Influence of the riparian zone phytophysiognomies on the longitudinal distribution of fishes: evidence from a Brazilian savanna stream

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The structure and composition of a fish community in a tributary stream of the Aquidauana River, located in the plateau region of the Paraguay River basin, central west Brazil are described, with special attention to the differential effects of the phytophysiognomies of the Cerrado (a tropical savanna), which are predominant in riparian zones all along their longitudinal gradient. A total of 1,166 individuals belonging to 44 species were captured. Similarity analyses of composition and abundance showed two groups: upstream reaches (R1 and R2) and downstream reaches (R3, R4 and R5), which presented 85.8% of the average dissimilarity. Although physical habitat and physicochemical descriptors varied along the longitudinal gradient of the Correntes stream, shoreline vegetation was the most important environmental feature predicting fish structure and composition. The Mantel test revealed a correlation between shoreline vegetation structure and fish composition and quantitative structure of the fish community (R > 0.65; p < 0.04). This relationship is driven by the prevalence of species occupying microhabitats associated with shoreline vegetation in contact with water in upstream reaches. Structural differences in shoreline vegetation along the longitudinal gradient correspond to the phytophysiognomic dichotomy observed in the Correntes stream, where riparian vegetation is made up of wet grassland upstream and of gallery forest downstream; this reinforces the importance of the phytophysiognomic heterogeneity of the Cerrado in maintaining ichthyofauna diversity.

São descritas a estrutura e composição da comunidade de peixes em um riacho afluente do rio Aquidauana, localizado na região planáltica da bacia do rio Paraguai, centro-oeste do Brasil, com atenção especial aos efeitos diferenciais das fitofisionomias de Cerrado predominantes nas zonas ripárias ao longo do seu gradiente longitudinal. Foram capturados 1.166 indivíduos pertencentes a 44 espécies. As análises de similaridade com a composição e abundância evidenciaram dois grupos: os trechos a montante (R1 e R2) e trechos a jusante (R3, R4 e R5), os quais apresentaram 85,8% de dissimilaridade média. Embora os descritores físico-químicos e do habitat físico tenham variado ao longo do gradiente longitudinal do córrego Correntes, a vegetação marginal foi o componente ambiental mais importante predizendo a estrutura e composição da ictiofauna. O teste de Mantel revelou correlação entre a estrutura da vegetação marginal com a composição e estrutura quantitativa da comunidade de peixes (R > 0.65; p < 0.04). Essa relação é representada pela prevalência de espécies que exploram micro-habitats associados à vegetação marginal em contato com a água nos trechos a montante. As diferenças na estrutura da vegetação marginal ao longo do gradiente longitudinal correspondem à dicotomia fitofisionômica observada no córrego Correntes, cuja vegetação marginal é constituída de campos úmidos à montante e por fisionomias florestais nos trechos à jusante, reforçando a importância da heterogeneidade fitofisionomica do Cerrado brasileiro para a manutenção da diversidade ictiofaunística.

Key words: Paraguay basin, Cerrado, Longitudinal gradient, River continuum concept, Riparian forest.

Introduction

The upper Paraguay River basin is one of the most important basins in the Neotropics, occupying an area of approximately 363,442 km² in Brazilian territory. It can be divided into two distinct regions: a floodplain called the Pantanal which is one of largest wetland areas in the world and a plateau around the Pantanal, including areas with an altitude of over 200 m. These two regions are distinguished by geologic and geomorphologic

characteristics, but they are interdependent in ecological terms since headwaters of the most important rivers that supply the Pantanal are situated in the plateau region, providing high hydrologic connectivity (Willink *et al.*, 2000).

The plateau region is biologically distinct from the floodplain (Chernoff & Willink, 2000), and its ichthyofauna, as well as the factors that modulate it, is poorly known when compared to the accumulated scientific knowledge about the Pantanal region (Catella *et al.*, 1996; Súarez *et al.*, 2004; Britski

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et al., 2007). Knowledge is especially scarce for small fishes from streams, which make up the greatest proportion of fish species richness of the Neotropics (Castro, 1999).

Most of the Paraguay basin plateau streams flow into the Brazilian Cerrado (savanna) biome, which is a world biodiversity hotspot due to its richness, high degree of endemism and anthropogenic threat (Ratter *et al.*, 1997; Myers *et al.*, 2001). Vegetation in these areas is very heterogeneous, and riparian vegetation is one example of this variation, showing phytophysiognomies ranging from grassland to closed canopy (Ratter *et al.*, 1997; Ribeiro & Walter, 1998). Considering the strong predictive power of riparian vegetation in structuring stream fish communities (Wichert & Rapport, 1998; Growns *et al.*, 2003), it is plausible that the spatial distribution of fish species can be affected by alterations in the longitudinal variation of riparian vegetation structure in Cerrado streams.

The purpose of this study was to describe fish community structure and composition in a stream located in the plateau region of the Paraguay basin, central west Brazil, with special attention to the differential effects of the predominant Cerrado phytophysiognomy in riparian zones. In this stream, shoreline vegetation of the upstream reaches is formed by wet grassland, a phytophysiognomy characterized by the dominance of herbaceous species, while in downstream reaches gallery forest predominates.

