



Response of fish communities to intense drought in Brazilian savanna streams

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ABSTRACT

The physical structures of streams are subjected to intense changes throughout the seasons. Intense drought in dry periods has been frequent and potentially harmful to aquatic species. In this study, we tested whether the changes in the habitat structure of the streams during the dry period determine the organization of fish communities. Five streams in the Upper Tocantins River were studied in the dry and rainy seasons. The species were characterized by 13 functional traits based on morphological measurements. The descriptors of functional diversity were: mean pairwise functional distance of species in the community (MPD) and mean functionally nearest species distance (MNTD). We also calculated the standardized effect size for MPD and MNTD, an indicator of functional redundancy, and compared the observed patterns with those expected by chance. Streams differed between seasons with respect to environmental variables. Functional diversity in the rainy season did not differ from the pattern expected by chance for both metrics. While functional diversity in the dry season has not differed from the pattern expected by chance for SES_{MPD} , a greater functional redundancy for SES_{MNTD} was found in this season. These results indicate that environmental changes in the streams during the dry season are important constraints for fish occurrence, preventing the occurrence of functionally original species. Therefore, a prospective scenario of dry-period intensification could result in functionally redundant communities, with functional homogenization of the regional species pool.

Keywords: ecomorphology, functional diversity, niche filtering.

Resposta das comunidades de peixes a intensa seca em riachos de savana brasileira

RESUMO

Os riachos são submetidos a intensas mudanças na sua estrutura física ao longo das estações. Secas intensas nos períodos de estiagem tem sido frequentes e potencialmente deletérias para as espécies aquáticas. Neste estudo, testamos se as alterações na estrutura do hábitat dos riachos no período da seca determinam a organização das comunidades de peixes. Foram estudados cinco riachos pertencentes à bacia do Alto rio Tocantins, amostrados no

período seco e chuvoso. As espécies foram caracterizadas por meio de 13 atributos funcionais baseados em medidas morfológicas. Os descritores de estrutura funcional das comunidades foram: distância média entre pares de espécies da comunidade (MPD) e distância média da espécie funcionalmente mais similar na comunidade (MNTD). Também calculamos o tamanho do efeito padronizado para MPD e MNTD, uma medida de redundância funcional, por meio da comparação dos padrões observados de MPD e MNTD com aqueles obtidos em comunidades formadas aleatoriamente em ambas as estações. A diversidade funcional da estação chuvosa não diferiu do padrão esperado ao acaso para ambas as métricas. Apesar da diversidade funcional na estação seca não ter diferido do padrão esperado ao acaso quando a métrica SES_{MPD} foi considerada, verificou-se uma maior redundância funcional nessa estação para a métrica SES_{MNTD} . Esses resultados indicam que as alterações nos riachos na estação seca representam filtros ambientais que restringem a ocorrência de espécies funcionalmente complementares. Nesse sentido, um cenário prospectivo de intensificação do período de seca poderia resultar em comunidades funcionalmente redundantes, com homogeneização funcional do pool regional de espécies.

Palavras-chave: diversidade funcional, ecomorfologia, filtragem de nicho.

1. INTRODUCTION

The environmental characteristics of tropical aquatic ecosystems are submitted to seasonal variations (Winemiller and Jepsen, 1998). These variations influence important factors related to the organization of aquatic communities (Casatti, 2005; Eros and Grossman, 2005), such as microhabitat availability, food resources, and flow and depth patterns (Eros e Grossman, 2005). In some regions, the small streams are submitted to intense changes in the structure of physical habitat throughout the seasons (Espírito-Santo et al., 2009). For example, in intense dry periods, the discharge of streams may be drastically reduced (Krupek et al., 2010).

Studies of the effect of seasonal variation on the pattern and process of biologic communities are especially important where the changes in the physical structure of the habitat are intense, such as in streams of Brazilian savanna (Cerrado). In this biome, the seasonal rainfall regime is composed of marked rainy (November to March) and dry (April to October) seasons (Scariot and Sevilha 2005). However, dry periods have become longer in recent years, and this effect has been intensified by climate change (Marengo, 2008).

