RESEARCH PAPER

Hierarchical analysis of the diversity of Trichoptera in the headwaters of the Cuiabá River Basin, Brazil

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The purpose of this study was to describe the spatial distribution of Trichoptera larvae in an area of fragmented Cerrado. We used additive partitioning for evaluating the most representative scale in terms of beta diversity and identifying differences in the pattern of partitioning between land uses. Four hierarchical levels were considered (substrate type, stream, microbasin, and land use) in five partitions (entire community, common genera, rare genera, livestock activity (LA), and subsistence activity). The most representative scale for the entire community was microbasin ($\beta_3 = 25.71\%$), for rare genera it was land use ($\beta_4 = 37.5\%$) and for common genera it was type of substrate ($\beta_1 = 28.75\%$). The comparison among land uses showed that the presence of LA changed the pattern of the distribution of beta diversity.

Keywords:

Beta-diversity / Cerrado / Diversity partitioning / Livestock activity / Type of substrate

1 Introduction

The Biome Cerrado, a "biodiversity hotspot" (Myers et al., 2000), is the second most endangered Brazilian ecosystem after the Atlantic Forest (Mittermeier et al., 1999). In the State of Mato-Grosso, central Brazil, following the implementation of agriculture during the 1980s, monocultures of soy and pastureland began to dominate the rural landscape (Ratter et al., 1997). As a result, over half of the native vegetation has been fragmented (Klink and Machado, 2005) resulting in loss of habitat and becoming the greatest threat to the biodiversity of the savannah (Nespstad et al., 2002). Incorporated in this backdrop are the headwaters of the Paraguay River Basin, which drains the largest wetland on the planet, the Pantanal. The expansion in terms of replacing the original landscape increases the erosion problems that significantly affect the aquatic communities during the rainy season (Wantzen, 2006). Considering that these environments are extremely

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Abbreviations: LA, livestock activity; SA, subsistence activity

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vulnerable, the scarcity of studies on aquatic diversity is alarming because species extinction estimates in the region are poorly known (Ribeiro et al., 2007).

Efficient conservation strategies depend on the understanding of patterns and processes related to the spatial organization of species diversity (Gaston et al., 2001; Summerville et al., 2001). Allan (1975a) discusses the different approaches that consider partitioning of the components of diversity and tries to demonstrate in which dimension and scale variations occur. From there, the spatial patterns of aquatic diversity were examined as dependent on the scale of the observations under different circumstances. Local scales, such as the type of substrate and microhabitats a few centimeters to meters (Beisel et al., 1998), in considering mesoscales streams, and small watersheds included in some kilometers (Wantzen, 2003; Ligeiro et al., 2009) or even at regional scale considering the entire watershed of hundreds of kilometers (Townsend et al., 1997) demonstrating that the variability can be detected and quantified within any range of scales.

The organizational structure of aquatic communities is regulated by a series of "environmental filters" that operate within a hierarchy of spatial scales (Poff, 1997). First, the filters operate on a large scale to determine the regional species pools. Thus, local communities are composed of a set of species that were not retained through large-scale

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filters (Heino et al., 2007). Among the regional filters, there are the drainage area characteristics, which can determine the different annual levels of discharge (Callisto and Goulart, 2005), the land use that can cause the extinction of species (Parson et al., 2003; Weigel et al., 2003) and in addition, historical events that may restrict dispersion (Heino et al., 2003). Within the local filters, the heterogeneity of the substrate, usually defined by particle size and availability of organic matter, is directly related to the micro-distribution of communities of aquatic invertebrates (Huamantinco and Nessimian, 1999).

Additive diversity partitioning, proposed by Allan (1975b) and reviewed by Lande (1996), is an analytical approach that evaluates the species distribution pattern in hierarchically organized sampling systems. In general, this approach has been used to identify the spatial patterns of diversity, assessing the relative contribution of alpha-(within site) and beta-diversity (between sites) through different spatial scales. In the additive approach, gamma diversity is the sum of the alpha and beta components ($\gamma = \alpha + \beta_1 + \beta_2 + \beta_n \dots$), as reported by Lande (1996). The partition identifies which scale is the most relevant for species substitution and such information can provide subsidies for definition of priority areas for conservation (Bennett et al., 2006).