Material and Methods

This study was carried out in the Correntes stream, a tributary on the left bank of the Aquidauana River (Fig. 1), located in Dois Irmãos do Buriti municipality, Mato Grosso do Sul State, central west Brazil, Paraguay basin. This stream is roughly 18.5 km in length and its catchment encompasses approximately 11,690 ha, where cattle pastures and eucalyptus plantations predominate. The region is located in the São Bento formation, represented by the Botucatu group. As to geomorphology, it belongs to the Maracaju plateau, a region characterized by plains topography and wide hills. The climate is wet mesothermal with a rainy summer (October to March) and a dry winter (April to September); annual precipitation ranges from 1,300 to 1,400 mm.

Five 100-m reaches were selected (R1-R5) along the longitudinal gradient of the Correntes stream (Table 1). The distance between each reach was 2.5 km, except between R4 and R5, where the distance was 5.2 km (Fig. 1). One sampling of the ichthyofauna was conducted in both the wet (February 2008) and dry seasons (September 2008). Fish were collected by use of a hand seine (2.5 m in width x 1.5 m in height, 3 mm mesh) and a dip net (0.9 m in width x 0.45 m in height, 3 mm mesh) during a period of 60 min. Fish were fixed in 10% formalin and afterward transferred to 70% EtOH. Voucher specimens were deposited in the fish collection at the Departamento de Zoologia e Botânica da Universidade Estadual Paulista (DZSJRP), São José do Rio Preto, São Paulo State, Brazil.

Eighteen habitat structure descriptors related to in-stream and shoreline physical structures were estimated visually

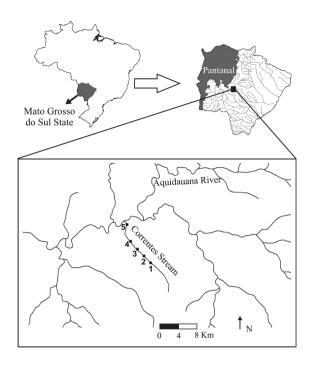


Fig. 1. Map showing localization of the sampled reaches of Correntes stream in the plateau region of the Paraguay basin, Mato Grosso do Sul State, Brazil.

along each reach in the wet and dry periods. These descriptors were divided into three categories related to shoreline vegetation structure, substrate composition and hydrological measurements. Descriptors related to shoreline vegetation comprise characteristics of shoreline vegetation in contact with the water as follows: proportion of shoreline occupied by grass, thin roots, large roots, bryophytes, pteridophytes, tree trunks, and bush leaves. Substrate composition was evaluated by estimating the proportion of bottom occupied by clay, sand, gravel, rock, algae, roots, litter, aquatic macrophytes and logs and branches. Hydrological descriptors included depth and width measurements obtained by means of transect measured along each reach. Additionally, a physicochemical analysis including measurement of dissolved oxygen, conductivity, pH, turbidity and temperature (all measured using electronic equipment, Horiba®, model U-10) was carried out. These analyses were only performed in the dry period due to operational problems with the equipment in the wet period.

Species diversity was calculated using the Shannon-Wiener index (H') as described by Magurran (2004), and species dominance was obtained using the Berger-Parker dominance index (where abundance of the dominant species is divided by the total abundance of the species, multiplied by 100). The spatial-temporal ordination of the reaches was evaluated by non-metric multidimensional scaling (NMDS) analysis, considering ichthyofauna composition and the quantitative structure of the community. This analysis resulted in stress values of 0.08 and 0.05, respectively, indicating good ordination and reliability of resulting interpretation (Clarke & Warwick, 2001). To complement the

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	Descriptors	Reach 1	Reach 2	Reach 3	Reach 4	Reach 5
(Coordinates	20°32'44.8"S	20°31'45.3"S	20°30'47.4"S	20°29'41.6"S	20°27'20.4"S
		55°21'56.1"W	55°22'53.1"W	55°23'47.3"W	55°24'46.6"W	55°25'16.8"W
	Altitude (m)	240	209	183	176	165
	Riparian phytophysiognomies*	wet grassland	wet grassland	gallery forest	gallery forest	gallery forest

run and pool

run and pool

run and pool

Table 1. Location and general characteristics of reaches (R1-R5) of the Correntes stream, central west Brazil. *sensu Ribeiro & Walter (1998).

ordination analysis, a two-way analysis of similarity (routine ANOSIM) was used to verify differences in the fish composition and quantitative structure of communities between rainy and dry seasons and between groupings determined by ordination analysis (NMDS). In order to investigate if spatial-temporal variation in the environmental descriptors had a pattern similar to fish abundance data, the same analysis was performed for shoreline vegetation structure, substrate composition and hydrological measurements. Additionally, a similarity percentage analysis (routine SIMPER) was applied to determine which species mainly explained differences in community composition between groupings established by NMDS.