Distributions of stream species facing such seasonal changes are not expected occur at random (Espírito-Santo et al., 2013). Many species are associated with specific habitat conditions and changes to abiotic characteristics after disturbances may influence their patterns of distribution and diversity. Further, alterations in the depth, width, flow and structure of the streambed throughout seasons influence the composition of fish species (Súarez and Petreire Júnior, 2005; Súarez; Lima-Júnior, 2009).

The importance of environment in driving community structure has been studied in light of the environmental filtering concept, according to which environmental constrains (filters) limit species occurrence, whose functional traits are incompatible with local conditions (Keddy, 1992; Poff et al., 1997). Communities structured by environmental filters tend to be composed of species that are functionally more similar, resulting in communities with lower diversity of functional traits than would be expected at random (Keddy, 1992, but see Kraft et al., 2015). In this study, we evaluated the importance of environment in structuring the fish communities of streams during dry periods. We studied the functional structure of fish communities in streams of the Brazilian savanna (Cerrado), and hypothesized that, during the dry period, only species with a particular set of traits will persist, and that the communities will therefore be functionally redundant.

2. MATERIALS AND METHODS

2.1. Study area

The Upper Tocantins River Basin covers an area of approximately 123,800 km² (Ferreira and Tokarski, 2007) and has been historically treated as an independent system of the Amazon Basin (Barthem and Schwassmann, 1994). This study was conducted in five streams (1st to 4th order) belonging to the Montividiu Microbasin (Figure 1). Samplings were conducted during the rainy season (February, 2013) and during the end of the dry season (September and early October, 2012). Monthly-accumulated precipitation in the region during sampling periods was 102 and 10 mm, respectively, according to the Instituto Nacional de Meteorologia (INMET).