In this study, we have chosen to assess a community of the insect order Trichoptera due to its representativeness concerning species richness and functional diversity in trophic webs (Huryn and Wallace, 1988; Erös and Podani, 2009). In addition, these organisms are sensitive to environmental changes, and as such widely used to monitor aquatic systems (Bispo et al., 2004).

The aim of this study was to describe the distribution of Trichoptera larvae in streams in a fragmented landscape of the Cerrado. We considered four spatial scales and evaluated which one is most representative in terms of its beta-diversity of Trichoptera larvae. The hierarchical sampling was organized in the following form: local scales (substrate types and streams) and regional scales (microbasins and land use). In addition, we are going to offer solutions to the following questions: (i) What is the relative contribution of beta-diversity to regional diversity at each spatial scale? (ii) Is the representativeness at each spatial scale different for common and rare genera? (iii) Do livestock activity (LA) and subsistence activity (SA) land uses present different patterns of diversity partitioning?

2 Methods

2.1 Study area

This study was conducted in the dry season of 2008 in firstto third-order streams in the Upper Cuiabá River Basin

Trichoptera of Brazilian headwater streams



Figure 1. Sampled streams in Upper Cuiabá River Watershed, evidencing the land uses studied (LA) livestock activity and (SA) subsistence activity and their respective microbasin.

(Fig. 1). This region is located in the South Central area of the State of Mato Grosso, Brazil. The climate is high altitude tropical (Cwb), with well-marked dry (April– September) and wet (October–March) seasons. The annual mean air temperature ranges from 17 to 18.5°C and annual rainfall between 1450 and 1800 mm (Nimer, 1989). The sampling covered different land use patterns uses and five microbasins, which contribute to the formation of the Cuiabazinho and Casca Rivers, the main tributaries of the Cuiabá River (Zeilhofer et al., 2006).

The criteria for the selection of the microbasin and their streams were based on location to pre-defined land uses representative of the Upper Cuiabá River watershed and definitions of stream order and microbasin according to the National Program of Water Resources MMA (Ministério do Meio Ambiente, 2006).

We plotted the streams coupled on the Socioeconomic and Ecological Zoning of the Mato Grosso State (Mato Grosso/SEPLAN/CENEC, 2008). From this, we identified the type of predominant land use around each stream in order to identify land use on a larger scale. In the LA scale, are included two categories of the SEZ: (i) areas with agricultural activity, requiring environmental remediation, (ii) protected areas with partial presence of agricultural activity. On the scale, LA has two types of soils, sandstone and limestone. The second pattern was SA, which is designated a special management area category due to the high hydric potential. This pattern of land use is localized on low fertility soils derived from sandstone containing small areas previously converted into pasture (Table 1).

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Table 1. Streams sampled in the Upper Cuiabá River Basin indicating their location, substrate availability (cla, clay;
san, sand; ped, pebbles; rif, riffles; lea, leaves; shv, shore vegetation; sbv, submerged vegetation), microbasin,
landscape (LA, livestock activity; SA, subsistence activity), and geological formation