Main mesohabitats

The relative importance of environmental descriptors (shoreline vegetation, substrate and hydrological measurements) structuring ichthyofauna in the Correntes stream was evaluated by 2Stage analysis. This analysis indicates which categories of the environmental descriptors are more correlated to biotic similarity matrices, calculating the rank correlation between all pairs of matrices. Afterward, the significance of the correlation between biotic and abiotic matrices was tested using the Mantel test in the Past software, version 1.68 (Hammer et al., 2001). In this case, data were pooled from the wet and dry seasons by summing species abundance (biotic data) and by means (abiotic data), except for physicochemical data which were obtained just in the dry period. In this case, abiotic data was correlated with biotic ones of the same period. Data were transformed according to the arcsin procedure for proportions (shoreline and substrate descriptors), $\log (x+1)$ procedure for hydrological measurements (Zar, 1999) and fourth root for abundance matrix. Similarity matrices were constructed using the Euclidean distance similarity measure for abiotic data (Clarke & Ainsworth, 1993), Jaccard similarity coefficient for ichthyofauna composition and Bray-Curtis similarity coefficient for quantitative structure of the communities. All analyses (except the Mantel test) were performed using Primer 6 (2006) software.

Results

Spatial variability on the environmental descriptors was greater than temporal variability (Table 2). Reaches 1, 2 and 3 were narrower and deeper than downstream reaches (Table 2). Grass and bush leaves were the most representative shoreline vegetation in contact with water in reaches 1 and 2, whereas in the downstream reaches, tree trunks and roots were the vegetation most representative (Table 2). Substrate

was uniform along the longitudinal gradient of Correntes stream with a predominance of sand in all reaches (Table 2). A total of 1,166 individuals were sampled, belonging to six orders, 18 families and 44 species (Table 3). Characiformes and Siluriformes represented 85.3% of the species recorded and approximately 97.2% of total abundance. The most abundant species were *Odontostilbe pequira* (24.3%), *Jupiaba acanthogaster* (14.0%), *Bryconamericus exodon* (9.0%), *Characidium* aff. *zebra* (7.9%), *Moenkhausia bonita* (6.4%), *Hemiloricaria lanceolata* (4.6%), *Hypostomus* sp. (4.6%) and *Astyanax abramis* (4.6%) (Table 3). Five species (11.4%) were recorded in all reaches in at least one sampling: *Astyanax abramis*, *Bryconamericus exodon*, *Jupiaba acanthogaster*, *Hypostomus* sp. and *Hemiloricaria lanceolata*.

run and pool

Total abundance obtained in the rainy season was greater than in the dry, except for reach 2 (Table 3). Reach 5 exhibited the greatest species richness, followed by reaches 1 and 4 which had greater species diversity but less dominance. Reach 2 had low species richness and diversity and high *Jupiaba acanthogaster* dominance. Reach 3 had the lowest species richness of all and low dominance. Although having the greatest species richness, reach 5 had low diversity and higher dominance due to the high relative abundance of *Odontostilbe pequira*.

The ordination generated by NMDS, considering the fish composition and quantitative structure of the communities, revealed two subsets formed by upstream reaches (sites 1 and 2) and downstream reaches (sites 3, 4 and 5), notwithstanding seasonality (Fig. 2). This was confirmed by two-way ANOSIM which indicated significant differences of ichthyofauna composition and quantitative structure between upstream and downstream reaches (R = 1.00; p = 0.01 for both), but not between rainy and dry seasons (p > 0.40).

The SIMPER procedure revealed that the two sub-sets indicated in the NMDS, *i.e.*, the upstream reaches (R1 and R2) and the downstream reaches (R3, R4 and R5), had an average dissimilarity of 85.8%. This pattern was principally obtained because of the differential contribution of *Jupiaba* acanthogaster, Odontostilbe pequira, Moenkhausia bonita, Characidium aff. zebra, Hemiloricaria lanceolata and Bryconamericus exodon along the longitudinal gradient of the Correntes stream (Table 4).

In a similar way, the shoreline vegetation structure differed significantly between upstream and downstream reaches (R = 0.79; p = 0.01), but not between wet and dry periods (R = 0.06; p = 0.37). Substrate composition and hydrological descriptors did not differ significantly between upstream and downstream reaches (p > 0.46) not between

