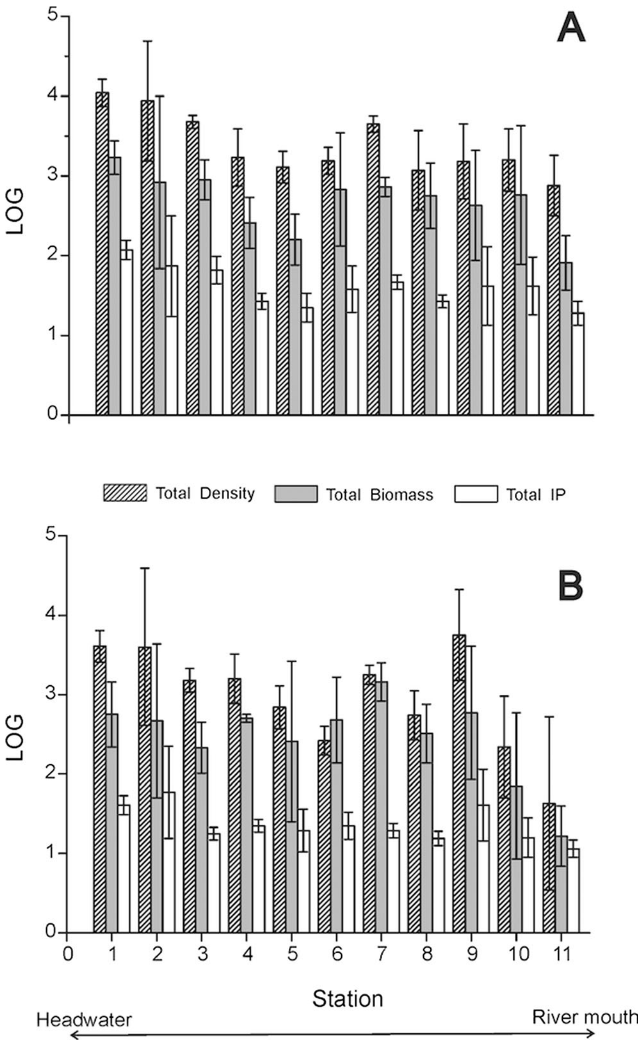

Fig. 2 Longitudinal variation in log-transformed total density (D, ind. m^{-2}), biomass (BM, mg DM m^{-2}), and instantaneous secondary production (IP, mg DM m^{-2} day^{-1}) of benthic invertebrates at the 11 stations in the Rio das Mortes (mean ± 1 SD) during the dry (**a**) and the rainy (**b**) season

Discussion

Catchment land cover, sediment structure, structural integrity, and water quality

Urban and agricultural land use affected the spatial variability in habitat variables and water quality in the Rio das Mortes. Urbanization is among the main threats to stream and river ecosystems around the world (Elmore and Kaushal 2008). Despite its generally low land cover in the Rio das Mortes catchment, urbanization was positively associated to both water quality and habitat structural integrity. Water quality and habitat integrity deteriorated toward midcatchment river stations, and the proximity to urban centers may help to understand the observed spatial patterns. For instance, ammonium concentrations were especially high downstream of urban centers, probably as a result of raw sewage discharge. Urban land cover was positively correlated to DIN and to the habitat integrity score in the present study, as well as to fatty acid indicators of sewage in the suspended organic matter of the Rio das Mortes in a previous study (Boëchat et al. 2014). In headwater streams of the Rio das Mortes catchment, small fractions of urban land cover (<8.3 % of total subcatchment area) increased stream ecosystem respiration, but diminished leaf decomposition rates (Silva-Junior et al. 2014). Thus, despite the larger areas of pasture and agriculture in continental Brazil, urbanization may be similarly or even more deleterious to water quality and ecosystem functioning of running waters than agriculture, a fact already well-established for temperate catchments (Paul and Meyer 2001).

Agricultural areas dominated the landscape of the Rio das Mortes catchment, but water quality variables and habitat structural integrity improved with higher percentages of agricultural land use. The headwater station, which was expected to serve as a reference station in our experimental design, was surrounded by agricultural land and already presented substantial degradation, both in water quality and habitat structural integrity. In such a high degradation scenario, from the headwaters to the river mouth, water quality variables and habitat structure may be insufficient to indicate strategic hotspots for management, and benthic community structure and function may be important additional ecological indicators for restoration purposes (Holt and Miller 2011).

