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Spatial and temporal variation in the trophic structure of fish assemblages in floodplain sediment banks

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DATA AVAILABILITY STATEMENT

The original data for this study are partially found in supplementary material and for full access upon request to the corresponding author.

CONFLICT OF INTEREST

The authors report no conflicts of interest.

Animal Ethics Committee

At the time this project was developed, issues related to the use of fish in research were evaluated and approved by the funding agency.

Abstract

In tropical floodplains, rivers have a high dynamic in space and time, which are determinants in the organization and trophic structure of fish assemblages. We evaluated the influence spatial and temporal on the trophic structure of fish assemblages in the sediment banks of the Bananal floodplain, in the Middle Araguaia river region. We identified the food preferences of the species by the analysis of the stomach content of 564 individuals distributed in 48 species of 22 families and six orders. We classified fish assemblages into eight trophic groups according to the Alimentary Index (IA_i). Analysis of the abundance and richness of the trophic groups indicated that fish assemblage trophic structure varied between environments the seasonal periods. Our results suggest that the composition and distribution of the fish trophic groups in the sediment banks of the Bananal floodplain are structured by spatial gradient and temporal. Together, the space and time determine high variability in the trophic organization of the fish fauna in these environments.

Key words: sandbanks, diet, trophic groups, fish fauna, Bananal floodplain

Resumo

Nas planícies de inundação tropicais a dinâmica fluvial confere alta heterogeneidade de habitats ao longo dos gradientes espaciais e temporais, aspectos que são determinantes na organização e estrutura trófica das assembleias de peixes. Avaliamos a influência da variabilidade espaço-temporal do habitat sobre a estrutura trófica das assembleias de peixes em bancos de sedimentos fluviais da planície de inundação do Bananal, na região do médio rio Araguaia. Identificamos a preferência alimentar das espécies pela análise do conteúdo estomacal de 564 indivíduos distribuídos em 48 espécies pertencentes a 22 famílias e seis ordens. Agrupamos as assembleias de peixes em oito grupos tróficos de acordo com o Índice de Importância Alimentar (IA_i). Análises da abundância e riqueza dos grupos tróficos mostraram que a estrutura trófica da assembleia de peixes varia entre os ambientes e os períodos sazonais. Nossos resultados sugerem que a composição e distribuição dos grupos tróficos da assembleia de peixes dos bancos de areia da planície de inundação do Bananal são estruturadas pelas variações na complexidade dos habitats ao longo do gradiente espacial e pelo regime hidrológico, que determinam alta variabilidade na organização trófica da ictiofauna nesses ambientes.

Palavras chaves: bancos de areia, dieta, grupos tróficos, ictiofauna, Planície do Bananal

Trophic structure of fish in the floodplain

Introduction

Characteristics of the floodplain habitats vary in the space and time and are structured by variation hydrological cycle (Winemiller, 1996; Arrington, Winemiller, 2006). The water level fluctuation with seasonal variations promotes physicochemical changes in the water, changes in the balance of production and respiration, and increased nutrient cycling (Junk, 1989; Junk, Wantzen, 2004). Moreover, there is an increase in food resources of autochthonous origin and microhabitat availability in these environments in the flood period, which consequently favors the maintenance of several ecological relationships, for example, reproduction and immigration between aquatic communities (Junk, 1989; Winemiller, 1996). Meanwhile, in dry period occur the decrease in the resources available (i.e, habitats and food), which in turn intensifies other ecological relationships, such as predation, competition for food resources and habitats (Winemiller, Jepsen, 1998). The trophic structure of fish assemblages in floodplains tends to be complex (Angelini, Agostinho, 2005; Layman *et al.*, 2005; Jepsen, Winemiller, 2007), since the high diversity of species and food resources result in a wide variety of trophic groups (Winemiller, 1991; Hahn *et al.*, 2004). Further, the spatial and temporal variation of the habitat adds even more complexity to the trophic structure of fish assemblages (Pouilly *et al.*, 2004; Quirino *et al.* 2015).

The environmental heterogeneity in the floodplains along of the space enable a taxonomic diversity great of fishes with behavior different and forms can to live and explorer those habitats, such conditions is determinant in the trophic structure of assemblages (Ward *et al.* 1999; Amoros, Bornnette, 2002). The intrinsic characteristics of each environment determine the patterns of habitat selection, which, in turn, alters the complexity and trophic composition of fish assemblages (Fernandes *et al.*, 2009; Brejão *et al.*, 2013; Wolff *et al.*,

2013). Thus, it is possible to find trophic groups with different composition in each geographical area (Rodríguez & Lewis Jr, 1997; Allan, 2004; Silva *et al.*, 2007).

Another remarkable feature of floodplains is the hydrological cycle (i.e., drought and flood), which plays a key role in maintaining the diversity of lotic, lentic and semi-aquatic habitats (Junk, 1989; Ward *et al.*, 1999; Thomaz *et al.* 2007; Silva *et al.*, 2014). In general, with the onset of rainfall events, there is an increase in the input of allochthonous food resources into the water bodies. This results from the input of organic matter accumulated during the drought in adjacent areas and through the removal of the soils by the water entering the river channel (Luiz *et al.*, 1998; Esteves, Aranha, 1999). In the flood period, habitat availability increases, allowing fish to disperse to explore new habitats, and in the dry period, fish distribution is limited to the river channel or lakes (Arthington *et al.*, 2005; Arrington *et al.*, 2005; Arrington, Winemiller, 2006; Silva *et al.*, 2007).

A common habitat in floodplains consists of marginal sediment banks formed by the deposition of material eroded by the river. They are habitats with homogeneous characteristics, since they have few internal structures, for example, usually do not have roots of trees the margins, banks of leaves or trunks and low stability due to the seasonal dynamics of flooding (Gordon *et al.*, 2004; Pereira *et al.*, 2007). These banks are important foraging, breeding and refuge areas for several small fish species and juvenile's fishes at different stages of development (Pereira *et al.*, 2007; Roach, Winemiller, 2011). Sandbanks are closely related to the natural flow regime (Arrington, Winemiller, 2004), in the Araguaia river, the presence of these areas is more accentuated, since the river has undergone geomorphologic and sedimentary changes because of the effect of high rates of deforestation during the last decades (Aquino *et al.*, 2009). Fish living in these locations are key to the maintenance of aquatic dynamics (Pereira *et al.*, 2007; Roach & Winemiller, 2011), since they are usually

small-sized, benthic species, and can serve as food for larger fish, thus sustaining a more complex trophic web (Pereira *et al.*, 2007).