	Order	Location			Su	bstrate	Availa		Land use			
Stream		South	West	cla	san	ped	rif	lea	shv	sbv	Microbasin	Geological formations
Cuiabazinho	1st	14°21′31.8″	55°45′33.8″	0.09	0.83	0.15	0.12	1.35	0.00	0.05	Vaquejador	LA/sandstone
Aguaçuzinho	3rd	14°20′55.1″	55°34′08.8″	0.18	0.69	1.77	0.33	1.26	0.09	0.00	Vaquejador	LA/limestone
Marzagão	3rd	14°39′45.2″	5554'11.3"	0.15	1.13	1.95	3.59	0.29	0.11	0.00	Marzagão	LA/limestone
Ribeirão	1st	14°40′30.9″	55°41′55.6″	0.72	0.00	4.45	0.18	0.68	0.71	0.00	Marzagão	LA/limestone
Limoeiro	3rd	14°17′44.2″	55°14′44.3″	0.00	0.42	0.00	6.31	0.26	0.34	0.00	Cbá da Larga	LA/sandstone
Piúva	1st	14°23′27.5″	55°15′22.9″	0.00	0.00	0.81	4.10	0.21	0.32	0.00	Cbá da Larga	LA/sandstone
Pulador	1st	15°13′14.2″	55°33′44.6″	0.00	0.23	0.00	0.24	0.83	0.06	0.20	Casca	SA/sandstone
Descalvado	2rd	15°16′51.1″	55°29′05.6″	0.00	3.05	0.00	1.48	0.24	0.11	0.00	Casca	SA/sandstone
Cambará	1st	15°14′16.2″	05°31′47.2″	0.00	1.29	0.29	0.59	0.12	0.30	0.05	Casca	SA/sandstone
Cervo	2rd	15°04′16.9″	55°27′13.9″	0.00	2.40	0.00	1.17	1.34	0.32	0.00	Roncador	SA/sandstone
Cascalho	2rd	15°06′47.8″	55°21′46.6″	0.00	2.07	0.00	2.07	0.59	0.47	0.00	Roncador	SA/sandstone
Balanço	1st	15°12′50.8″	55°24′28.9″	0.00	1.22	0.00	0.00	0.00	0.15	1.43	Roncador	SA/sandstone

2.2 Experimental design

We performed a hierarchically nested sampling design, each corresponding to a different spatial scale. Four hierarchical levels comprised the nested design: substrate type, stream, microbasin, and land use (Fig. 2 and Table 1).



Figure 2. Relationship among spatial scales and the model of additive partitioning of the diversity in Upper Cuiabá River. Adapted from Gering et al. (2003).

The study was extended to include the mosaic formed by different types of substrates of each of the 12 streams into the 5 microbasins in the Upper Cuiabá River watershed. We selected 50 m of each stream in order to capture a greater variability of the substrates available. The substrate categories were based on Minshall (1984). The types of substrates were: clay, sand, pebbles, riffles, litter deposit, shore vegetation, and submersed vegetation (Table 1).

2.3 Trichoptera sampling

At each stream site, we sampled five transects of 10 m, cross-cutting the stream flow. Each substrate type was individually sampled using a Surber (0.125 mm mesh and sampled area of 0.093 m^2). The area of each substrate type sampled varied according to their transverse extent occupied in each transect (Table 1). Samples from the same type of substrate were combined totaling 49 samples. Caddisfly were identified to genera and to species where possible using specialized literature and with the help of experts.

2.4 Data analysis

We tested the null hypothesis that the Trichoptera community was randomly distributed across different spatial scales. A null model was used to create randomized distributions of the number of Trichoptera individuals at each spatial scale. Values obtained in field were compared with the corresponding distribution generated by the null model (Gering et al., 2003). Based on this test, we evaluated whether the observed richness was significantly different from that expected at random. This is a two-tailed test and we used a 10% significance-level threshold. The test can produce three different results: (i) a significant and

low richness estimate, when 95% or more of the randomized values are higher than the values observed (p > 0.95); (ii) a significant and high richness estimate, when <5% of the randomized values are higher than the values observed (p < 0.05); (iii) richness similar to that expected by our null model, when the percentage of the values obtained that are higher than the randomized ones are within 5 and 95%. The analyses were conducted using PARTITION (Veech and Crist, 2006).

To describe the Trichoptera spatial distribution, we carried out two models and five partitions. The first model was the regional partitioning of richness (regional distribution of richness = $\alpha + \beta_1 + \beta_2 + \beta_3 + \beta_4$), where α = mean richness in each substrate type; β_1 = difference among substrate types; β_2 = difference among streams; β_3 = difference among microbasin and β_4 = difference between land uses. In this model, we performed three partitions with different treatments. The treatments were: the entire community of Trichoptera, only common genera (abundance >0.5% of the total community) and rare genera (abundance <0.5%). The second model (richness distribution in land use = $\alpha + \beta_1 + \beta_2 + \beta_3$) was used to compare the richness partitioning pattern among different land uses LA and SA.