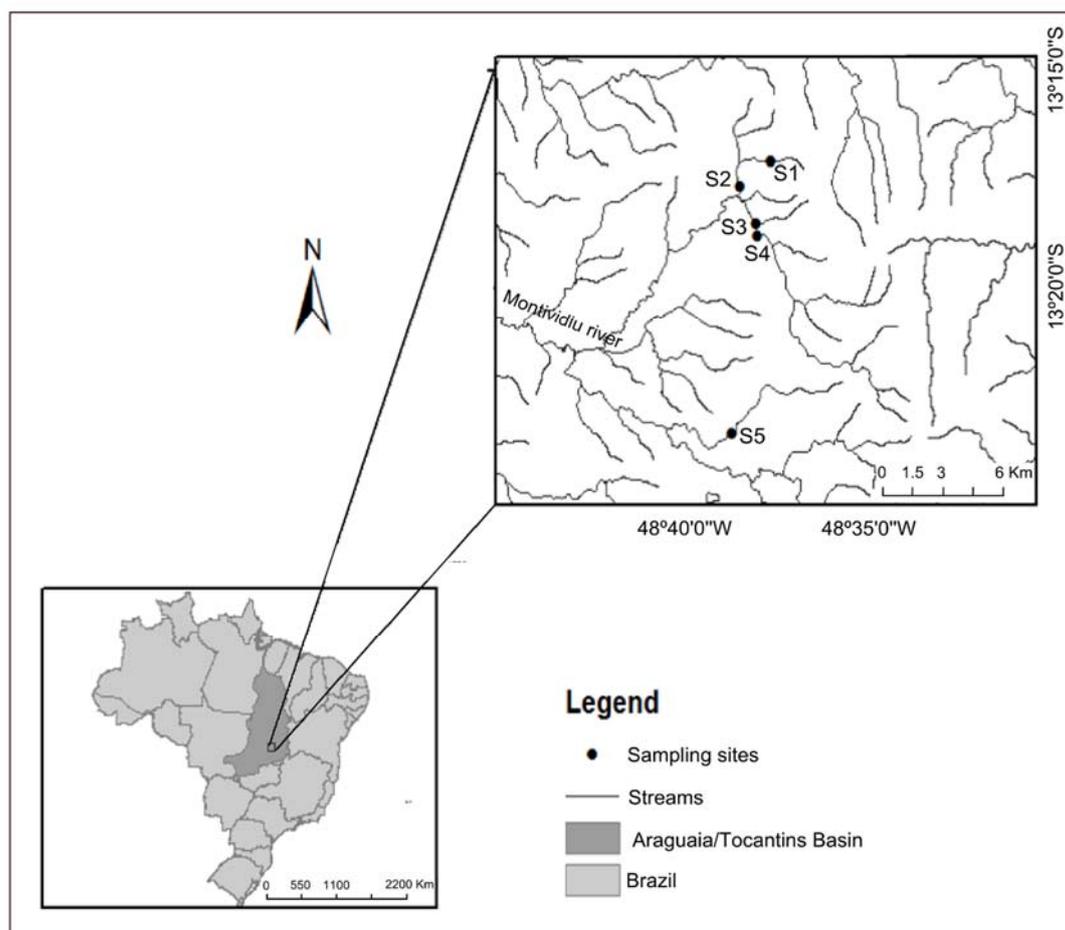


Figure 1. Locations of the sampled streams in the Araguaia/Tocantins Basin, Goiás State, Brazil.

2.2. Fish sampling and environmental variables

We sampled stream fish communities in 80-meter long stretches using seine- (2.50 x 1.20 m) and dip-nets for one hour in each stream each season. Fish were captured and fixed in a solution of formaldehyde (10%) and, after 72 hours, they were transferred to an ethanol solution (70%). Species were identified by a taxonomy specialist (Fernando R. Carvalho, Universidade Federal do Mato Grosso do Sul, Brazil).

We performed local-habitat characterization by dividing sampled stretches into nine transversals and equidistant transects where we measured width, depth, superficial water current velocity, substrate composition and cover. Widths were measured along the transversal transects and depths in five equidistant points along these transects. Substrate compositions

were represented by the proportion of each component: silt, sand, gravel, rock, clay and pebble. Cover was represented by trunks and branches in the inner habitat. Estimated values for each variable were averaged in order to obtain the mean values for each stream.

2.3. Functional diversity

We characterized fish according to habitat use and trophic ecology based on 13 ecomorphological indices calculated from 18 morphometric measurements: compression index, depression index, relative depth, relative length of caudal peduncle, caudal peduncle compression index, index of ventral flattening, relative area of pectoral fin, aspect ratio of pectoral fin, relative area of caudal fin, relative eye position, relative length of head, relative width of mouth, and mouth orientation (Gatz, 1979; Freire and Agostinho, 2001; Casatti and Castro, 2006; Oliveira et al., 2010). We obtained morphological measurements by using a digital caliper on 10 adult individuals of each species (except for those whose abundance was lower than 10 individuals). Fin areas were estimated using millimetered paper.

Functional diversity (FD) was calculated using two metrics: MPD (mean pairwise distance) and MNTD (mean nearest neighbor distance). These metrics were originally described to assess phylogenetic diversity (Tucker et al., 2017), but have been widely used in functional ecology studies (Hidasi-Neto et al., 2012; Casatti et al., 2015). The MPD is the average of the species' pairwise distances obtained from the community trait matrix including the entire species pool. While MNTD is similar, the calculation is based on the average distance between each species of the community with its respective functionally more-similar species (Webb, 2000). Thus, while MPD is more influenced by changes in the root of the dendrogram, MNTD is more sensitive to changes in the terminal branches of the functional dendrogram. We obtained the functional dendrogram using the Unweighted Pair Group Method Using Arithmetic Mean (UPGMA) from a Euclidean distance matrix of standardized (z-score) ecomorphological indices.