Analyses on the trophic ecology of the fish fauna provide information on the behavior of species on a range of spatial and temporal variation in the supply of food resources available in the environment (Melo *et al.*, 2007). This allows the analysis of fish assemblages at different levels and of the interrelationships of individuals of different communities (Pereira *et al.*, 2007). In this context, the present study evaluated the effects of spatial and seasonal on the trophic structure of fish assemblages associated with marginal sediment banks in the middle Araguaia river, in the Bananal Floodplain. More specifically, we evaluate if the fish trophic organization: (i) is different between the three environments (Araguaia river, Crixás-Açu river and Montaria lake)? (ii) is it different between periods of drought and flood? (iii) is there a difference between trophic groups? and (iv) which group most contributes to the differences between environments and periods? We expected that the fish assemblages have differentiation in the trophic structure across the space and time.

Material and methods

Study area

Samplings were conducted in marginal sediment banks associated of the main channel of the Araguaia river (S 13°19'51,4" and W 50°37'22,5"), a tributary, Crixás-Açu river (S 13°21'07,6" and W 50°36'35,7"), and of Montaria lake (S 13°22'37,9" and W 50°40'28,1"), a meandering lake permanently connected to the Araguaia river. All environments are in the floodplain Bananal within the Environmental Protection Area (EPA) Meanders of the Araguaia river (**Fig. 1**).

The Bananal floodplain is an important flood area in the middle region Araguaia basin, which has characteristics of a lacustrine-marshy environment, such as several alluvial

sedimentation areas, formed by the geological composition of the region (Latrubesse, Steavux, 2006; Aquino et al. 2008; Morais *et al.*, 2005). The flood and drought events in the floodplain vary mainly with rainy season durability. The rainy periods start generally in the end from October for June or July. The sediment banks stay cover by water generally till July, but the drought period begins in March or April. We considered the month of June as the flood period for these environments because most of the beaches are still submerged during this part of the ebb period.

The Araguaia river has the drainage in Cerrado biome and maintains great aquatic biodiversity (Latrubesse, Steavux, 2006). The Araguaia river basin has a total length of 2,110 km, covering an area of 379,836 km² and your course runny by four states (Goiás, Mato Grosso, Pará and Tocantins) (Morais *et al.*, 2005). The Araguaia river has a discharge of 6,000 m³s⁻¹, in the hydrological station of Araguatins (Aquino *et al.*, 2008). Its middle section flows through a vast seasonal alluvial plain of about 106,000 km² called Bananal floodplain (Valente, Latrubesse, 2012).

The Crixás-Açu river is located on the right bank of the Araguaia river being one of its main tributaries. This river presents a complex plain with a meandriform pattern and along with the other tributaries of the Araguaia river form the largest sedimentation area of the State of Goiás (Aquino *et al.*, 2009). The sediment banks of the Crixás-Açu river are characterized by a heterogeneous substrate composed mainly of sand-clay, sandy and pebble sediments with variable depth.

Situated to the left Araguaia river, the Montaria lake is connected to the channel of the river by a channel of 90 meters of width. The lake presents on its banks riparian vegetation that suffers flood (Morais *et al.*, 2005). The sediment banks are formed by fine sand and sandy-clayey substrate and are generally deeper.

Fish sampling

Fish were sampled in two collections, in September 2012 (dry period) and in June 2013 (flood period) in three environments (Araguaia river, Crixás-Açu river and Montaria lake). Fish were collected with a seining net 10m long and 2m high, with 5.0mm mesh size, “picaré” type, in four sediment banks in each environment, totaling 12 sampling sites. In each sediment bank, we sampled an area of 100m² during daytime and nighttime (n = 24 samples in each collection). After the capture, fish were fixed in 10% formalin. Later in the laboratory they were transferred to 70% alcohol to be preserved, measured (standard length in cm) and identified. Fishes were collected according governmental laws (Permit n° 33663-1 ICMBio). All specimens are deposited in the laboratory of biological sciences of the Universidade Estadual de Goiás, Porangatu, state of Goiás, Brazil.

Diet analysis

We determined diet of each species by analysis of fish stomach contents. We considered only the species with total abundance greater than or equal to five individuals and with at least one individual with stomach content. We dissected and analyzed the stomachs with the aid of stereomicroscope and optical microscope. Food items were identified and quantified by the volumetric method (Hyslop, 1980) using a gridded dish, standardizing the height to 1 mm and then converting to milliliters (1 cm³ = 1mL) (Hellowell, Abel, 1971) for small items. For larger items, we obtained the volume by displacement of water in a graduated cylinder.

We grouped the identified items were in broad food categories as follows: terrestrial invertebrates - Coleoptera, Diptera, Araneae, Zygotera, Lepidoptera; aquatic invertebrates - Diptera, Ephemeroptera, Plecoptera, Trichoptera, Megaloptera and Coleoptera, Acarina and Decapoda; fish; Periphyton - filamentous and diatom algae and microorganisms associated with substrate; Mollusks – Bivalves; Scales and fins; Plant material - leaves, fruits, flowers,

trunks and roots; Plankton - zooplankton (Cladocera and Copepoda) and planktonic algae (e.g. diatom); Detritus - organic matter/macroorganisms and microorganisms associated with the substrate; Blood; Other - category consisting of rare (e.g. amphibian) or unidentified items.

Data analysis

Fish species were classified into trophic groups according to the predominance of a given food category, given by the Alimentary Index (IA_i) (Kawakami, Vazzoler, 1980), represented by the following formula: $IA_i = F_i \times V_i / \sum_{i=1}^L F_i \times V_i \times 100$, where, F_i is the frequency of occurrence (%) of a given item, and V_i is the volume (%) of a given item.

