

The influence of physical instream spatial variability on Chironomidae (Diptera) assemblages in Neotropical streams



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ABSTRACT

In this study, the Chironomidae assemblages were studied in order to test the following hypotheses: a) mesohabitat type and substrate complexity affect the richness, abundance, and composition of the fauna; b) mesohabitat type is a good predictor for Chironomidae composition. To test the hypotheses, experiments were carried out in two mesohabitats (riffle and pool) using two substrate complexities (high and low) in 12 streams from Central Brazil. The mesohabitat type and substrate complexity did not affect the richness and abundance of the local fauna. The mesohabitat affected the faunistic composition. The assemblages of riffles and pools were distinct. Indicator Species Analysis showed that *Paratendipes* sp., *Polypedilum* sp. 2, *Pentaneura* sp., *Rheotanytarsus* sp. 1, *Corynoneura* sp. 2, *Cricotopus* sp. 2, *Lopescladius* sp., *Nanocladius* sp. 2, *Parametriocnemus* sp., and *Thienemanniella* sp. had preference for riffles and *Chironomus* sp., *Ablabesmyia* sp. 1, *Ablabesmyia* sp. 2, *Djalmabatista* sp., *Fittkauimyia* sp., and *Labrundinia* sp. for pools. Our results highlight the importance of physical instream variability on fauna structure, suggesting that habitat homogenization due to anthropic action may cause drastic effects on the diversity of chironomids and, probably, other benthic macroinvertebrates. Therefore, maintaining instream morphology, including the different mesohabitats, is fundamental for biodiversity conservation in streams.

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1. Introduction

Streams are ecosystems with high spatial variability on different scales, creating mosaics with different environment conditions and resource availability. This variability is responsible for spatial variation of abundance and high alpha and beta diversity in these ecosystems (Taniguchi and Tokeshi, 2004; Clarke et al., 2008; Costa and Melo, 2008). Therefore, understanding the influence of environmental variability on stream biota is critical to understand the ecological processes that determine the biodiversity in these ecosystems.

High instream spatial variability can be observed in meso and microhabitat scales (Frissell et al., 1986; Pardo and Armitage, 1997). This variability affects biotic structure and ecological dynamics in streams (Pardo and Armitage, 1997; Brooks et al., 2005; Ortiz et al., 2006; Brown, 2007; Costa and Melo, 2008). A simple visual inspection of these ecosystems allows to identify many mesohabitats

(Pardo and Armitage, 1997), among these, riffles and pools. Riffles are erosive habitats with predominance of rock and gravel sediment beds, characterized by rapid, turbulent, and irregular water currents. On the other hand, pools have low water velocity and are deposition habitats with organic debris, sand, and fine sediment. Due to the great environmental differences between these two mesohabitats, their faunal assemblages generally are also different. Thus, many studies indicate that mesohabitat types can be a good predictor of stream macroinvertebrate fauna (Pardo and Armitage, 1997; Buss et al., 2004; Silveira et al., 2006; Crisci-Bispo et al., 2007).

Inside each mesohabitat, the specific substrate characteristics also affect aquatic macroinvertebrate assemblages. For example, type, localization, presence of refuges, and substrate complexity influence the role of predation, faunal composition, body size, species richness, and abundance of aquatic macroinvertebrates (Dudgeon, 1996; Lancaster, 1996; Taniguchi et al., 2003; Taniguchi and Tokeshi, 2004; Gibbins et al., 2005; Costa and Melo, 2008; Thomaz et al., 2008). Thus, the experimental manipulation of substrate characteristics, such as the substrate complexity, has been used to understand their effects on macroinvertebrate assemblages (Taniguchi et al., 2003; Taniguchi and Tokeshi, 2004).

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Riffle substrates are composed of different size rocks, which create interstitial spaces with distinct sizes and a complex mosaic of water currents. On the other hand, pool substrates are composed of fine and coarse organic deposits as well as soft inorganic sediments. Thus, on riffles, substrate and hydraulic conditions are apparently more complex than on pools, which could explain the greater fauna diversity in riffle mesohabitats often observed in streams (Buss et al., 2004; Brooks et al., 2005). However, riffle and pool substrates present distinct natures; thus, this factor requires control. One way to solve this question is to make experimental studies manipulating the substrate characteristics in both mesohabitats. Our experiment was based on the premises that substrate complexity may affect the aquatic macroinvertebrates (Taniguchi et al., 2003; Taniguchi and Tokeshi, 2004) and that it is possible to manipulate the complexity by the disposition of particles with different shapes and sizes, mimicking the natural substrate of the stream.