2.4. Data analysis

We conducted a Principal Components Analysis (PCA) to describe the spatial and temporal variations of stream habitat characteristics. In order to test whether the drought acts as an environmental filter, we measured the standardized-effect size (SES_{MPD} e SES_{MNTD}) for each community in each season (Equation 1), which is based on a comparison of the observed values with those obtained in null communities (1000 permutations).

$$SES_{MPD \text{ or } SES_{MNTD}} = \frac{\text{obsMPD or obsMNTD} - \text{average MPD}_{\text{null or MNTD}_{\text{null}}}}{\text{standard deviation of MPD}_{\text{null or MNTD}_{\text{null}}}} \quad (1)$$

where:

obsMPD and obsMNTD are observed values of MPD and MNTD, respectively, and MPD_{null} and MNTD_{null} correspond to values of randomized communities.

The null models were built by a random shuffling of traits across species in the dendrogram. We tested whether the mean values of SES_{MPD} and SES_{MNTD} were different than random expectation (mean 0) by using the one-sample t test. Statistically significant negative values of SES indicate functional redundancy, which is compatible with the hypothesis of environmental filtering acting on species assembly (Webb et al., 2002). We compared the species richness and FD metrics between dry and rainy seasons using the t-test ($p < 0.05$). The assumptions of normality and homoscedasticity were met. Indices of functional diversity were calculated using the picante package of R software (R Development Core Team, 2012).

3. RESULTS

Principal Components Analysis (PCA) summarized environmental variation found in the stream' stretches into two dimensions. The first two axes of PCA explained 61.1% of the variation of the data (Figure 2). The first axis explained 32.8% of the data variation, represented by substrate (litter and pebble), flow and width, and distinguished the samples of dry and rainy seasons (Figure 2). The dry season stretches exhibited higher proportions of litter, lower proportions of pebble (loadings: -0.87 and 0.71, respectively), were narrower, and had slower waterflow (loadings: 0.81 and 0.86, respectively). The second axis explained 28.3% of the data variation and represented spatial variation among stream' stretches in relation to substrate (gravel and rocks), and depth and tree branches in the inner habitat (loadings: -0.80, 0.73, 0.78 and -0.73, respectively). This axis represented the differences among deeper stretches with higher proportions of rocks (Streams 1, 2, and 5), and those (Streams 3 and 4) with higher proportions of gravel and tree branches in the inner habitat (Figure 2).

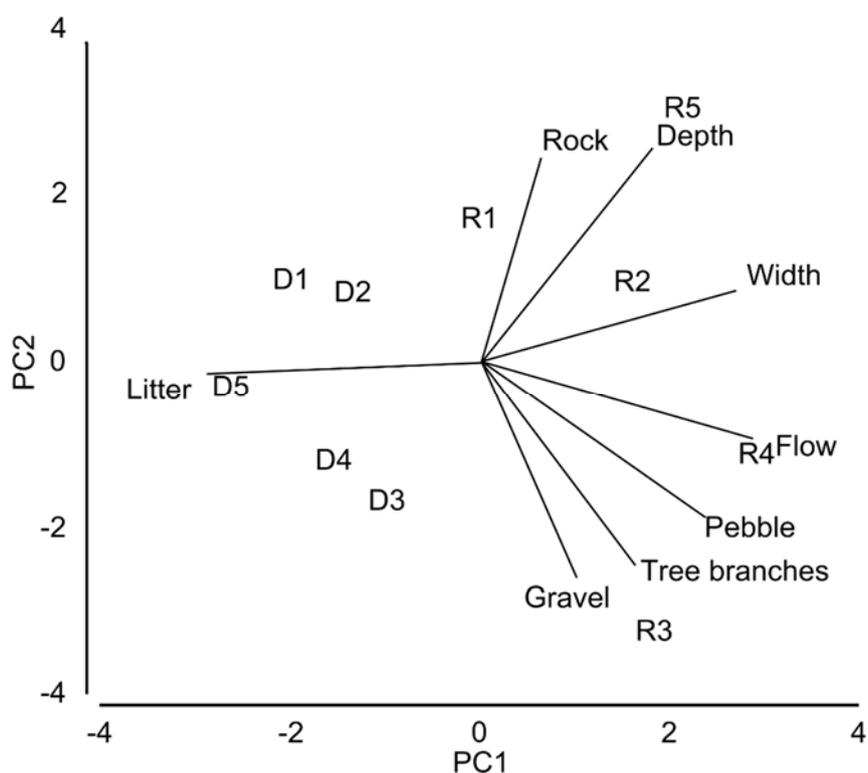


Figure 2. Ordination obtained in the Principal Component Analysis (PCA) of the five stream stretches in the dry (D) and rainy (R) seasons, according to the descriptors of physical habitat. Stream numbers according to Figure 1.