The species that have the IA_i less than 60% for all food category were classified as omnivores. Species that presented $IA_i \geq 60\%$ for a specific food item group were classified into the following trophic groups: Detritivore, Invertivore (allochthonous and autochthonous), Lepidophagous, Omnivore, Periphytophagous, Piscivore, Planktivore, and Hematophagous.

For evaluated the patterns in the trophic organization of the fish fauna in relation to the spatial (Araguaia river, Crixás-Açu river, Montaria lake) and temporal/seasonal (drought and flood) variation we use a Non-Metric Multidimensional Scaling Analysis (NMDS) from the matrices of abundance and richness of the trophic groups, based on Bray-Curtis distance measures. For analyze the effects of local and seasonal variation on the fish assemblage we use a factorial Analysis of Similarity (ANOSIM). For check the average dissimilarity between the trophic groups and to determine the groups that contributed most to the observed spatial and temporal differences, we used the Similarity Percentage Analysis (SIMPER) (Clarke, Warwick, 2001). These analyses were run in the R program (R Core Team, 2015) using the vegan package (Oksanen et al., 2015) and used the significance level $\alpha = 0.05$.

Results

We collected a total of 5587 fish (1631 in Araguaia river, 1715 in Crixás-açu river, 2241 in Montaria lake), distributed into 106 species and nine orders. We analyzed the diet of 564 individuals of 48 species, belonging to 22 families and six orders (Characiformes, Clupeiformes, Gymnotiformes, Perciformes, Siluriformes and Tetraodontiformes). From this total, we analyzed 140 individuals of 27 species for the Araguaia river, 138 individuals of 39 species for the Crixás-Açu river and 138 individuals of 40 species for Montaria lake. Fish species were classified into eight trophic groups according to food preference (**Tab. S1, Fig. 2**). The most abundant trophic groups were the invertivores in the rivers, and detritivores and planktivores in the lake (**Tab. 1**).

Values of the Alimentary Index (IA_i) indicated that 87.5% of the total species sampled showed a preference for a given food resource, i.e., they presented $IA_i \geq 60\%$ (**Tab. S1**). Only six species had IA_i less than 60%. When analyzing IA_i considering the environments, 88.88% of the analyzed species of Araguaia river, 84.6% of Crixás river and 85% of Montaria lake preferred a food item. Only three species (*Colomesus asellus*, *Geophagus neambi*, and *Tetragonopterus* gr. *chalceus*) were classified as omnivores in the Araguaia River, six species in Crixás-Açu River (*C. asellus*, *G. neambi*, *Retroculus lapidifer*, *T. chalceus*, *Tetragonopterus* sp. 2, and *Triphorteus trifurcatus*), and 5 species in Montaria lake (*G. neambi*, *Poptella compressa*, *T. chalceus*, *Tetragonopterus* sp. 2, and *T. trifurcatus*). The trophic structure of fish assemblages varied in relation to the composition, richness, and abundance of the trophic groups between the sites and periods. Piscivores were not registered in the Araguaia and showed a low abundance in Crixás-Açu and in the lake, being represented by *Pygocentrus nattereri* and *Hoplias malabaricus*. Planktivores (e.g. *Metynnis* sp. and *Moenkhausia dichrourea*) were present in all environments, more abundant in Araguaia and in the lake. Lepidophagous (e.g. *Serrasalmus rhombeus* and *Roeboides* sp.) were not recorded in

Araguaia and showed greater abundance in the lake. Periphytofagous (e.g. *Leporinus friderici*, *Aphanotorulus emarginatus* and *Apareidon* sp.) were observed in all samples, but with low abundance in Araguaia and Crixás rivers (**Tab.1**). Finally, hematophagous (e.g. *Stegophilus* sp. and *Vandellia* sp.) were present only in Araguaia and Crixás rivers but were not very abundant when compared to other groups.

Invertivores exhibited the highest number of species in all environments (**Fig. 3**) and were dominant in number of individuals in both lotic (Araguaia and Crixás-Açu rivers) and lentic (Montaria lake) environments. The group of detritivores presented higher abundance and richness in Montaria lake (535 individuals of seven species) and in Crixás-Açu river (114 individuals of 6 species) and was not found in samples of the Araguaia river.

The abundance of trophic groups in sediment banks of the three environments varied between periods (**Tab. 2**). For the group of detritivores, in the dry period, we caught 441 individuals (80 individuals in Crixás river, 361 in Montaria lake, and none in Araguaia river), while in the flood period, 211 individuals were captured (three in the Araguaia River, 34 in Crixás, 174 in the lake). Abundance of invertivores varied between 1671 in the dry period (877 in Araguaia, 572 in Crixás and 222 in the lake), and 1854 individuals (483 in Araguaia, 573 in Crixás, 399 in the lake) in the flood period.

The richness of the trophic groups did not vary widely between dry and flood periods (46 species in the drought and 42 species in the flood period) within each environment, not exceeding the difference of two species between the periods (**Fig. 3**). Sampling of the detritivore species (*Steindachenerina* sp.) in Araguaia river occurred only in the flood, and no piscivore was caught in Crixás-Açu river in the flood period.

The Ordination by Nonmetric Multidimensional Scaling indicated differences in the trophic structure of the fish assemblages between the sampled sites in relation to the data of abundance and richness of trophic groups (**Fig. 4**). In general, samples of the lentic

environment (Montaria lake) formed a larger grouping, and lotic samples, mainly from the Araguaia River, formed a smaller grouping.

Patterns of temporal and spatial variation obtained by the NMDS were confirmed by the Analysis of Similarity (ANOSIM), in which the paired tests evidenced significant differences between the environments in relation to the richness and the abundance of the trophic groups (**Tab. 3**).