The Chironomidae family distinguishes itself from other freshwater macroinvertebrates regarding high richness (Ferrington, 2008) and a wide range of feeding behaviors represented by predators, detritivores, and filterers, in addition to leaf, wood, and fruit miners (Berg, 1995; Trivinho-Strixino and Strixino, 1995; Nessimian and Sanseverino, 1998). Another characteristic is its wide geographic distribution and different preferences for specific microhabitats (e.g. litter, fine sediment, rocks, mosses, macrophytes among others) (Sanseverino and Nessimian, 1998, 2001; Sodr e et al., 2010). High diversity and fast colonization of Chironomidae make them an ideal faunal group for testing ecological theories using an experimental approach. Thus, the Chironomidae family was used to evaluate the following hypotheses on the role of physical instream variability for aquatic insects: 1) mesohabitat type and substrate complexity affect the taxa richness, abundance and composition of the fauna; 2) mesohabitat type is a good predictor for Chironomidae composition. These hypotheses were tested experimentally in two mesohabitats (riffle and pool), using substrates with two complexities (high and low) in streams from Central Brazil.

2. Materials and methods

2.1. Study area

This study was carried out during the dry season (August and September) in 12 streams (classified as first and second order according to Strahler, 1957) of municipalities of Ipor a, Ivol andia, and Amorin opolis, between 50°54' W 16°39' S and 51°3' W 16°40' S, in the Southwest region of Goi as State, Brazil (Fig. 1). This region presents Cerrado (Brazilian Savanna), a biome that comprises the headwaters of three important Brazilian hydrographic basins (Paran a, S o Francisco, and Amaz onica Basins). The seasonality is well defined with two periods: dry (May to October) and rainy (November to April).

2.2. Environmental characterization

The following environmental variables were recorded in the studied streams: water temperature ( C), current (m/s), discharge (m³/s), potential hydrogen (pH), electrical conductivity ( S/cm), dissolved oxygen (mg/l), and turbidity (NTU). The water current was measured using a current meter (Swoffer model 3000) and the discharge was calculated by multiplying water current average by stream section area (Lind, 1979). A multi-parameter probe (Horiba) was used to measure water temperature, pH, electric conductivity, and dissolved oxygen. Turbidity was measured with Hach probe (model 2100P). The characterization of studied mesohabitats of the streams is presented in Table 1.

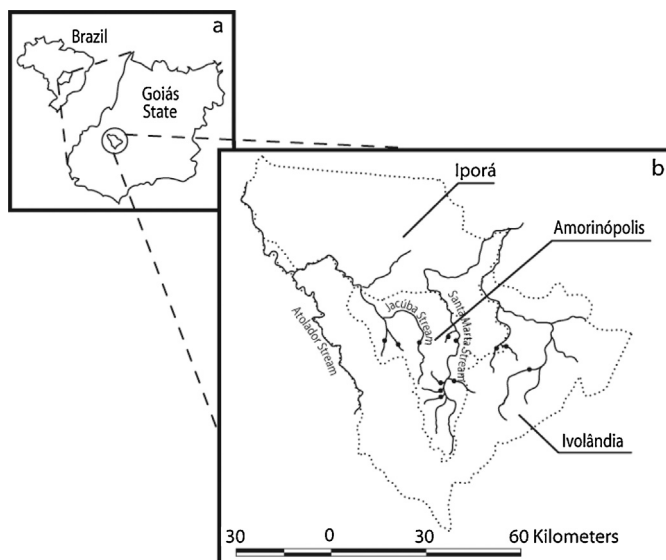


Fig. 1. a- Study region in the southwest of Goi as State, Brazil. b- Points marking the stations where the experiments were performed. Dotted lines delineate limits of Amorin opolis, Ipor a, and Ivol andia Municipalities.

Table 1

Means and standard deviations (sd) of physical-chemical variables measured in riffle and pool mesohabitats, and of discharge of 12 streams of Ipor a, Amorin opolis, and Ivol andia Municipalities, Goi as State, Brazil.