Category	Category Descriptor		Reach 1		Reach 2		Reach 3		Reach 4		Reach 5	
Category	Descriptor	W	D	W	D	W	D	W	D	W	D	
•	Dissolved oxygen(mg.l ⁻¹)	ND	6.40	ND	7.89	ND	8.03	ND	8.51	ND	8.52	
	Conductivity (mS.cm ⁻¹)	ND	0.054	ND	0.017	ND	0.049	ND	0.048	ND	0.049	
Physicochemical	pН	ND	6.58	ND	6.83	ND	6.70	ND	6.25	ND	7.18	
	Turbidity (NTU)	ND	14	ND	07	ND	10	ND	25	ND	28	
	Water temperature (°C)	ND	24.6	ND	27.4	ND	24.2	ND	21.3	ND	23.2	
TT-darlasias1	Mean depth (m)	0.68	0.54	0.85	0.70	0.82	0.65	0.45	0.35	0.26	0.20	
Hydrological	Mean width (m)	2.14	2.04	1.65	1.52	2.4	2.32	3.95	3.87	6.62	6.50	
	Grass (%)	0.44	0.35	0.43	0.30	-	-	0.01	-	-	-	
	Thin roots (%)	0.07	0.25	0.13	0.20	0.33	0.75	0.14	0.40	0.24	0.25	
	Large roots (%)	-	0.25	-	0.10	0.33	0.25	0.21	0.15	-	-	
Shoreline vegetation	Bryophytes (%)	-	-	-	-	0.33	-	0.25	0.15	-	-	
	Pteridophytes (%)	0.07	0.10	0.26	0.15	-	-	0.21	-	-	-	
	Tree trunks (%)	-	-	0.02	-	-	-	0.14	0.15	0.33	0.35	
	Bush leaves (%)	0.36	-	0.17	0.25	-	-	-	0.05	-	-	
	Sand (%)	0.67	0.85	1.00	0.90	0.70	0.50	0.90	0.85	0.75	0.75	
	Clay (%)	-	-	-	-	-	0.05	-	0.05	-	-	
	Gravel (%)	0.17	0.05	-	-	0.10	0.10	0.05	-	-	-	
	Rock (%)	0.17	-	-	-	-	-	0.05	-	0.04	0.05	
Substrate	Adhered algae (%)	-	-	-	-	-	-	-	-	0.06	0.05	
	Roots (%)	-	-	-	-	-	0.25	-	-	-	-	
	Litter (%)	-	-	-	-	-	0.05	-	0.05	-	-	
	Aquatic macrophytes (%)	-	0.10	-	-	-	-	-	-	-	-	
	Logs and branches (%)	-	-	-	0.10	0.20	0.05	-	0.05	0.16	0.15	

Table 2. Values of physicochemical (absolute) and physical habitat (proportion) descriptors of reaches (R1-R5) of the Correntes stream in the wet (W) and dry period (D), central west Brazil. ND = no data available.

seasons (p > 0.30). Shoreline vegetation structure was more related to fish composition and quantitative structure of community (2Stage analysis: R = 0.63 and 0.62, respectively) than substrate composition and hydrological measurements (0.28 > R > -0.32). This was confirmed by Mantel tests which revealed a significant correlation of fish composition and quantitative structure of the fish communities with the shoreline vegetation (R > 0.65; p < 0.04), but not with substrate composition, width and depth and physicochemical measurements (p > 0.12). Qualitatively, it was shown that Gymnotiformes species such as Apteronotus albifrons, Brachyhypopomus sp., Eigenmannia trilineata and Gymnotus sp. and the loricariids Farlowella paraguayensis, Hemiloricaria lanceolata and Rineloricaria cacerensis were always captured associated with thin roots, shrub leaves and grass in contact with the water.

Discussion

The two most abundant species, Odontostilbe pequira and Jupiaba acanthogaster, were also the ones that most contributed to the dissimilarity between up- and downstream reaches in the Correntes stream. Jupiaba acanthogaster was more restricted to upstream reaches, while *Odontostilbe* pequira was exclusive to downstream reaches and was predominant in R5. Marginal areas with moderate water flow seem to favor O. pequira in this reach. The occurrence of Jupiaba acanthogaster in upstream reaches of the Correntes stream is compatible with findings of their preferential occurrence in headwater streams of the Serra da Bodoquena (L. Casatti & R. M. Romero, pers. comm.).

The greater species abundance recorded during the rainy

season can be explained by the increased volume of the habitat, which provides a higher availability of microhabitats and increases the amount of allochthonous material in the stream, increasing the availability of food and substrates that can be used as shelter and as reproductive sites (Schlosser, 1982; Angermeier & Karr, 1983; Casatti, 2005). Moreover, the rainy season is also the reproduction period for many tropical species when there is an increase in abundance, especially of young in the streams (Casatti, 2005; Súarez et al., 2007). Reach 2 with its lower abundance in the rainy season may be due to a sampling artifact, since there are limitations to the collecting methodology used in deeper localities, as is the case with this reach in rainy periods. Despite potential limitation of the sampling techniques used in this study (Wiley & Tsai, 1983; Mercado-Silva & Escandón-Sandoval, 2008), there was no evidence of differential catchability between reaches along the longitudinal gradient of the Correntes stream, except between dry and wet period in reach 2. In this case, abundance rather than richness seems to have been underestimated, but this did not affect the results because relations obtained from fish composition and quantitative structure of communities were congruent in all analyses.

Despite the tendency for an increased abundance during the rainy season, similarity analyses results indicate that such differences were not enough to alter the structure of the communities. Studying the fish communities in headwater streams of Paraguay and Paraná basins, Valério et al. (2007) found little seasonal influence on the organization of communities, a pattern comparable to that seen in this study. The increase in richness and diversity along the longitudinal gradient predicted by the River Continuum Concept (Vannote et al., 1980) has been confirmed in rivers and streams in

Table 3. Species abundance during the wet (W) and dry period (D) and ichthyofauna descriptors of the five reaches of the Correntes stream, central west Brazil.