The Factorial Similarity Percentage Analysis (SIMPER) indicated which trophic groups contributed most to the dissimilarity of the trophic structure between the environments (**Tab. 4**). For the seasonal periods, the trophic groups that contributed most to the dissimilarity in abundance were planktivores, invertivores, and hematophagous. Regarding the sites, the trophic groups that contributed most to the dissimilarity between the Araguaia and Crixás-Açu rivers were detritivores, omnivores, and planktivores. For the dissimilarity between Araguaia river and Montaria lake, detritivores, lepidophagous, and omnivores were the groups that most contributed, and for the sediment banks of Crixás-Açu river and Montaria lake, the groups that contributed most were the planktivores, detritivores, lepidophagous, and piscivores. In terms of species richness, SIMPER indicated that hematophagous, omnivores, and planktivores were the groups that contributed most to dissimilarity between the periods (**Tab. 4**). As for the sites, the most important trophic groups for the dissimilarity observed between Araguaia river and Montaria lake were the detritivores, lepidophagous, and omnivores; for Araguaia river and Crixás-Açu river were the detritivores, omnivores, and planktivores; and for Crixás-Açu river and Montaria lake were the piscivores, detritivores, and lepidophagous.

Discussion

In this study, we observed that the trophic structure (i.e., abundance and richness) of the fish assemblages of sandbanks of the floodplain Bananal change across space and time. We find

eight trophic groups in the three environments (Araguaia river, Crixás-Açu river, Montaria lake) studied in the floodplain. The difference of abundance and richness of the fish trophic groups of sandbanks in the space can be resulted of variability of environmental and the food available. Once fish species can be dispersal between environments of floodplain, but are selected by environmental filters (Poff, 1997). The seasonal variation in the floodplains is determined by pulse of flooding, so the shift structure of habitat and the amount of food available (Junk *et al.*, 1989). These changes which occur across time in the habitats of the floodplain provoke alterations in the organizations of fish assemblages and too in the structure trophic (Tejerina-Garro *et al.*, 1998, Li, Gelwick 2005). Whenever, if the composition of the fish assemblages varies with space and time, we hope soon too which trophic groups of fishes in the floodplain change between habitats and seasonal. As observed the fish fauna of the tropical region presents high flexibility in diet, consuming food with greater availability in the environments, according to its supply in space and time (Abelha *et al.*, 2001; Pereira *et al.*, 2007).

Our study demonstrates that fish species of the Bananal floodplain have preference for a food type, generally are invertivores. Species that have a more specific feeding behavior seek to live in environments where the conditions are more suitable for foraging, while species with general characteristics tend to forage on different types of habitats and consume different types of food of various origins. The diet variation verified for these fish assemblages may be the result of morphological adaptation related to the capture or ingestion of food and/or greater stability in the supply of food resources (Winemiller *et al.*, 2008). Like this the trophic organization of a fish assemblages in a habitat can be determined by food type and available, for example, if the alimentary items are for allochthons or autochthons origin (Willis *et al.*, 2001). For example, lentic environments such as the lake, or with low flow, allow greater deposition of organic material in the substrate, favoring the species that exploit

this type of food, as the species sampled in the Montaria lake (*Prochilodus nigricans*, *Curimatella dorsalis*, *Curimatella immaculata*) and supporting a high diversity of fish at low trophic levels in floodplains (Winemiller *et al.*, 2008).

However, some species of which live in the sandbanks of the floodplain showed a generalist feeding habit. As observed for many other fish species tropical (Melo *et al.* 2007; Pereira *et al.*, 2007). Most tropical fish species tend that had a behavior feeding generalists (Lowe-MCconnel, 1999; Abelha *et al.*, 2001; Wolff & Hahn, 2013), as exploring the foods more abundant in the environment. In a study with fish associated with sandbanks in the Tocantins River, Pereira *et al.* (2007) also found greater abundance of invertivore fish, indicating a large supply of invertebrates in these shallow marginal habitats.

In general, the fish assemblage trophic structure varied both in relation to the spatial and seasonal gradients in sandbanks of the Bananal floodplain, with a greater difference when comparing lentic environments (Montaria lake) with lotic ones (Araguaia and Crixás-Açu rivers). These variations are caused by changes in the habitats, which stabilizes the fish communities (Gido *et al.*, 1997), thus is possible find trophic groups with different structures between the sandbanks.

The spatial distribution of the fish fauna is associated with the structural complexity of habitats along a gradient in a certain environment, and abiotic characteristics (e.g. depth, temperature, turbidity) have a strong influence on the distribution of fish assemblages in the habitat (Lowe-MCconnel, 1999; Oliveira, Goulart, 2000). Likewise, differences in biological characteristics influence the heterogeneity in species richness and density (Willis *et al.*, 2005). In general, the sediment banks located in places of slower or absent flow (Crixás-Açu river and Montaria lake) presented a higher richness and abundance of trophic groups in relation to the Araguaia river. In the Crixás-Açu river and in the lake, sediment banks are more stable and heterogeneous, with greater proximity of the marginal vegetation, and in the bottom, are

found remains of organic matter and other resources that can be used by fish, thus increasing the trophic structure complexity. The more complex the environment, the greater the number of microhabitats available, allowing the coexistence of species in the same environment sharing the spatial and food resources (Pianka, 1994; Jepsen, 1997; Esteves, Aranha, 1999; Melo, 2007).

We conclude that the trophic structure of fish assemblages varied between sites/environments (spatial) and time (seasonal), which can be explained by the spatial and temporal variability in the habitat structure. This variation affects the distribution, abundance and richness of the trophic groups, allowing us to find different trophic groups along the habitats and time in the floodplains. The fish of sediment banks tend to show diet specialization, with few omnivore species, and aquatic invertebrates are the main resource used by most species. The species present significant differences in diet, resulting from the variety of food resources available in the sediment banks, favoring the exploitation of the habitat by a high diversity of species with different functional aspects. The high number of trophic groups as well as their patterns of composition, richness, and abundance suggests that fish assemblages of sediment banks have a rich and complex trophic structure.

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Tables

Tab. 1. Abundance in number of individuals (N) and species richness (S) of trophic groups by environment and for total samples from the sediment banks in the Bananal Floodplain.