Temporal and spatial patterns in D, BM and IP and land-use impacts

Regarding seasonal effects on benthic invertebrate variables, both the ANOSIM and the dbRDA clearly showed differences on invertebrates D, B, and IP between seasons. In the dry, cold season, water temperatures were 3–5 °C lower than in the rainy warm season. Temperature is a key factor affecting density and biomass of benthic invertebrates, as it directly affects hatching, growth, life cycle patterns, and trophic interactions (Allan 2004), but it is also an important component associated to bioenergetics and metabolic rates (Sweeney 1978), causing important deviations in allometric relationships, according to the metabolic theory of ecology (MTE, Brown et al. 2004). According to the MTE, under high temperatures, populations tend to exhibit higher densities of individuals, but individuals tend to be smaller. For instance, individuals of the mayfly *Ephemerella dorothea* emerging from cool tributaries of a US headwater stream had nearly twice the mass of those emerging from a warm tributary (Vannote and Sweeney 1980).

The dbRDA pointed to a seasonal effect of water temperature on benthic invertebrate D, B, and IP; however, temperature was the only strongly seasonal variable included in our model. Thus, temperature may be a proxy for other seasonal

Table 5 Single taxa (indicator values, $p<0.05$, are given in parentheses) significantly affected by seasonality or sampling station in the Rio das Mortes, according to ANOSIM and indicator taxa analysis performed separately for D, B, and IP

Season	Density (D)	Biomass (B)	Instantaneous secondary production (IP)
Dry season	Chironomidae not Tanypodinae (0.85), Tanypodinae (0.64), Apobaetis (0.55), Phyllocycla (0.46)	Apobaetis (0.55), Phyllocycla (0.46)	Apobaetis (0.55), Phyllocycla (0.46)
Rainy season	Progomphus (0.48), Tricorythopsis (0.40)	Progomphus (0.48), Tricorythopsis (0.41)	Progomphus (0.48), Tricorythopsis (0.41)
Sampling stations			
1	Xenelmis (0.68)	Xenelmis (0.69)	Xenelmis (0.70)
7	Perlidae (0.82), Glossosomatidae (0.80), Thraulodes (0.78), Bivalvia (0.76)	Perlidae (0.82), Glossosomatidae (0.80), Thraulodes (0.79), Bivalvia (0.72)	Perlidae (0.82), Glossosomatidae (0.80), Thraulodes (0.79), Bivalvia (0.75)
1, 7	Empididae (0.60)	Empididae (0.58), Simuliidae (0.58)	Simuliidae (0.58)
1, 8	Hexacylloepus (0.65)	Hexacylloepus (0.72)	Hexacylloepus (0.69)
1, 2, 4, 9	Ceratopogonidae (0.74)	Ceratopogonidae (0.77)	Ceratopogonidae (0.77)
1, 3, 7, 8, 9	Acerpena + Americabaetis (0.67)	Acerpena + Americabaetis (0.68)	Acerpena + Americabaetis (0.68)

effects in our study. Especially in tropical river systems, additional seasonal features associated to the dry or rainy season are likely to affect benthic invertebrate occurrence and distribution (Jacobsen et al. 2008). For example, hydraulic stress caused by frequent flash flood events in the warm rainy period (Dudgeon 2000), as well as higher water column and sediment stability in the colder, dry period (Cressa 1998; Maldonado et al. 2001) have to be considered as additional or alternative causes of the differences observed in benthic invertebrate variables in the Rio das Mortes.

Larger rivers are less subjected to temperature variation, due to their greater volume, although temperature differences between headwater and middle reach stations can be expected as a result of longitudinal patterns in shading and groundwater influence (Allan 2004). In our study, within season longitudinal variability in water temperature was small and may thus also not be an important determinant of the observed longitudinal patterns in invertebrate D, BM, and IP. In our study, sampling stations 1 and 7 differed from all other stations in both structural (density, biomass) and functional (IP) characteristics of the invertebrate community. Local sediment characteristics, i.e., the percentage of sandy sediment, clearly separated these stations from all other sampling stations in the Rio das Mortes. Moreover, sediment structure was the only environmental variable that was related to the spatial distribution of the invertebrate community. Interestingly, sampling station 7 also had one of the highest percentages of urban land use in the catchment, a habitat integrity score of 6 (highly disturbed), high nutrient concentrations, but a sediment structure composed completely of pebbles. These results support findings that overall water quality and habitat quality were impacted throughout the catchment and specific local habitat variables (i.e., sediment structure) represented the only important determinant of the benthic invertebrate community. Local variation in habitat heterogeneity creates patchy environments and allows invertebrate populations to select patches with better features, thus affecting spatial distribution and production (Godbold et al. 2011). A recent study showed that both structural and functional features of benthic invertebrate communities in temperate streams are affected by sediment composition, with lower diversity and abundance associated with increasing contribution of sandy sediment (Larsen et al. 2011). Sandy sediments are a key feature of larger rivers (Wantzen et al. 2014) and could be a major determinant of benthic community structure and functioning in these systems.