3 Results

We collected 1498 caddisfly larvae distributed into 10 families and 26 genera, considering that two morphospecies were distinguished in the genera Nectopsyche, two in Oecetis and one in the family Sericostomatidae, Genus A. Most genera were rare, 85.7% occurred at an abundance of <5%. The most abundant genera were Smicridea. (Hydropsychidae), comprising 35% of the individuals sampled and Nectopsyche (Leptoceridae) at 29.97%. The genera Macronema (Hydropsychidae) and Nectopsyche (Leptoceridae) was the most frequent genera collected, occurring in 11 of the 12 streams sampled (91.66%). Setotes and Synoestropsis occurred exclusively in limestone streams and Triplectides, Triaenodes, Oxyethira, and Atopsyche only in sandstone streams. The distribution of Setodes (Leptoceridae) and Genus A (Sericostomatidae) was restricted to streams categorized as LA land use, whereas Triplectides, Nectosyche sp3. (Leptoceridae) and Oxvethira sp. (Hvdroptilidae) only occurred in streams categorized as SA land use (Table 2). The richer stream was Ribeirão (15 genera). The streams with the lowest richness were Aguaçuzinho and Cambará, both with seven genera. The Casca microbasin showed the highest accumulated richness (19 genera) and Roncador microbasin showed the least (14 genera: Table 2).

Partitioning of the entire community showed only a small difference in the representation of the scales, where the microbasin scale ($\beta_{3 \text{ entire community}} 25.71\%; p > 0.05$)

represented the most. The results of the partitioning of rare genera showed that the scale of land use (β_4 rare genera 37.5%, p < 0.05) presents the largest portion of beta diversity, different from that observed for common genera where the substrate scale was the most important ($\alpha_{genera\ common\ }21.25\%,\ p < 0.05$ and $\beta_{1genera\ common\ }28.75\%\ p < 0.05$; Fig. 3). The comparison between different land uses showed that in LA land use the microbasin scale was the most representative ($\beta_{3\ LA}$ 38.8% p < 0.05) and in SA land use it was the stream scale ($\beta_{2\ SA}$ 42.17%; p < 0.05; Fig. 4; Table 3).

4 Discussion

Partitioning considering the entire community indicated that the representativeness of the beta diversity for local and regional scales showed a balanced distribution (Fig. 3). The diversity observed in the microbasin scale ($\beta_{3entire community}$ 27.5%) was lower than the estimated at randomization. This demonstrates that in this study the microbasin scale exhibited a larger heterogeneous environment, containing different levels of land use and types of geological formations at this scale. We suggest that those factors added together with geographical distance between microbasins can produce different species compositions of Trichoptera throughout the study region. Galbraith et al. (2008) studied the contribution of local and regional variables in structuring the community of Trichoptera in the Ouachita Mountain Rivers, USA. Their results showed a similar pattern to this study, where local habitat conditions and patterns of land use are equally important for predicting the Trichoptera community composition. However, we observed a strong interaction among local and regional factors, indicating the importance of biogeographic processes.

When rare and common genera are considered separately, the representativeness of the local scales (type of substrate and streams) and regional variables (microbasin and land use) are expressed differently (Fig. 3). For rare genera, the scale of land use was more representative (β_4 rare genera 37.5% p < 0.05) (Fig. 3), and the value of the diversity observed was higher than expected from randomization (Table 3). This indicates that the environmental differences between land use patterns affect the rare genera more than the common genera. We know that in the geological formations such as sandstones and limestones that occur in the study area, the physical and chemical characteristics of the water, especially the electrical conductivity, are influenced by the mineral matrix. We observed two genera that occurred exclusively in limestone streams (Setotes and Synoetrosis) and four in sandstone streams (Triplectides, Triaenodes, Oxyethira, and Atopsyche), but richness was considerably higher in

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Table 2. List of families and genera of the Trichoptera sampled in headwaters of the Cuiabá River Basin showing specific composition in streams, microbasin, and patterns of land use (LA) and (SA)