Trophic group	Araguaia		Crixás		Lake	
	N	S	N	S	N	S
Detritivore	3	1	114	6	535	7
Hematophagous	22	2	29	2		
Invertivore	1358	16	1145	15	621	15
Lepidophagous			52	3	164	3
Omnivore	19	3	202	6	232	6
Periphytophagous	4	2	39	1	41	2
Piscivore			4	2	33	2
Planktivore	134	3	63	4	409	5
Total	1540	27	1648	36	2035	40

Tab. 2. Abundance of trophic groups in number of individuals in the dry and flood periods by environment and for total samples from the sediment banks in the Bananal Floodplain.

Trophic group	Araguaia		Crixás		Lake	
	Drought	Flood	Drought	Flood	Drought	Flood
Detritivore	-	3	80	34	361	174
Hematophagous	2	20	2	27	-	-
Invertivore	877	483	572	573	222	399

Lepidophagous	-	-	5	47	61	103
Omnivore	12	7	132	70	163	69
Periphytophagous	2	2	10	29	40	1
Piscivore	-	-	4	-	18	15
Planktophagous	113	21	2	61	331	78
Total	1006	536	807	841	1196	839

Tab. 3. Results of Factorial Analysis of Similarity (ANOSIM) and pairing of trophic groups for abundance and richness of environments based on 1000 permutations at a level of significance of 5%.

Comparison between groups	R	P
Abundance		
R Global Season	<i>0.424</i>	<i>0.003</i>
R Global Site	<i>0.773</i>	<i>0.001</i>
Araguaia x Crixás	<i>0.766</i>	<i>0.001</i>
Araguaia x Lake	<i>0.891</i>	<i>0.001</i>
Crixás x Lake	<i>0.891</i>	<i>0.001</i>
Richness		
R Global Season	<i>0.333</i>	<i>0.003</i>
R Global Site	<i>0.639</i>	<i>0.001</i>
Araguaia x Crixás	<i>0.516</i>	<i>0.007</i>
Araguaia x Lake	<i>0.885</i>	<i>0.001</i>
Crixás x Lake	<i>0.76</i>	<i>0.001</i>

Tab. 4. Similarity Percentage Analysis (SIMPER) for the factors site and period based on the matrix of abundance and richness of species sampled in the Bananal Floodplain. DM(%) Percentage of average dissimilarity; IA – Invertivores; DT – Detritivores; ON – Omnivores; PL – Planktivores; LP – Lepidophagous; PX – Piscivores; HM – Hematophagous; Cumu. – cumulative percentage.

Paired comparisons	DM (%)	Contribution of trophic groups (%)*							
		IA	DT	ON	PL	LP	PX	HM	Cumu.
Abundance									
Araguaia x Crixás	46.0		21.1	20.9	14.4				57.5
Araguaia x Lake	55.8		23.9	15.2		18.4			57.5
Crixás x Lake	27.5		15.3		19.8	13.9	13.5		62.5
Period (drought x flood)	28.8	15.8			23.1			14.7	53.6
Richness									
Araguaia x Crixás	35.9		20.1	16.1	14.9				51.2
Araguaia x Lake	44.8		22.7	13.9		17.4			54.0
Crixás x Lake	22.4		16.3			14.9	18.9		50.1
Period (drought x flood)	23.1			18.7	18.6			18.9	56.2

Figures

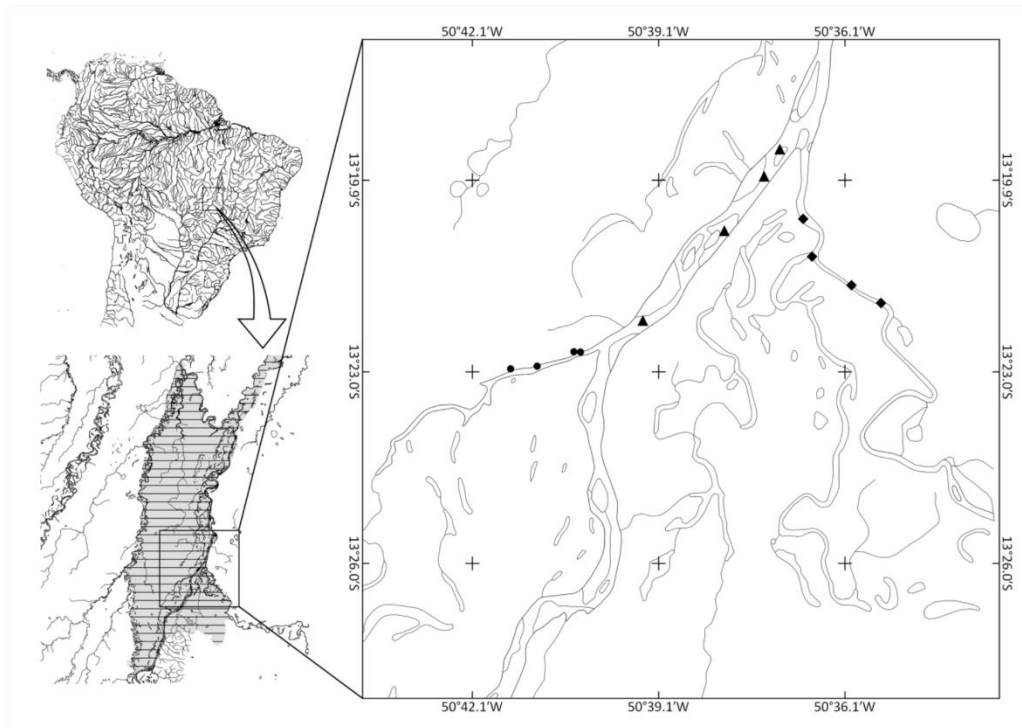


Fig.1. Study area in the middle Araguaia River, Bananal Floodplain. Black triangles indicate the sampled sites in the Araguaia River; black squares, sites in the Crixás-Açu River; and black circles, sites in the Montaria Lake, in the EPA Meanders of the Araguaia river.