Species	Voucher	Rea			ch 2	Read		Rea		Read	
Characiformes	number	W	D	W	D	W	D	W	D	W	D
Characidae Characidae											
Aphyocharax cf. dentatus	12436	_	_	_	_	_	_	_	_	2	_
Astyanax abramis	12424	-	1	-	1	21	-	11	1	18	1
Astyanax marionae	12411	-	-	-	-	1	1	-	-	1	-
Bryconamericus exodon	12426	1	4	-	3	15	4	7	-	59	12
Bryconops melanurus	12416	7	3	-	-	-	-	1	-	-	
Creagrutus meridionalis	12428	-	-	25	-	4	1	6	2	-	4
Jupiaba acanthogaster Moenkhausia bonita	12404 12441	29 66	44 3	25	44 -	5	3	12 1	-	5	1
Moenkhausia sanctaefilomenae	12448	-	1	-	4	_	-	-	-	2	-
Odontostilbe paraguayensis	12429	_	-	_		_	_	1	_	-	_
Odontostilbe pequira	12433	-	-	-	-	44	3	57	15	157	7
Piabarchus torrenticola	12409	-	-	-	-	12	6	1	3	-	5
Serrapinnus calliurus	12415	-	2	-	-	-	-	-	-	-	-
Xenurobrycon macropus	12431	-	-	-	-	-	-	12	13	-	14
Anostomidae	12420										
Leporinus lacustris Leporinus striatus	12439 12438	-	-	-	-	-	-	-	-	1 1	-
Parodontidae	12436	-	-	-	-	-	-	-	-	1	-
Apareiodon affinis	12434	_	_	_	_	_	_	3	_	2	_
Parodon nasus	12445	_	_	_	_	_	_	1	_	-	_
Crenuchidae											
Characidium aff. zebra	12432	-	11	-	-	5	12	11	7	9	38
Lebiasinidae											
Pyrrhulina australis	12442	-	10	-	-	-	-	-	-	-	-
Curimatidae	12419	7	1					1			
<i>Cyphocharax gillii</i> Erythrinidae	12419	7	1	-	-	-	-	1	-	-	-
Hoplias malabaricus	12420	_	2	1	_	_	_	_	_	_	_
Gymnotiformes	12420		2	1							
Apteronotidae											
Apteronotus albifrons	12407	1	-	-	-	-	-	-	-	-	-
Hypopomidae											
Brachyhypopomus sp.	12406	7	2	1	2	-	-	-	-	-	-
Sternopygidae	10444	2									
Eigenmannia trilineata	12444	3	1	-	-	-	-	-	-	-	-
Sternopygus macrurus Gymnotidae	12440	-	1	-	-	-	-	-	-	1	-
Gymnotus sp.	12407	1	_	1	_	_	_	_	_	_	_
Siluriformes	12 107			1							
Loricariidae											
Ancistrus sp.	12427	-	-	-	2	2	3	3	9	2	1
Farlowella paragyayensis	12405	7	7	5	15	4	4	-	-	-	-
Hemiloricaria lanceolata	12408	5	5	11	26	1	3	1	1	-	1
Hypostomus cochliodon	12437	-	-	1	-	1	-	1	-	3	-
Hypostomus boulengeri	12423	-	-	-	-	-	-	-	-	-	1
Hypostomus sp. Otocinclus vittatus	12403 12422	4	9	6	4	1	-	6	2	16	6 1
Rineloricaria cacerensis	12422	-		1	-	-			-	-	1
Heptapteridae	12440	_	_	1	_	_	_	_	_	_	_
Imparfinis cf. schubarti	12413	_	_	6	4	_	_	_	_	_	_
Imparfinis sp.	12421	-	4	-	2	_	-	7	11	-	1
Phenacorhamdia hoehnei	12410	-	-	-	-	-	1	-	-	-	-
Auchenipteridae											
Tatia neivai	12435	-	-	-	-	-	-	-	-	3	-
Cetopsidae											
Cetopsis gobioides	12430	-	-	-	-	-	-	1	-	-	-
Cyprinodontiformes											
Rivulidae Rivulus punctatus	12414	_	_	_	1	_	_	_	_	_	_
Perciformes	12717	-	-	-	1	-	-	-	-	-	-
Cichlidae											
Aequidens plagiozonatus	12443	-	3	-	-	_	-	-	_	-	_
Crenicichla lepidota	12418	1	4	-	1	-	-	-	-	-	-
Synbranchiformes											
Synbranchidae											
Synbranchus marmoratus	12425	-	-	-	-	-	-	1	-	-	1
Abundance		139	118	58	109	116	41	145	64	282	94
Richness Total richness		13	20	10	13	13	11	21 2	10	16	15
LODAL HUBBESS					7	1				2:	
Diversity (Shannon-Wiener)		2.	28		84	2.	14	., .	28	1.9	

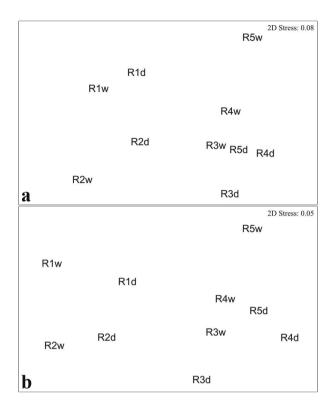


Fig. 2. Two-dimension ordinations based on Jaccard similarity coefficient (a) and on Bray-Curtis (b), considering the ten samples from the wet and dry seasons from the Correntes stream, central west Brazil.