	Land use	Livestock activity (LA)							Subsistence activity (SA)						
	Microbasin	Vaquejador		Marzagao		CbaLarga		Casca			Roncador				
	Stream	Cuiabazinho	Aguaçuzinho	Ribeirão	Marzagao	Limoerio	Piuva	Pulador	Descalvado	Cambará	Cervo	Cascalho	Balanço		
Family	Genera														
Leptoceridae	Nectopsyche sp. Muller		Х	х	х	х	Х	х	Х	х	х	х	х		
	Nectopsyche sp.2 Muller				Х	Х									
	Oecetis sp. McLachlan	х	Х	Х	Х	Х		Х	х						
	Oecetis sp.2 McLachlan		Х	Х				Х					Х		
	Triplectides sp. Kolenati									Х	Х				
	Triaenodes sp. MacLachlan									Х					
	Setodes sp. Rambur		х												
Polycentropodidae	Cernotina sp. Ross			Х	Х	х		х		х	х		х		
	Polycentropus sp. Curtis	х	х												
	Polyplectropus sp. Ulmer	х	х	Х		х					х				
	Cyrnellus sp. Banks			х	Х	х		х							
Hydropsychidae	Macrostemum sp. Kolenati	х					Х	х	х		х		х		
	Macronema sp. Pictet	х	х	х	Х	х	Х	х	х	х	х	Х	х		
	Smicridea sp. McLahlan			х	Х	х	х	х	х		х	х	х		
	Leptonema sp. Guérin	х						х							
	Synoestropsis sp. Ulmer				Х										
Hydroptilidae	Neotrichia sp. Morton	х		Х	Х		х	х	х	х	х	х	х		
	Metrichia sp. Ross			Х					х						
	Oxvethira sp. Eaton								х		х				
	Hvdroptila sp. Dalman			х		х	х					х			
	Flintiella sp. Angrisano			х							х	х			
Sericostomatidae	Genus A	х		х	х										
Hvdrobiosidae	Atopsvche sp. Banks					х									
Ecnomidae	Austrotinodes sp. Schmid	х		х	х				х						
Odontoceridae	Marilia sp. Müller	х				х		х	х	х	х	х	х		
Helicopsvchidae	<i>Helicopsvche</i> sp. Sielbold			х	х	х	х		х		х		х		
Calamoceratidae	Phylloicus sp. Müller	х			х			х	х						
Philopotamidae	Wormaldia sp. McLachlan	х					х		х						
Accumulated richness (microbasin)		15		18		15		19			14				
Total riv	chness (streams)	12	7	15	10	10	9	10	10	7	10	7	٩		

sandstone streams (Table 3). However, in other studies conducted in the Cerrado it has not been possible to demonstrate the influence of the physical and chemical characteristics (e.g., conductivity) of water in predicting the composition of the Trichoptera community (Bispo and Oliveira, 1998; Oliveira and Bispo, 2001).

Another factor that may explain beta diversity of rare genera is the "isolation" and distance between the two areas (LA and SA) caused by the large expanse of land used for farming in around LA. This leads to a hypothesis of landscape divergence proposed by Laurence et al. (2007), which suggests that different landscapes tend to generate increasingly distinct compositions over time. Poole (2002) and Finn and Poff (2005) demonstrated that the discontinuity of the forest may limit the spread of invertebrate adults, producing isolation in the community. Other factors that may influence the distribution of genera is emergence of adults and stream characteristics. However, the



Figure 3. Percentage of Trichoptera richness at different scales: α_1 : mean of each substrate type; β_1 : difference among substrate types; β_2 : difference among streams; β_3 : difference among microbasin; β_4 : difference among land use.

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Figure 4. Comparison of Trichoptera partitioning between landscapes LA (livestock activity) and SA (subsistence activity); α_1 : mean of each substrate type; β_1 : difference among substrate types; β_2 : difference among streams; β_3 : difference among microbasin.

samples were taken in the dry season, which features stability, besides the fact that we did not observe large differences in stream richness between those of 1st and 3rd order (Tables 1 and 2).