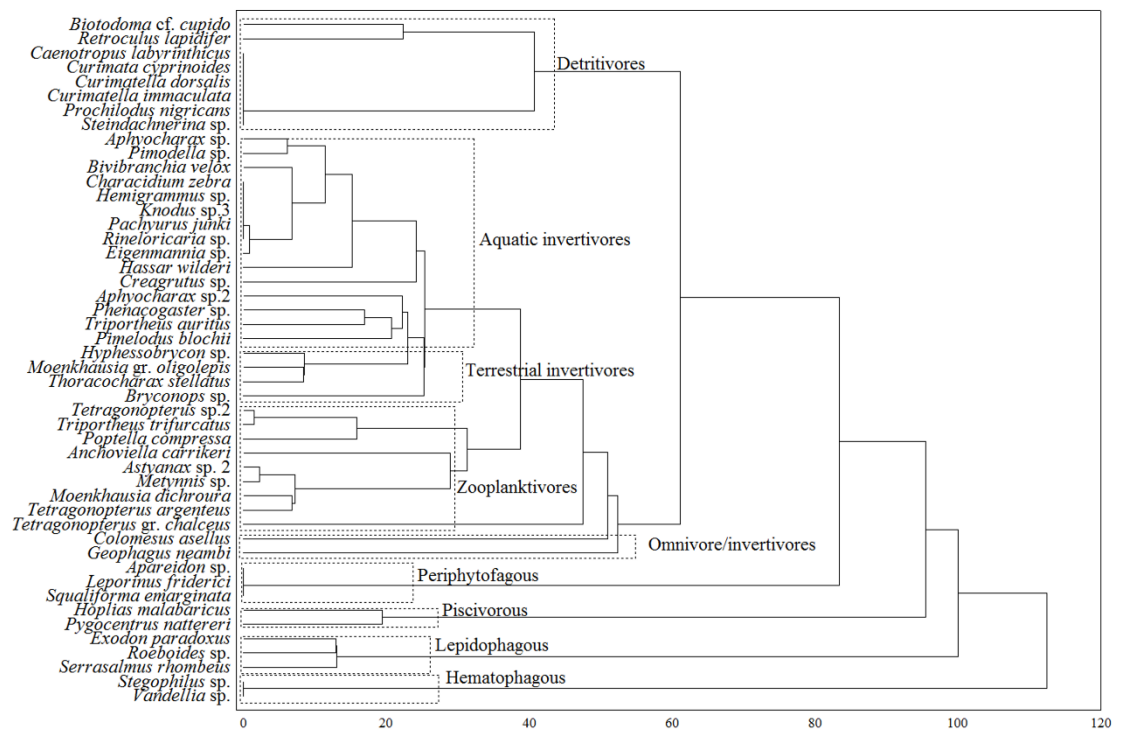


Fig. 2. Grouping in trophic groups of species found in Montaria lake, Crixás-açu and Araguaia rivers based on the diet similarity, from the values of the Alimentary Index.

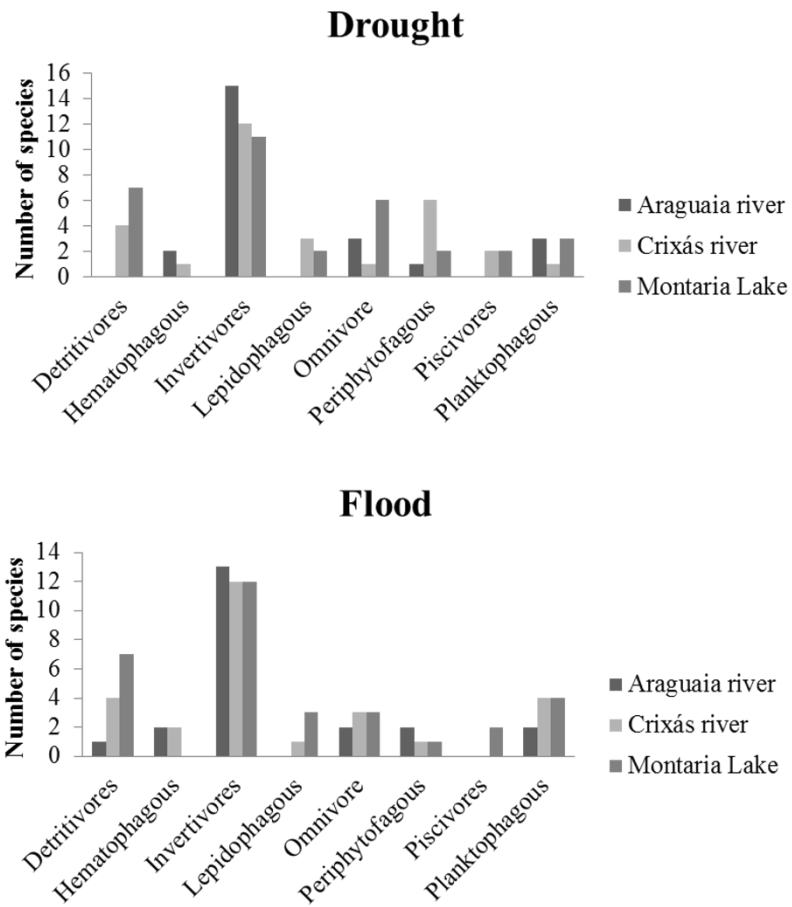


Fig. 3. Total number of species (S) in the drought and flood periods per trophic group in Araguaia and Crixás-Açu rivers and Montaria lake.