different zoogeographic regions (Sheldon, 1968; Evans & Noble, 1979; Garutti, 1988; Oberdorff *et al.*, 1993; Casatti, 2005; Petry & Schulz, 2006). In the Correntes stream, this pattern was especially evident from the intermediate reach (R3) to the extreme downstream reach (R5) (14 to 25 species), apparently following the increase in habitat volume (Angermeier & Schlosser, 1989; Casatti, 2005). Moreover, fish migration from bigger rivers to tributaries is also a factor that contributes toward an increase in species richness in reaches of the stream near the mainstem (Gorman, 1986; Fernandes *et al.*, 2004). Therefore, the proximity of R5 to the Aquidauana River (less than 600 m) could also have contributed to the maintenance of richer communities in the downstream reaches.

Surprisingly, headwater reaches, normally with smaller species richness (Whiteside & McNatt, 1972; Garutti, 1988; Casatti, 2005), had high species richness and diversity in the Correntes stream. This happens when the headwaters have singular characteristics such as a high structural heterogeneity, making the occurrence of richer communities feasible (McNeely, 1986; Ferreira & Casatti, 2006). In fact, upstream reaches of the Correntes stream maintain high structural diversity, especially the abundance of shoreline vegetation in contact with the water; notably grasses, bushes and roots. The high structural diversity of the banks was a marked characteristic of upstream reaches, allowing the occurrence of diverse species, notably fishes of the orders Gymnotiformes and Siluriformes, which were abundant at these sites. These

results reinforce the predictive role of the structural composition of the habitat for the structuring of fish communities (Gorman & Karr, 1978; Schneider & Winemiller, 2008).

The addition of species was the most important process in the downstream reaches (R3 to R5), which is generally the result of increased habitat volume and complexity along the longitudinal gradient of the streams, providing favorable conditions for the occurrence of a greater number of species (Sheldon, 1968; Angermeier & Schlosser, 1989). Nevertheless, the high species richness in upstream reaches, among which 12 were exclusive, and its high dissimilarity in relation to downstream reaches, evidenced by NMDS and SIMPER, also suggests species substitution as an important process in the structuring of fish communities in the Correntes stream. Species substitution is predominant when environmental changes along the longitudinal gradient are sudden, causing physical or biological impediments to ichthyofauna longitudinal colonization (Burton & Odum, 1945; Tramer & Rogers, 1973). In fact, the structural composition of habitats in upstream areas is quite distinct from that of downstream reaches, apparently limiting the occurrence of some species while favoring others.

Although physical habitat and physicochemical descriptors varied along the longitudinal gradient of the Correntes stream, the shoreline vegetation was the most important environmental feature predicting fish structure and composition as evidenced by 2Stage analysis and Mantel tests. Structural differences between upstream and downstream reaches correspond to the phytophysiognomy dichotomy observed in the Correntes stream whose shoreline vegetation consists of wet grassland upstream and gallery forest downstream. Wet grasslands are characterized by the dominance of herbaceous and shrubby vegetation adapted to hydromorphic soil (Ribeiro & Water, 1998). In upstream reaches, the small size of the abundantly present shoreline vegetation on the low banks favors their contact with the stream water. Foliage leaning over the channel and roots extending internally increase the spatial heterogeneity of in-stream habitats, creating specific microhabitats (Collier et al., 1999; Rocha et al., 2009) usually explored by species with specialized needs. In fact, some species such as Apteronotus albifrons, Brachyhypopomus sp., Eigenmannia trilineata and Gymnotus sp. were captured exclusively in upstream reaches (Table 3) and always associated with shoreline vegetation in contact with the water. This is probably associated with preferential use of submerged vegetation by Gymnotiformes species for diurnal shelter and feeding (Ferreira & Casatti, 2006; Ferreira, 2007; Rocha et al., 2009). Two other species, Farlowella paraguayensis and Hemiloricaria lanceolata, also occurred associated with marginal areas with dense vegetation and were important for the dissimilarity between upstream and downstream reaches according to the similarity percentage analysis. These data are in agreement with the Mantel test result which indicated an association between shoreline vegetation in contact with water and the composition and quantitative structure of the fish community. On the other hand, most of the species associated with downstream areas that contributed toward dissimilarity

Table 4. Species contribution to dissimilarity between the upstream reaches (R1 and R2) and downstream reaches (R3, R4 and R5) of the Correntes stream, central west Brazil. ^a = Contribution of each species to the mean dissimilarity between groups. ^b = Mean dissimilarity between groups ± standard deviation. ^c = Contribution percentage of each species (> 3.0%) to the dissimilarity between groups.