In the partitioning of common genera, the greatest portion of the regional richness was assigned to the substrate scale ($\alpha_{\text{common genera}}$ 21.25% and $\beta_{1 \text{ common genera}}$ 28.75%) (Fig. 3),

Table 3. Results of the significance tests of the
richness estimates observed for richness of
the Trichoptera genera, realized in the
PARTITION program; where (+) indicates
significant and high values (p < 0.05), (-)
indicates significant and low values (p > 0.95),
and (ns) indicates not significant (p between
0.06 and 0.94)

Partitioning	Level	Result
Entire community	α	_
,	β1	_
	β_2	+
	β_3	+
	β_4	+
Rare genera	α	+
·	β_1	ns
	β_2	ns
	β_3	_
	β_4	+
Commom genera	α	+
	β_1	+
	β_2	—
	β_3	_
	β_4	ns
Land use (LA)	α	—
	<i>β</i> 1	—
	β_2	+
	β_3	+
Land use (SA)	α	—
	<i>β</i> 1	ns
	β_2	+
	β_3	+

and the value of beta-diversity observed was higher than expected from randomization (Table 3). This result demonstrates that significant changes occur in the community structure among the types of substrate. Ligeiro et al. (2009), in using additive partitioning, also showed that beta-diversity of macroinvertebrates among habitats in streams depended on the type of substrate. Some studies have shown that there is a specialization of some genera of Trichoptera in respect to type of substrate (Fidelis et al., 2008), which can maximize differences in composition at this scale. Matthaei et al. (1996) demonstrated that an increase in flow during floods does not generally affect homogeneously the beds of the streams, there are types of substrates that are more protected, favoring the differentiation of the community structure at this scale.

Our partitioning analysis indicated that the land uses considered in this study resulted in different patterns of spatial distribution of richness. In land use LA, the microbasin scale ($\beta_{3 LA}$ 38.8%; Fig. 4) was the most representative and the value of the diversity observed was higher than expected from randomization (Table 3). The higher representativeness of the microbasin scale in LA demonstrates greater heterogeneity resulting from the different geological formations and levels of environmental changes in land use. Other factor is that the geographical distance between streams in land use LA is bigger than compared with land use SA (Fig. 1).

Land use SA presented small beta-diversity in the microbasin scale, which demonstrates the environment homogeneity in this scale. Beta-diversity among streams ($\beta_{2 SA}$ 42.17% p < 0.05) was a more representative scale in land use SA (Fig. 4), where the value observed was higher than expected from randomization (Table 3). On this scale, beta diversity is more associated with the orders of streams than land use. (Table 1). In land use SA, beta-diversity among the substrates was the only non-significant scale (Table 3), which may be related to the better environmental conditions of this land use. Strand and Merritt (1999) and Braccia and Voshell (2007) suggested that the absence of fine sediment input, typical of conserved areas, could

provide equivalent conditions to colonization in different substrate types, minimizing the differences in composition.

According to Poff (1997), environmental filters primarily act in regional and intermediate scales, restricting the distribution of some species, for subsequent action of local filters. The results of this study suggest that the microbasin scale operates as a preliminary filter, being also the most important, since this is representative and higher than expected from the randomization of all the partitions generated (β_3 entire community 25.71%; p > 0.05), of both common (β_3 common genera 24.38%; p > 0.05) and rare genera (β_3 rare genera 27.50%; p > 0.05).

In this study, we observed that the action of the local filter (type of substrate) is more influential on the most abundant organisms in the community (common genera).

Overall, our results demonstrated that the spatial distribution of Trichoptera richness in the Upper Cuiabá River is controlled by both regional and local filters, where scale of the microbasin is highlighted, reflecting both management-related features, as well as the geology of each microbasin. It is important to highlight that the influence of such filters is different when we analyzed the entire community and when we separated it into common (local scales more important) and rare genera (regional scales more important). Thus, we suggest that inventories of invertebrates seek to capture both, heterogeneity in the streams (types of substrates), prioritizing beta-diversity of the dominant genera at a local scale and heterogeneity of the landscape (land use and geology) adding to inventories of rare genera.

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