	Pool		Riffle	
	Mean	sd	Mean	sd
Dissolved oxygen (mg/l)	7.26	1.25	8.24	0.94
Turbidity NTU	7.33	5.47	5.08	1.88
pH	6.65	0.94	6.52	0.97
Temperature (�C)	23.79	2.44	23.8	2.35
Water current (m/s)	0	0	0.46	0.18
Electrical conductivity (�S/cm)	<6.0		<6.0	
	Mean	sd	Min	Max
Stream discharge (m ³ /s)	0.08	0.1	0.003	0.257

2.3. Experimental design

This experiment was carried out in riffles and pools of 12 streams. Riffle habitats had water currents greater than 0.255 m/s, and pools had absence of currents (considering the current meter used). Streams were used as blocks and substrates were put in one riffle, and in one pool on each stream. Two samplers were fixed in each mesohabitat, one with high and another with low complexity substrate. The position of samplers in relation to stream margins was selected randomly.

Samplers were composed by a substrate in trays with 228 cm² of basal area. To mimic natural substrate, different shapes and sizes of substrate particles were combined to create similar (low complexity) or distinct (high complexity) spaces. The low complexity substrate was composed by marbles (glass) (2 cm diameter) and two concrete plaques (13 × 3.5 × 1 cm) arranged in parallel to each other. The high complexity substrate was composed by two size marbles (2 and 4 cm diameter) and three concrete cylinders (4 cm height and 4 cm diameter) randomly arranged. The sum of marbles and concrete objects was similar in both treatments in order to exclude area bias in posterior statistical analyses. Marbles were sandblasted to make them rough prior to the experiment.

As Chironomidae larvae are fast colonizers, an exposure time of 20 days on the mesohabitats was considered enough (Carvalho and Uieda, 2004). After the colonization period, samplers were removed with the help of a D net (0.250 mm) to avoid organisms loss. In the

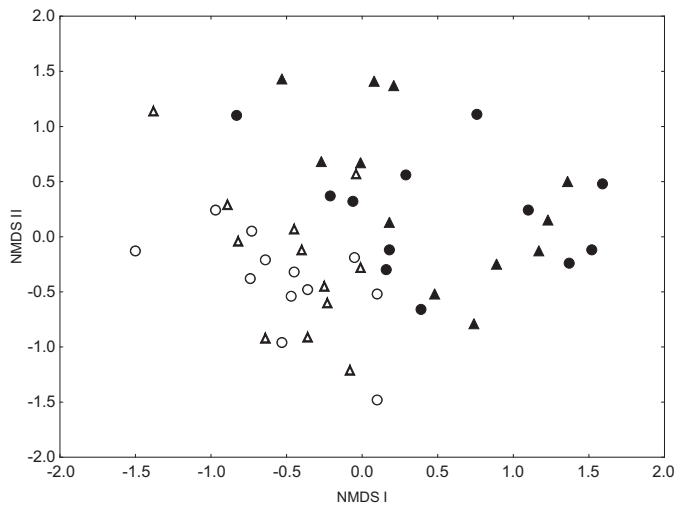


Fig. 2. Faunal composition ordination according to NMDS of Chironomidae assemblages collected in streams of Amorinópolis, Iporá, and Ivolândia Municipalities, Goiás State. Riffles and pools are represented by filled and empty symbols, respectively; low substrate complexity by triangles and high by dots. Stress = 0.15.

field, substrates were washed using a soft brush. The material was stored in jars and fixed in 4% formaldehyde solution. Chironomidae family individuals were mounted on semi-permanent slides using Hoyer, identified at a genus level and separated according to morphotypes, using the keys: [Wiederholm \(1983\)](#); and [Trivinho-Strixino and Strixino \(1995\)](#).

2.4. Data analysis

The data collected was assessed after logarithmization (base 10). We tested the effects of mesohabitat type and substrate complexity on richness (taxa number), abundance (number of individuals) and composition of the fauna. As the streams have different characteristics, we used an experimental randomized block design and each stream was considered a block ([Gotelli and Ellison, 2004](#)). As the number of collected individuals affects richness ([Gotelli and Graves, 1996](#)), this variable was assessed by a blocked ANCOVA using the streams as a block and abundance (log 10) as covariate. In this case, ANCOVA was used to control the effects of abundance on richness. A blocked ANOVA and a blocked PERMANOVA ([Gotelli and Ellison, 2004](#); [Anderson et al., 2008](#)) were used to test the effects of the mesohabitat (riffle and pool) and substrate complexity (high and low) on Chironomidae abundance and composition, respectively. Faunal composition was assessed using the NMDS (Non Metric Multidimensional Scaling) ([Legendre and Legendre, 1998](#)). Both PERMANOVA and NMDS were calculated based on a Bray-Curtis similarity matrix ([Legendre and Legendre, 1998](#)). The Indicator Species Analyses (ISA) ([Dufrene and Legendre, 1997](#)) was used to identify which taxa are associated with riffle or pool mesohabitats.