Species	Mean a	bundance ^a	- Mean dissimilarity ^b	Contribution9/¢	
Species	Upstream Downstream		- wican dissimilarity	Contribution/0	
Odontostilbe pequira	0.0	47.2	16.48 ± 1.19	19.21	
Jupiaba acanthogaster	35.5	3.5	15.50 ± 2.36	18.07	
Moenkhausia bonita	17.2	1.0	7.16 ± 0.59	8.35	
Characidium aff. zebra	2.7	13.7	6.10 ± 0.96	7.11	
Hemiloricaria lanceolata	11.7	1.12	5.22 ± 1.14	6.08	
Bryconamericus exodon	2.0	16.2	5.14 ± 1.03	5.99	
Xenurobrycon macropus	0.0	6.5	3.33 ± 0.91	3.88	
Farlowella paraguayensis	8.5	1.33	3.30 ± 1.52	3.84	
Astyanax abramis	0.5	8.67	3.19 ± 0.91	3.72	

between upstream and downstream reaches were water column swimmers such as *Bryconamericus exodon* and *Astyanax abramis*. Their preference for downstream reaches was probably related to the increased habitat volume.

The Correntes stream ichthyofauna is structured into two biologically distinct zones, with upstream reaches having particular structural and biological conditions. This reinforces the importance of preserving headwaters to maintain regional biodiversity (Paller, 1994). The composition of ichthyocenosis and structure differences along the longitudinal gradient are differential contributions influenced by phytophysiognomies in determining specific structural patterns on stream banks. This provides support for the generalization that phytophysiognomic diversity is fundamental for the maintenance of biodiversity in the Brazilian Cerrado (Mares et al., 1986; Ratter et al., 1997; Oliveira & Marquis, 2002; Almeida & Louzada, 2009).

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Literature Cited

Almeida, S. S. P. & J. N. C. Louzada. 2009. Estrutura da comunidade de Scarabaeinae (Scarabaeidae: Coleoptera) em fitofisionomias do Cerrado e sua importância para a conserva-

ção. Neotropical Entomology, 38(1): 32-43.

Angermeier, P. L. & J. R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Environmental Biology of Fishes, 9: 117-135.

Angermeier, P. L. & I. J. Schlosser. 1989. Species-area relationship for stream fishes. Ecology, 70(5): 1450-1462.

Britski, H. A., K. Z. S. Silimon & B. S. Lopes. 2007. Peixes do Pantanal: manual de identificação. Brasília, Embrapa, 184p.

Burton, G. W. & E. P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology, 26(2): 182-194.

Casatti, L. 2005. Fish assemblage structure in a first order stream, southeastern Brazil: longitudinal distribution, seasonality, and microhabitat diversity. Biota Neotropica, 5(1): 1-9.

Castro, R. M. C. 1999. Evolução da ictiofauna de riachos sul-americanos: padrões gerais e possíveis processos causais. Oecologia Brasiliensis, 6: 139-155.

Catella, A. C. & M. Petrere-Jr. 1996. Feeding patterns in a fish community of Baía da Onça, a floodplain lake of the Aquidauana river, Pantanal, Brazil. Fisheries Management and Ecology, 3: 229-237.

Chernoff, B. & P. W. Willink. 2000. Ecological and geographical structure in assemblages of freshwater fishes in the Pantanal, Mato Grosso do Sul, Brasil. Pp. 183-201. In: Willink, P. W., B. Chernoff, L. E. Alonso, J. R. Montambault & R. Lourival (Eds.). A Biological Assessment of the Aquatic Ecosystems of the Pantanal, Mato Grosso do Sul, Brazil. Washington, Bulletin of Biological Assessment 18, Conservation International, 307p.

Clarke, K. R. & R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth, Plymouth Marine Laboratory, 144p.

Collier, K. J., P. D. Champion & G. F. Crocker. 1999. Patch-and reach-scale dynamics of a macrophyte-invertebrate system in a New Zealand lowland stream. Hydrobiologia, 392: 89-97.

Evans, J. W. & R. L. Noble. 1979. The longitudinal distribution of fishes in an east Texas stream. American Midland Naturalist, 101(2): 333-343.

Fernandes, C. C., J. Podos & J. G. Lundberg. 2004. Amazonian ecology: tributaries enhance the diversity of electric fishes. Science, 305: 1960-1962.

Ferreira, K. M. 2007. Biology and ecomorphology of stream fishes from the rio Mogi-Guaçu basin, Southeastern Brazil. Neotropical Ichthyology, 5(3): 311-326.

Ferreira, C. P. & L. Casatti. 2006. Influência da estrutura do hábitat sobre a ictiofauna de um riacho em uma micro-bacia de pastagem, São Paulo, Brasil. Revista Brasileira de Zoologia, 23(3): 642-651.