A total of 2,383 individuals belonging to 30 species, 11 families and five orders were sampled (Table 1, Figure 3). A functional dendrogram summarized the pairwise functional dissimilarities between species (Figure 3). The species' richness and functional diversity (MPD and MNTD) did not change between seasons ($p > 0.14$). The values of SES_{MPD} in the rainy and dry seasons were not different from mean zero ($p > 0.26$). However, SES_{MNTD} in the dry season was negative and significantly different from the pattern expected by chance ($p=0.023$) (Figure 4).

Table 1. Fish species sampled in streams of the Upper Tocantins River Basin in the dry (D) and rainy (R) seasons. Streams numbers are according to Figure 1.

Order, FAMILY, <i>Species</i>	Code	D1	D2	D3	D4	D5	R1	R2	R3	R4	R5
Characiformes											
ANOSTOMIDAE											
<i>Leporinus</i> sp.	Lepsp					1					
CHARACIDAE											
<i>Astyanax elachylepis</i>	Astela	1			2		4		14	5	
<i>Astyanax goyacensis</i>	Astgoy	13		12	3	26	2		2		
<i>Bryconops melanurus</i>	Brymel		2	2		1		4		11	3
<i>Creagrutus britskii</i>	Crebri			1	10					2	10
<i>Hyphessobrycon heterorhabdus</i>	Hyphet	104	73	29	5	264	4	14	3	3	35
<i>Jupiaba apenina</i>	Jupape	1	9	4	1	5	2		1	1	
<i>Knodus cf. chapadae</i>	Knocha	68	71	92	259	186	57	27	77	102	23
<i>Moenkhausia oligolepis</i>	Moeoli	10	3	10		39	8	5	6		4
<i>Moenkhausia pankilopteryx</i>	Moepan		17		1	3	4		3		
<i>Serrapinnus</i> sp.	Sersp		2								
CRENUCHIDAE											
<i>Characidium zebra</i>	Chazeb			13	22	74	2	2	2		1
CURIMATIDAE											
<i>Steindachnerina amazonica</i>	Steama					3					
Perciformes											
CICHLIDAE											
<i>Cichlasoma araguaiense</i>	Cicara										1
<i>Crenicichla labrina</i>	Crelab		2			10	1	1			49
Siluriformes											
CALLICHTHYIDAE											
<i>Aspidoras aff. poecilus</i>	Asppoe	3	8	28	1						
HEPTAPTERIDAE											
<i>Imparfinis schubarti</i>	Impsch			1	8				1		
<i>Phenacorhamdia</i> sp.	Phesp	3		15	4			1	14	4	
<i>Pimelodella</i> sp.	Pimsp				1					1	
<i>Rhamdia quelen</i>	Rhaque	2					4		1		
LORICARIIDAE											
<i>Ancistrus</i> sp.	Ancsp	4	2	4	14	14	2	2	2		1
<i>Farlowella oxyrhyncha</i>	Faroxy									3	
<i>Hypostomus</i> sp.	Hypsp				2	1	1	3		6	4
<i>Loricaria</i> sp.	Lorsp				2			2		1	
<i>Otocinclus hasemani</i>	Otohas				1	19					10
<i>Rineloricaria lanceolata</i>	Rinlan				1		1	4		1	
Continua...											