3. Results

A total of 4149 individuals was collected. The list of taxa is presented in [Table 2](#). The Chironomidae faunistic composition was affected by mesohabitat type, but not by substrate complexity (PERMANOVA, [Table 3](#)). On the other hand, richness and abundance were not influenced by mesohabitat type nor by substrate complexity ([Table 3](#)).

The assemblages of Chironomidae from riffle and pool mesohabitats were distinct according with NMDS ordination ([Fig. 2](#)). On the other hand, the assemblages were not distinct between high

Table 2

List of taxa and results of Indicator Species Analysis to riffle and pool mesohabitats in streams of Amorinópolis, Iporá, and Ivolândia Municipalities, Goiás State, Brazil. IV (indicator value); p (significance level) obtained by Monte Carlo test (5000 permutations). The bold values indicate statistical significance ($p < 0.05$).

Taxa	Mesohabitat	IV (%)	p
<i>Beardius</i> sp. 1	Pool	8.3	0.725
<i>Chironomini</i> sp.	Pool	23.1	0.198
<i>Chironomus</i> sp.	Pool	28.6	0.023
<i>Cryptochironomus</i> sp.	Pool	9.5	0.332
<i>Dicrotendipes</i> sp.	Riffle	8.3	0.506
<i>Endotribelos</i> sp.	Pool	4.2	1.000
<i>Fissimentum</i> sp.	Pool	4.2	1.000
<i>Pelomus</i> (?) sp. 1	Pool	12.5	0.223
<i>Pelomus</i> (?) sp. 2	Pool	4.2	1.000
<i>Pelomus</i> (?) sp. 3	Riffle	20.8	0.052
<i>Manoa</i> cf. sp.	Pool	8.3	0.491
<i>Nilothauma</i> sp.	Riffle	12.5	0.216
<i>Parachironomus</i> sp.	Pool	19.7	0.192
<i>Paratendipes</i> sp.	Riffle	33.2	0.002
<i>Phaenopsectra</i> sp.	Pool	35.9	0.544
<i>Polypedilum</i> sp. 1	Pool	36.7	0.275
<i>Polypedilum</i> sp. 2	Riffle	60.3	0.018
<i>Polypedilum</i> sp. 3	Riffle	15.6	0.368
<i>Pseudochironomus</i> (?) sp.	Pool	27.8	0.152
<i>Robackia</i> sp.	Riffle	4.2	1.000
<i>Stenochironomus</i> sp.	Riffle	32.1	0.146
<i>Zavreliella</i> sp.	Pool	4.2	1.000
<i>Ablabesmyia</i> sp. 1	Pool	52.4	0.006
<i>Ablabesmyia</i> sp. 2	Pool	71.7	0.001
<i>Coelotanyptus</i> sp.	Pool	8.3	0.477
<i>Denopelopia</i> sp.	Pool	4.2	1.000
<i>Djalmabatista</i> sp.	Pool	25	0.019
<i>Fittkauimyia</i> sp.	Pool	20.8	0.05
<i>Labrundinia</i> sp.	Pool	71.5	0.001
<i>Larsia</i> sp.	Riffle	13.4	0.883
<i>Macropelopia</i> sp.	Pool	4.2	1.000
<i>Pentaneura</i> sp.	Riffle	66	0.019
<i>Pentaneurini</i> sp.	Pool	4.2	1.000
<i>Caladomyia</i> sp. 1	Pool	24.8	0.206
<i>Caladomyia</i> sp. 2	Pool	45.5	0.200
<i>Caladomyia</i> sp. 3	Pool	4.2	1.000
<i>Caladomyia</i> sp. 4	Pool	51.4	0.354
<i>Rheotanytarsus</i> sp. 1	Riffle	77.5	0.001
<i>Rheotanytarsus</i> sp. 2	Riffle	18	0.160
<i>Stempellinella</i> sp.	Riffle	5.4	0.864
<i>Stempellina</i> sp.	Pool	4.2	1.000
<i>Tanytarsini</i> sp.	Pool	42.6	0.316
<i>Tanytarsus</i> sp. 1	Pool	2.1	1.000
<i>Tanytarsus</i> sp. 2	Pool	4.2	1.000
<i>Tanytarsus</i> sp. 3	Pool	4.2	1.000
<i>Corynoneura</i> sp. 1	Pool	13.9	0.555
<i>Corynoneura</i> sp. 2	Riffle	34.7	0.023
<i>Cricotopus</i> sp. 1	Riffle	4.2	1.000
<i>Cricotopus</i> sp. 2	Riffle	37	0.011
<i>Lopescladius</i> sp.	Riffle	25	0.028
<i>Nanocladius</i> sp. 1	Riffle	23.5	0.428
<i>Nanocladius</i> sp. 2	Riffle	25	0.021
<i>Onconeura</i> sp.	Riffle	28.6	0.064
<i>Parametrioctenus</i> sp.	Riffle	57.8	0.001
<i>Thienemanniella</i> sp.	Riffle	52.4	0.001