- Garutti, V. 1988. Distribuição longitudinal da ictiofauna de um Córrego na região noroeste do Estado de São Paulo, Bacia do rio Paraná. Revista Brasileira de Biologia, 48: 747-759.
- Gorman, O. T. 1986. Assemblage organization of stream fishes: the effect of rivers on adventitious streams. The American Naturalist, 128(4): 611-616.
- Gorman, O. T. & J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology, 59: 507-515.
- Growns, I., P. C. Gehrke, K. L. Astlea & D. A. Pollard. 2003. A comparison of fish assemblages associated with different riparian vegetation types in the Hawkesbury-Nepean River system. Fisheries Management and Ecology, 10: 209-220.
- Hammer, Ø., D. A. T. Harper & P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4(1): 1-9.
- Magurran, A. E. 2004. Measuring Biological Diversity. United Kingdom, Blackwell Publishing, 256p.
- Mares, M. A., K. A. Ernest & D. D. Gettinger. 1986. Small mammal community structure and composition in the Cerrado Province of central Brazil. Journal of Tropical Ecology, 2: 289-300.
- McNeely, D. L. 1986. Longitudinal patterns in the fish assemblages of an Ozark stream. Southwestern Naturalist, 31: 375-380.
- Mercado-Silva, N. & D. S. Escandón-Sandoval. 2008. A comparison of seining and electrofishing for fish community bioassessment in a Mexican Atlantic slope montane river. North American Journal of Fisheries Management, 28: 1725-1732.
- Myers, N., R. Mittermeier, C. Mittermeier, G. Fonseca & J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature, 403(6772): 853-858.
- Oberdorff, T., E. Guilbert & J. C. Lucchetta. 1993. Patterns of fish species richness in the Seine River basin, France. Hydrobiologia, 259: 157-167.
- Oliveira, P. S. & R. J. Marquis. 2002. The cerrados of Brazil: ecology and natural history of a Neotropical savanna. Irvington, Columbia University Press, 398p.
- Paller, M. H. 1994. Relationships between fish assemblage structure and stream order in South Carolina coastal plain streams. Transactions of the American Fisheries Society, 123: 150-161.
- Petry, A. C. & U. H. Schulz. 2006. Longitudinal changes and indicator species of the fish fauna in the subtropical Sinos river, Brazil. Journal of Fish Biology, 69: 272-290.
- Ratter, J. A., J. F. Ribeiro & S. Bridgewater. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. Annals of Botany, 80: 223-230.
- Ribeiro, J. F. & B. M. T. Walter. 1998. Fitofisionomias do Bioma Cerrado. Pp. 89-166. In: Sano, S. M. & S. P. Almeida (Eds.). Cerrado: ambiente e flora. Planaltina, Embrapa/CPAC, 556p.
- Rocha, F. C., L. Casatti, F. R. Carvalho & A. M. Silva. 2009. Fish assemblages in stream stretches occupied by cattail (Typhaceae, Angiospermae) stands in Southeast Brazil. Neotropical Ichthyology, 7(2): 241-250.
- Schlosser, I. J. 1982. Fish Community structure and function along two habitat gradients in a headwater stream. Ecological Monographs, 52(4): 395-414.
- Schneider, K. N. & K. O. Winemiller. 2008. Structural complexity of woody debris patches influences fish and macroinvertebrate species richness in a temperate floodplain-river system. Hydrobiologia, 610: 235-244.
- Sheldon, A. L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology, 49(2): 194-198.
- Súarez, Y. R., M. Petrere-Jr. & A. C. Catella. 2004. Factors regulating diversity and abundance of fish communities in Pantanal

- lagoons, Brazil. Fisheries Management and Ecology, 11: 45-50. Súarez, Y. R., S. B. Valério, K. K. Tondado, A. C. Florentino, T. R. A. Felipe, L. Q. L. Ximenes & L. S. Lourenço. 2007. Fish species diversity in headwaters streams of Paraguay and Paraná basins. Brazilian Archives of Biology and Technology, 50(6): 1033-1042.
- Tramer, E. J. & P. M. Rogers. 1973. Diversity and longitudinal zonation in fish populations of two streams entering a metropolitan area. American Midland Naturalist, 90(2): 366-374.
- Valério, S. B., Y. R. Súarez, T. R. A. Felipe, K. K. Tondato & L. Q. L. Ximenes. 2007. Organization patterns of headwater-stream fish communities in the Upper Paraguay-Paraná basins. Hydrobiologia, 583:241-250.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedel & C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science, 37: 130-137.
- Whiteside, B. G. & R. M. McNatt. 1972. Fish species diversity in relation to stream order and physicochemical conditions in the Plum creek drainage basin. American Midland Naturalist, 88(1): 90-101.
- Wichert, G. A. & D. J. Rapport. 1998. Fish community structure as a measure of degradation and rehabilitation of riparian systems in an agricultural drainage basin. Environmental Management, 22(3): 425-443.
- Wiley, M. L. & C. F. Tsai. 1983. The relative efficiencies of electrofishing vs. seines in Piedmont streams of Maryland. North American Journal of Fisheries Management, 3: 243-253.
- Willink, P. W., O. Froehlich, A. Machado-Alisson, N. Menezes, O. Oyakawa, A. Catella, B. Chernoff, F. C. T. Lima, M. Toledo-Piza, H. Hortega, A. M. Zanata & R. Barriga. 2000. Fishes of the Rio Negro, Negrinho, Taboco, Aquidauana, Taquari and Miranda, Pantanal, Brasil: diversity, distribution, critical habitats and value. Pp. 63-81. In: Willink, P. W., B. Chernoff, L. E. Alonso, J. R. Montambault & R. Lourival (Eds.). A Biological Assessment of the Aquatic Ecosystems of the Pantanal, Mato Grosso do Sul, Brazil. Washington, Bulletin of Biological Assessment 18, Conservation International, 307p.

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