Contrary to our hypothesis, no direct effect of land use, water quality, or habitat structural integrity on benthic invertebrate variables was observed. Nevertheless, impacts of bank erosion and riparian clear cutting can cause increased sediment transport and alterations of the sediment structure in downstream river sections (Wantzen and Mol 2013), suggesting that land use may have indirectly affected the benthic invertebrate community. Moreover, we expected that IP, as a functional characteristic of the invertebrate community, should provide complementary information to structural variables (D, BM) for assessing land use impacts in the investigated tropical catchment. However, D, BM, and IP were similarly affected by sediment structure and by seasonality in our study, and IP did not contribute a single additional indicator taxon to our analysis. In a recent study carried out in the Paraná river floodplain in Argentina, biomass and annual secondary production of benthic invertebrates were also similarly affected by river connectivity, substrate structure, and water transparency (Zilli 2013).

A major problem for the evaluation of land use impacts on the Rio das Mortes, and probably also for many other tropical rivers in developing countries, is the absence of true reference conditions. The Rio das Mortes exhibited substantial human impacts on water quality, e.g., in comparison with regional reference conditions for low-order streams (Fonseca et al.

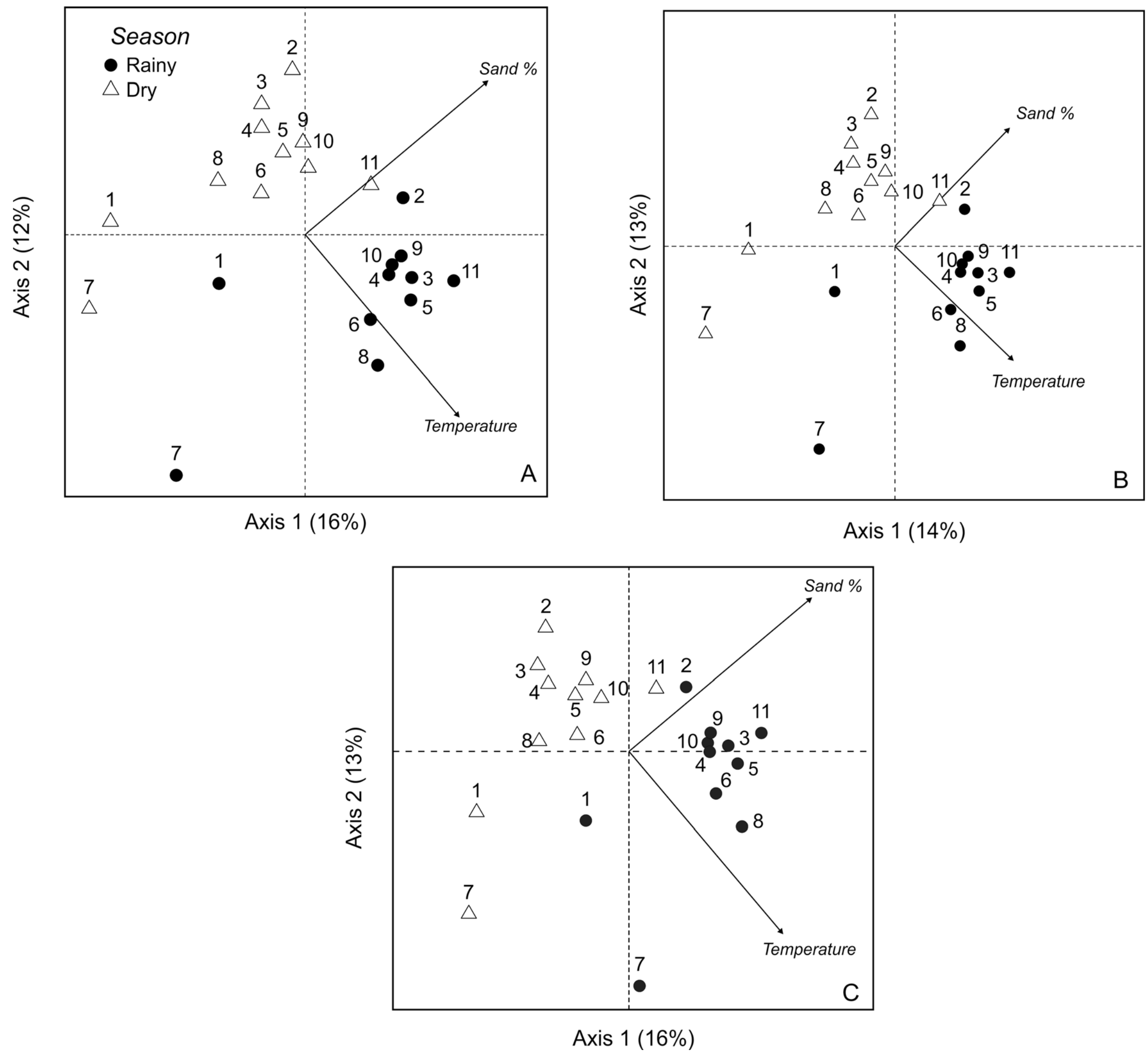

Fig. 3 Distance-based RDA performed to identify environmental variables explaining seasonal and spatial differences in benthic community density (**a**), biomass (**b**), and instantaneous secondary production (**c**) in the Rio das Mortes

2014), and habitat integrity from its headwaters to the river mouth. The high percentage of agricultural areas around the headwater station has possibly contributed to the already impacted condition of this station that was expected to be a local reference site. Accordingly, it was not possible to find direct relationships between catchment-scale land use change and the investigated benthic invertebrate community variables. Seasonality and local sediment structure affected the invertebrate community structure of the Rio das Mortes, and stations rich in pebbled sediment and low in sand were associated with higher IP, D, and B of a larger number of taxa than sand dominated stations.