and low complexity substrates ([Fig. 2](#)). The Indicator Species Analyses showed that *Paratendipes* sp., *Polypedilum* sp. 2, *Pentaneura* sp., *Rheotanytarsus* sp. 1, *Corynoneura* sp. 2, *Cricotopus* sp. 2, *Lopescladius* sp., *Nanocladius* sp. 2, *Parametrioctenus* sp., and *Thienemanniella* sp. had preference for riffles and *Chironomus* sp., *Ablabesmyia* sp. 1, *Ablabesmyia* sp. 2, *Djalmabatista* sp., *Fittkauimyia* sp., and *Labrundinia* sp. for pools ([Table 2](#)).

4. Discussion

Streams show high spatial variability on different scales (hydrographic basin, segment, section, mesohabitat, and microhabitat) ([Frissell et al., 1986](#)) which affect aquatic macroinvertebrate assem-

Table 3

Results of the Blocked Analysis of Covariance testing substrate complexity (high and low complexities) and mesohabitat (riffles and pools) effects on Chironomidae richness (using abundance as covariate); and Blocked Analysis of Variance, and Blocked PERMANOVA testing substrate complexity and mesohabitat effects on abundance and faunal composition, respectively, in streams of Amorinópolis, Iporá, and Ivólândia Municipalities, Goiás State, Brazil. In the case of PERMANOVA, it was used 1000 permutations. The bold values indicate statistical significance ($p < 0.05$).

Factors	F	P
Blocked ANCOVA Richness		
Abundance (Log 10)	30.845	<0.001
Streams (Blocks)	1.405	0.218
Substrate complexity	0.209	0.651
Mesohabitat	0.148	0.703
Complexity*Mesohabitat	0.210	0.650
Blocked ANOVA Abundance		
Streams (Blocks)	15.131	<0.001
Substrate Complexity	0.205	0.653
Mesohabitat	1.991	0.165
Complexity*Mesohabitat	0.1	0.753
Blocked PERMANOVA		
Composition	Pseudo F	
Streams (Blocks)	2.749	0.001
Substrate complexity	0.836	0.592
Mesohabitat	9.073	0.001
Complexity*Mesohabitat	0.487	0.928

blages (Vison and Hawkins, 1998; Heino et al., 2004; Clarke et al., 2008). On small scale, environmental conditions and resources may drastically change in a few meters. Considering instream physical variability, riffles, and pools differ in hydraulic and substrate characteristics; two important variables that affect aquatic macroinvertebrates (Barmuta, 1990; Beisel et al., 2000; Boyero, 2003). The results of this study show a significant effect of mesohabitat type on Chironomidae composition, as well as literature (Sanseverino et al., 1998; Amorim et al., 2004). In addition, this study used the same artificial substrate composition (marbles and concrete) in both mesohabitats, which allows to assume that faunal differences among riffles and pools observed here are mainly due to: 1) proximity of the artificial substrate from the source of colonization of particular taxa of each mesohabitat; 2) differences in hydraulic characteristics of each mesohabitat. These two assumptions are supported by studies showing that the distance of the colonizing source (Mormul et al., 2011) and hydraulic variability (e.g. distinct water currents) (Barmuta, 1990; Boyero and Bailey, 2001) can play an important role in structuring the macroinvertebrate fauna.