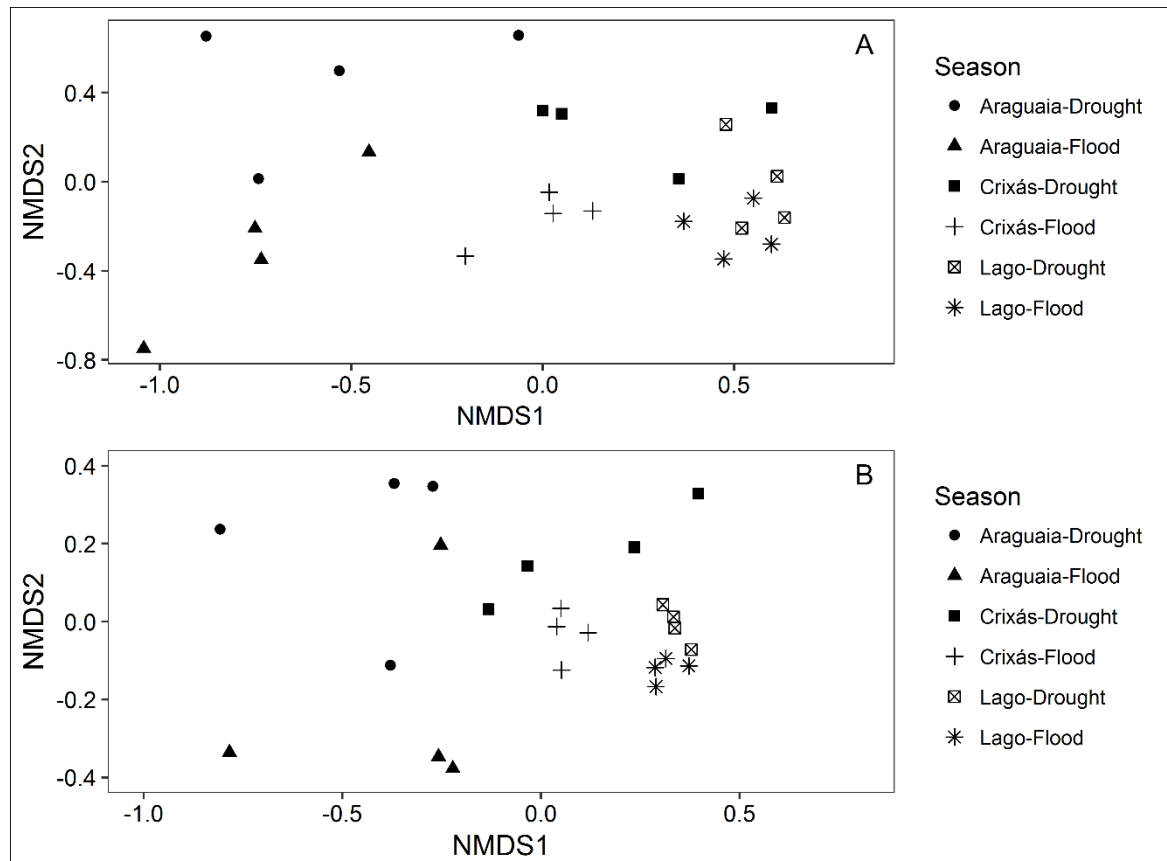


Fig. 4. Ordination by Non-metric Multidimensional Scaling (NMDS) based on abundance (A) and richness (B) of trophic groups registered in sediment banks during the drought and flood periods. *Stress 2D* = 0.099 for abundance, *stress 2D* = 0.091 for richness after 1000 permutations.

Supplementary material

Tabela S1. General classification of fish species into trophic groups (TG) based on the values of the Alimentary index (≥ 60 in bold) for food categories for all the samples. DT – Detritus; IT – Terrestrial invertebrates; IA – Aquatic invertebrates; PX – Fish; PE – Periphyton; MO – Mollusks; ES – Scales and fins; AF – Filamentous algae; MV – Plant material; OU – Others; SG – Blood; PL – Plankton; N – Number of stomachs with content.

Species	DT	IT	IA	PX	PE	MO	ES	AF	MV	OU	SG	PL	TG
<i>Biotodoma cf. cupido</i> (Heckel 1840)	71.2		28.8										Detritivore
<i>Caenotropus labyrinthicus</i> (Kner 1858)	100.0												Detritivore
<i>Curimata cyprinoides</i> (Linnaeus 1766)	100.0												Detritivore
<i>Curimatella dorsalis</i> (Eigenmann & Eigenmann 1889)	100.0												Detritivore
<i>Curimatella immaculata</i> (Fernández-Yépez 1948)	100.0												Detritivore
<i>Prochilodus nigricans</i> Spix & Agassiz 1829	100.0												Detritivore
<i>Steindachnerina</i> sp.	100.0												Detritivore
<i>Stegophilus</i> sp.											100.0		Hematophagous
<i>Vandellia</i> sp.											100.0		Hematophagous

<i>Aphyocharax</i> sp.	9.3	90.7							Invertivore
<i>Aphyocharax</i> sp.2	22.8	56.7			2.2			18.3	Invertivore
<i>Bivibranchia velox</i> (Eigenmann & Myers 1927)		94.9					5.1		Invertivore
<i>Bryconops</i> sp.	83.4	16.4			0.2				Invertivore
<i>Characidium zebra</i> Eigenmann. 1909		100.0							Invertivore
<i>Creagrutus</i> sp.	3.9	72.5			1.8	5.3	0.4	16.2	Invertivore
<i>Eigenmannia</i> sp.	0.1	99.4				0.5			Invertivore
<i>Hassar wilderi</i> Kindle 1895		87.2		12.8					Invertivore
<i>Hemigrammus</i> sp.		100.0							Invertivore
<i>Hyphessobrycon</i> sp.	65.6	34.4							Invertivore
<i>Knodus</i> sp.3		100.0							Invertivore
<i>Moenkhausia</i> gr. <i>oligolepis</i> (Günther 1864)	51.7	41.6		1.9			1.9	2.9	Invertivore
<i>Pachyurus junki</i> Soares & Casatti 2000		100.0							Invertivore
<i>Phenacogaster</i> sp.	28.2	71.8							Invertivore
<i>Pimelodus blochii</i> Valenciennes 1840	21.3	56.5	11.2		3.9	6.4	0.2	0.4	Invertivore
<i>Pimodella</i> sp.	6.4	88.7				5.0			Invertivore
<i>Rineloricaria</i> sp.		100.0							Invertivore
<i>Thoracocharax stellatus</i> (Kner 1858)	58.7	37.8						3.5	Invertivore