One of the major present-day challenges for ecologists is to understand how land use alterations affect community structure, diversity, and ecosystem processes, as well as to understand the links between communities and ecosystem functioning. Ecosystem processes have increasingly gained attention as important indicators of human impacts, both in temperate and tropical freshwater systems (Woodward 2009; Bunn et al. 1999; Clapcott et al. 2010; Silva-Junior et al. 2014). Structural and functional features of benthic invertebrate communities have been used to assess land use impacts on rivers and streams (Lenat and Crawford 1994) and are expected to provide complementary information. Whereas changes in community structural features are closely related to adaptation processes of organisms to local environmental conditions, secondary production may be an interesting indicator of functional responses of populations or communities to a broader set of environmental stressors, such as eutrophication, chemical contaminants, climate change, non-native species invasion, among others (Whiles and Wallace 1995; Cardoso et al. 2008; Sousa et al. 2008; Dolbeth et al. 2011). In a long-term study in estuarine sites, the years with the highest density or biomass values not necessarily were the years with the highest secondary production and vice versa (Dolbeth et al. 2007), and thus, structure and function may exhibit opposing patterns. Accordingly, combined approaches including both community structural and process-based, functional variables appear to be a promising way to evaluate land use impacts on river benthic communities.

Conclusions

In our study, taxon density, biomass, and IP differed similarly among sampling stations along the river and between seasons, suggesting that these invertebrate metrics had the same bioindication potential in the high-impact scenario encountered in the tropical Rio das Mortes. More resolved assessments of secondary production, such as complete multi-year assessments of annual secondary production, might provide additional information on invertebrate community functioning and its relation to land use in tropical catchments. Our study also suggests that the consistently high degradation status of the investigated river from its headwaters to its mouth—a typical scenario for many tropical catchments—weakened relationships between invertebrate community metrics and specific land use impacts, and that only local habitat characteristics and seasonality exerted effects in the encountered high-impact scenario. Our study suggests that large-scale melioration of water and especially habitat quality, i.e., catchment-wide sewage treatment and erosion prevention, are necessary to achieve notable restoration effects on benthic invertebrate communities in the studied tropical catchment.

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