The presence of distinct Chironomidae assemblages between the mesohabitats studied was confirmed. Among all recorded taxa (Table 2), 15 (28% of total) had preference by riffles (10) or by pools (5). Most taxa that preferred riffles were represented by Orthocladinae, as found by Sanseverino et al. (1998). Other taxa that preferred riffles were *Rheotanytarsus* sp., a genus generally associated to this habitat (Amorim et al., 2004), *Paratendipes* sp., *Polypedilum* sp. 2 and *Pentaneura* sp. On the other hand, except *Pentaneura* sp., Tanypodinae taxa preferred pools, as found by Roque and Trivinho-Strixino (2001). The mesohabitat type was considered a good predictor to approximately 30% of taxa collected.

Despite the effects of mesohabitat type on fauna, many abundant taxa were equally represented in both riffles and pools. Most Chironomidae are generalist feeding (Nessimian and Sanseverino, 1998) and commonly enter in drift (Callisto and Goulart, 2005; Hay et al., 2008), which suggest that redistribution of individuals in streams is common. Furthermore, we used similar substrate material in both mesohabitats. Thus, widespread occurrence of the most abundant taxa on both mesohabitats may be explained by the similar experimental substrate, generalist life strategies and the high redistribution capacity of Chironomidae.

The results of the present study also indicate that the assemblage traits (abundance, richness, and compositions) respond differently to different mesohabitats. Unlike composition, richness, and abundance were not distinct among riffles and pools. Streams normally present high macroinvertebrate abundance associated to riffles (Kikuchi and Uieda, 1998; Kobayashi and Kagaya, 2002; Buss et al., 2004; Rezende, 2007). On the other hand, in this paper, Chironomidae abundance was similar in both mesohabitats and differently than expected. The low importance of mesohabitats type on Chironomidae abundance may also be explained by similar experimental inorganic substrate, in which food resource and productivity are probably similar.

In relation to richness, some studies found higher values in riffles (Buss et al., 2004; Silveira et al., 2006). However, results of these studies may vary and the higher richness can change spatially and temporally between riffles and pools (see data from Baptista et al., 2001). Most studies aforementioned did not standardize richness by number of individuals; therefore, those results may be biased by abundance (see McCabe and Gotelli, 2000). Crisci-Bispo et al. (2007) found higher richness associated with riffles; however, when standardized by the same number of individuals, richness became similar in both mesohabitats. Several papers (Crisci-Bispo et al., 2007; Costa and Melo, 2008) and our results suggest that mesohabitat effects on richness are less significant than previously thought. Hence, differences in richness among mesohabitats detected in many studies may be amplified due to abundance bias. Thus, it is fundamental to adopt richness-standardized methods (see McCabe and Gotelli, 2000) in spatial and temporal comparisons.

Streams show high habitat complexity, including mesohabitats (e.g. riffles, and pools discretization) and microhabitats (e.g. fissures, gaps, holes, cavities, and roughness). The substrate complexity determines local diversity of macroinvertebrate fauna and other aquatic organisms (Taniguchi et al., 2003; Vieira et al., 2007). It may also influence organic particle deposition and algae establishment, and provide a large number of refuges and niches (Taniguchi and Tokeshi, 2004). On this view, complexity substrate has been used to explain the richness of lotic biota (Beisel et al., 2000; Taniguchi and Tokeshi, 2004). Shape, size, and position of stream bed rocks create interstitial spaces of different sizes and thus a variety of substrate complexity levels and hydraulic characteristics. Nevertheless, in our study, Chironomidae richness and abundance did not respond to complexity generated by the manipulation of shape and size of substrate particles. The high redistribution of Chironomidae, as suggest by high drift rates (Callisto and Goulard, 2005), could explain part of this result.

In summary, mesohabitat types affect Chironomidae faunal composition even considering the same substrate type and taxa with great redistribution capacity. Therefore, mesohabitat variability in streams provides different combinations of physical conditions and resources, enabling the establishment of taxa with different environment requirements, and increasing the diversity in streams. On the other hand, levels of substrate complexity created by the disposition of different size and shape of particles did not affect Chironomidae fauna. The high rates of redistribution and the complexity scales used in this study could explain this result. Our results, as well as the literature (Pardo and Armitage, 1997; Crisci-Bispo et al., 2007; Costa and Melo, 2008), highlight the importance of instream variability, at least on mesohabitat level, on biota, suggesting that habitat homogenization due to anthropic action may cause drastic effects on diversity of chironomids and, probably, of other benthic macroinvertebrates. Therefore, maintaining the stream physical structure, including the different mesohabitats, is fundamental for diversity conservation in these ecosystems.

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