Continuação

Gymnotiformes

GYMNOTIDAE

<i>Gymnotus</i> aff. <i>carapo</i>	Gymcar	13	5	2	1	1
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STERNOPYGIDAE

<i>Eigenmannia trilineata</i>	Eigtri	1				
<i>Sternopygus macrurus</i>	Stemac		2	3		

Synbranchiformes

SYNBRANCHIDAE

<i>Synbranchus marmoratus</i>	Synmar	2			1	
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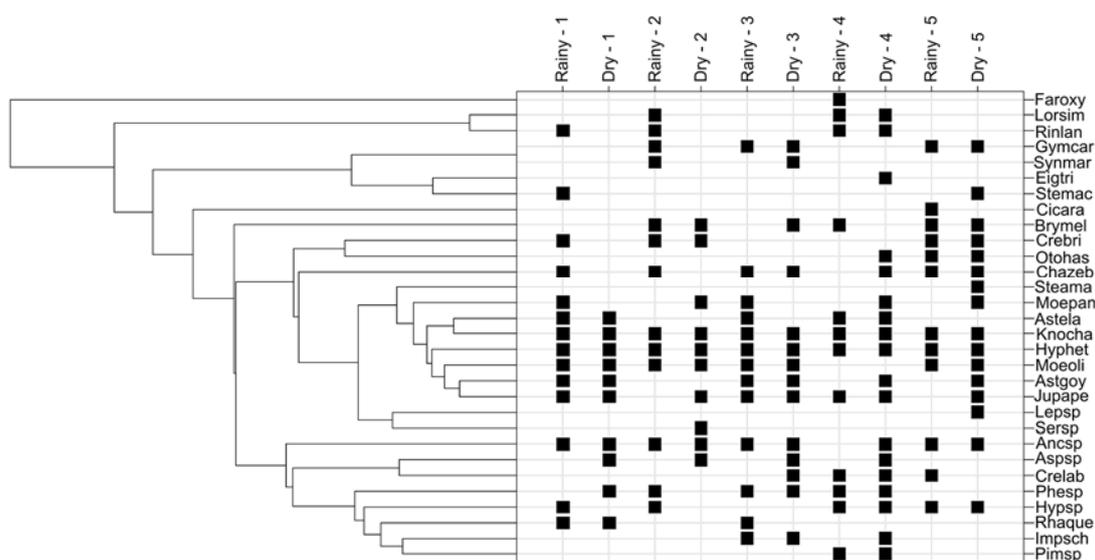


Figure 3. Functional dendrogram with squares indicating the species occurrence in the sampled streams (1 to 5) in dry and/or rainy seasons. Species codes are according to Table 1.

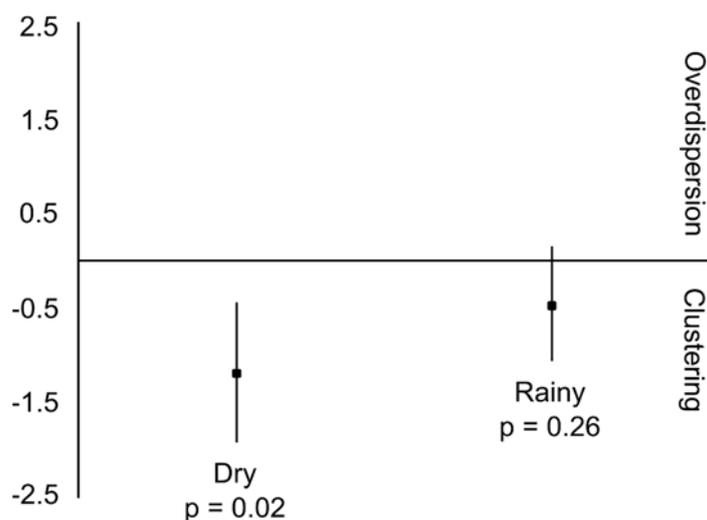


Figure 4. Mean \pm standard deviation of the standardized-effect sizes of functional diversity (MNTD) in stream fish communities in the dry and rainy season. p-value are shown.