<i>Triportheus auritus</i> (Valenciennes 1850)	36.2	57.6			4.8		1.3	Invertivore
<i>Exodon paradoxus</i> Müller & Troschel 1844			9.2		90.8			Lepidophagous
<i>Roeboides</i> sp.					100.0			Lepidophagous
<i>Serrasalmus rhombeus</i> (Linnaeus 1766)					88.7	2.8	8.6	Lepidophagous
<i>Colomesus asellus</i> (Müller & Troschel 1849)		38.9	32.2	29.0				Omnivore
<i>Geophagus neambi</i> Lucinda, Lucena & Assis 2010		30.0	15.0			30.0	25.0	Omnivore
<i>Retroculus lapidifer</i> (Castelnau 1855)	54.4	43.4			2.2			Omnivore
<i>Tetragonopterus</i> gr. <i>chalceus</i> Spix & Agassiz 1829	1.3	14.6			3.6	36.8	43.7	Omnivore
<i>Tetragonopterus</i> sp.2	1.1	49.3			0.2		49.3	Omnivore
<i>Triportheus trifurcatus</i> (Castelnau 1855)		50.0					50.0	Omnivore
<i>Apareidon</i> sp.				100.0				Periphytophagous
<i>Leporinus friderici</i> (Bloch 1794)				100.0				Periphytophagous
<i>Aphanotorulus emarginatus</i> (Valenciennes 1840)				100.0				Periphytophagous

<i>Hoplias malabaricus</i> (Bloch 1794)			100.0				Piscivore
<i>Pygocentrus nattereri</i> Kner 1858			84.4	5.5	10.1		Piscivore
<i>Anchoviella carrikeri</i> Fowler 1940	16.2	13.6				70.2	Planktivore
<i>Astyanax</i> sp. 2		1.6				98.4	Planktivore
<i>Metynnis</i> sp.						100.0	Planktivore
<i>Moenkhausia dichrourea</i> (Kner 1858)	5.4	0.8				93.8	Planktivore
<i>Poptella compressa</i> (Günther 1864)		38.8				61.2	Planktivore
<i>Tetragonopterus argenteus</i> Cuvier 1816	0.6	3.6			3.6	92.3	Planktivore

Table S2. Comparação par-a-par da abundância e riqueza de grupos tróficos de peixes de bancos de areia marginais do Rio Araguaia, Rio Crixás- Açú e Lago Montaria, Planície do Bananal.

	Site vs Site	<i>F</i>	<i>R</i>²	<i>P</i>	<i>P</i> adjusted
Abundance	Araguaia vs Crixás	9.296	0.399	0.002	0.004
	Araguaia vs Lago	22.237	0.614	0.002	0.004
	Crixás vs Lago	6.830	0.328	0.001	0.003
Richness	Araguaia vs Crixás	7.342	0.344	0.002	0.003
	Araguaia vs Lago	22.142	0.613	0.001	0.003
	Crixás vs Lago	8.174	0.369	0.001	0.003

Table S3. Comparação par-a-par da abundância e riqueza de grupos tróficos de peixes entre dois períodos hidrológicos (dry and ebb) de bancos de areia marginais do Rio Araguaia, Rio Crixás- Açú e Lago Montaria, Planície do Bananal. Prefixo dos locais: ARA – Rio Araguaia; CRI – Rio Crixás-Açú; MON – Lago Montaria.

	Dry vs EBB	F	R²	P	p.adjusted
Abundance	ARA-EBB vs CRI-EBB	8.476	0.586	0.033	0.345
	ARA-EBB vs MON-EBB	14.863	0.712	0.031	0.345
	ARA-EBB vs ARA-DRY	2.882	0.324	0.108	0.345
	ARA-EBB vs CRI-DRY	8.712	0.592	0.023	0.345
	ARA-EBB vs MON-DRY	16.727	0.736	0.035	0.345
	CRI-EBB vs MON-EBB	8.089	0.574	0.043	0.345
	CRI-EBB vs ARA-DRY	9.401	0.610	0.023	0.345
	CRI-EBB vs CRI-DRY	7.936	0.569	0.026	0.345
	CRI-EBB vs MON-DRY	9.056	0.601	0.037	0.345
	MON-EBB vs ARA-DRY	13.513	0.693	0.038	0.345
	MON-EBB vs CRI-DRY	9.512	0.613	0.025	0.345
	MON-EBB vs MON-DRY	2.417	0.287	0.108	0.345
	ARA-DRY vs CRI-DRY	8.330	0.581	0.026	0.345
	ARA-DRY vs MON-DRY	16.205	0.730	0.024	0.345

	CRI-DRY <i>vs</i> MON-DRY	8.259	0.579	0.030	0.345
	ARA-EBB <i>vs</i> CRI-EBB	6.590	0.523	0.022	0.33
	ARA-EBB <i>vs</i> MON-EBB	17.129	0.741	0.035	0.364
	ARA-EBB <i>vs</i> ARA-DRY	3.169	0.346	0.068	0.364
	ARA-EBB <i>vs</i> CRI-DRY	6.412	0.517	0.029	0.364
	ARA-EBB <i>vs</i> MON-DRY	18.868	0.759	0.032	0.364
	CRI-EBB <i>vs</i> MON-EBB	14.804	0.712	0.026	0.364
	CRI-EBB <i>vs</i> ARA-DRY	8.110	0.575	0.035	0.364
Richness	CRI-EBB <i>vs</i> CRI-DRY	3.194	0.347	0.034	0.364
	CRI-EBB <i>vs</i> MON-DRY	15.151	0.716	0.036	0.364
	MON-EBB <i>vs</i> ARA-DRY	13.261	0.688	0.027	0.364
	MON-EBB <i>vs</i> CRI-DRY	5.178	0.463	0.031	0.364
	MON-EBB <i>vs</i> MON-DRY	3.031	0.336	0.049	0.364
	ARA-DRY <i>vs</i> CRI-DRY	5.287	0.468	0.03	0.364
	ARA-DRY <i>vs</i> MON-DRY	14.581	0.708	0.034	0.364
	CRI-DRY <i>vs</i> MON-DRY	3.918	0.395	0.03	0.364

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