4. DISCUSSION

Studies on how biodiversity is influenced by fluctuation on environmental conditions are important, mainly in a context in which alterations are anthropogenically induced. While seasonal alterations of stream conditions are influenced by natural seasonal climate cycles, longer dry periods and hence the intensification of drought has been attributed to climate change (Marengo, 2008). Our results highlight the influence of the drought to the physical and biological components of streams. The results suggest that environmental changes drive functional structures of fish communities across seasons, resulting in redundant communities during dry periods.

The changes in physical habitat that we detected throughout the seasons resulted from the reduction of width and water flow during the dry period due to the lack of rain and hence the reduction of water volume (Casatti, 2005; Espírito-Santo et al., 2009). Moreover, slow water flow, associated with the loss of leaves by riparian vegetation contributes to the deposition of a greater amount of litter. Despite evident alterations in the physical structure of the habitat, changes in the community structure were less drastic. While some streams showed increased species number during the dry season, others showed reductions. This variability is compatible with the differences in the physical structure among streams, as shown by the PCA, and contributed to the lack of differences in species' richness between seasons.

Streams that showed increased numbers of species during the dry season were composed mainly of redundant species. On the other hand, the streams exhibiting reductions in species number during the dry season mainly lost more original species. In both conditions, communities tend to become more functionally redundant. These patterns were supported by the results of standardized effect size of MNTD, which indicates functional redundancy during the dry season, and is compatible with the constraints imposed by environmental filters (Mouillot et al., 2007). MNTD is a measurement of functional diversity that is more influenced by changes in the terminal branches of the functional dendrogram (Webb, 2000). The functional redundancy observed for this index and not for MPD suggests that, during the dry season, the communities are composed by functionally more-similar species; but at the same time, these communities still have species of different functional groups, maintaining unchanged patterns in the base of the functional dendrogram (sensible to MPD).

Streams during the dry season included mainly species occupying the middle of the functional dendrogram. These species (e.g. *Moenkhausia pankilopteryx* and *Astyanax elachylepis*, and *A. goyacensis*) shared characteristics with other characid species that are compatible with the slow water flow during the dry season, such as compressed body, greater body depth, and compressed caudal peduncle. Pairs of functionally similar species (e.g. *A. goyacensis* and *Jupiaba apenima*) were more commonly found during the dry season. Bottom-dwelling fish with redundant traits, such as *Aspidoras* aff. *poecilus* and *Crenicichla labrina*, and with cylindrical body shape, were also common during the dry season, mainly associated with the banks and trunks and roots. Therefore, even when richness was increased during the dry season, species were packed in some parts of the functional space. This pattern could be interpreted as within-site heterogeneity (Kraft et al., 2015), associated with filters acting in a microhabitat scale.

Functional redundancy has been interpreted as evidence of environmental filtering, as environmental constraints would select only species with a particular set of traits adapted to local conditions (Kraft et al., 2015). However, phenotypic similarities among co-occurring species can hinder other processes (e.g. competition) (Mayfield and Levine, 2010). For example, the covariance between competitive exclusion with the influence of environment on species survival implies that the species-environment relationship with a clustering of

functionally similar species can be simultaneously determined by different mechanisms (Cadotte and Tucker, 2017). However, evidence from literature has provided little support for the role of competition in structuring the fish communities of streams (Oberdorff et al., 1998; Mouillot et al., 2007). Furthermore, traits we used to characterize fish species (*i.e.* habitat use and trophic ecology) are strongly associated with the response of fish species to physical habitat structure (Teresa and Casatti, 2012; 2017). Therefore, while our results suggest direct influence of environment on fish community structure via habitat filtering, more studies are needed in order to disentangle the relative influence of other ecological mechanisms underlying seasonal shifts in the functional structure of fish communities.

In summary, our results evidence seasonal changes in the physical habitat structure of Cerrado streams. Such changes are sufficient to alter biological processes, generating a pattern of functional redundancy during the dry period, when environmental conditions are more restrictive. These constraints probably involve not only aspects of physical habitat structure *per se*, influencing the availability of microhabitat and food resources, but physico-chemical features as well. Therefore, our study provides evidence of the importance of environment in driving seasonal species turnover in streams.

5. ACKNOWLEDGMENTS

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