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The influence of environmental variables on the functional structure of headwater stream fish assemblages: a study of two tropical basins in Central Brazil

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We investigated functional patterns of fish assemblages of two adjacent basins (Araguaia and Tocantins) to test whether their headwater stream fish assemblages are more functionally (dis)similar than expected by chance and whether these (dis)similarities are related to differences of environmental conditions between basins. We used an analysis of similarities (ANOSIM) on a functional dissimilarity matrix to test for (dis)similarities between fish assemblages of both basins. We performed RLQ and fourth-corner analyses to determine fish species trait-environment relationship. Our results revealed functional dissimilarities between fish assemblages of both basins and significant species trait-environment relationships, suggesting that environmental conditions are driving such dissimilarities. Inter-basin dissimilarities are mainly driven by altitudinal and water temperature gradients, whereas dissimilarities among streams within the basins are influenced by channel depth, turbidity and conductivity. These five environmental variables mostly affected six fish species traits (body mass, water column position, substrate preference, parental care, foraging locality and migration) in different manners. This study is an attempt to understand functional trends of fish assemblages in a tropical region that remains poorly known but severely threatened.

Nós investigamos os padrões funcionais das assembleias de peixes de duas bacias adjacentes (Araguaia and Tocantins) para testar se as assembleias de peixes de seus riachos de cabeceira são funcionalmente mais (dis)similares do que o esperado ao acaso e se estas (dis)similaridades estão relacionadas a diferenças nas condições ambientais entre as bacias. Nós utilizamos uma análise de similaridades (ANOSIM) sobre uma matriz de dissimilaridade funcional para testar por (dis)similaridades entre as assembleias de peixes das duas bacias. Nós realizamos análises de RLQ e fourth-corner para determinar a relação entre o ambiente e a estrutura funcional das assembleias de peixes. Nossos resultados revelaram dissimilaridades funcionais entre as assembleias de peixes de ambas as bacias e relações significativas entre atributos das espécies e o ambiente, sugerindo que as condições ambientais estão direcionando tais dissimilaridades. As dissimilaridades entre bacias são influenciadas principalmente pelos gradientes de altitude e temperatura da água, enquanto as dissimilaridades entre os riachos na bacia pela profundidade do canal, turbidez e condutividade. Estas cinco variáveis ambientais afetaram principalmente seis atributos das espécies de peixes (massa corporal, posição na coluna de água, preferência por substrato, cuidado parental, local de forrageio e migração) de diferentes maneiras. Este estudo é uma tentativa para entender os padrões funcionais das assembleias de peixes de uma região ainda pouco conhecida, mas, seriamente ameaçada.

Keywords: ANOSIM, Community ecology, Functional ecology, RLQ analysis, Tocantins-Araguaia river basin.

Introduction

A central challenge of ecological research relies on revealing how diversity is structured through space and which factors are responsible for such organization. An observed pattern in ecology is the decrease of compositional similarity between localities as distance increases (Nekola & White, 1999), often as a consequence of dispersal limitation through geographic barriers or spatially structured environmental gradients (Olden *et al.*, 2010). In freshwater systems, remarkable differences in fish species composition among localities of distinct basins have been observed in temperate (Cross *et al.*, 1986; Swift *et al.*, 1986; Matthews & Robinson, 1988) and tropical (Mendonça *et al.*, 2005)

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regions, reinforcing the idea that the regional biogeography of fish assemblages is frequently limited by drainage basin limits (Gilbert, 1980). In this context, one may expect a higher degree of similarity between species composition of any localities within a basin than with species composition of localities at neighboring basins (Matthews, 1998). However, while species composition of fish assemblages is strongly influenced by historical and geographical factors, functional traits composition is mainly structured by local environmental drivers (Hoeinghaus *et al.*, 2007), such as: hydrological factors (Poff & Allan, 1995; Lamouroux *et al.*, 2002), habitat features (Hoeinghaus *et al.*, 2007; Teresa & Casatti, 2012), environmental gradients (Ibañez *et al.*, 2007; Pease *et al.*, 2012) and urbanization (Cunico *et al.*, 2011).

The hypothesis of community convergence predicts that distant and unrelated communities (or assemblages) will converge in their species traits composition when living under similar environmental conditions (Ricklefs, 2006). As a consequence, fish assemblages' traits composition of separated hydrographic basins will be dissimilar if abiotic characteristics of their environments are different. Several studies described species traits similarities among fish assemblages of distinct regions. For example, Lamouroux *et al.* (2002) found out that fish assemblages from European and North American streams are similar along geomorphic and hydraulic gradients for most biological traits evaluated in their study. Ibañez *et al.* (2009) described similar patterns for invertivorous and omnivorous fish species among fish assemblages of tropical and temperate regions. Logez *et al.* (2010) demonstrated that stream fish assemblages from Mediterranean and western European responded in a similar way along environmental gradients. Cunico *et al.* (2011) also found similarity between species functional traits of fish assemblages from Brazil and USA urban streams despite their differences in species composition. In freshwater systems, headwater streams are suitable habitats to test the consequences of community convergence hypotheses since they, as all lotic systems, are usually regulated by similar physical processes (Lamouroux *et al.*, 2002), which together with other abiotic factors may predominate over biotic interactions (Ostrand & Wilde, 2002; Grenouillet *et al.*, 2004).

In this paper, we used a dataset of 25 headwater streams distributed between two adjacent basins of Central Brazil (Araguaia and Tocantins river basins) to unveil functional patterns of their fish assemblages. In consequence of community convergence, we expect that headwater stream fish assemblages of both basins will be more functionally similar than expected by chance because of similar environmental conditions. Our main goal in this study is to answer the following questions: *i*) Are headwater fish assemblages of the Araguaia and Tocantins basins more functionally (dis)similar than expected by chance?; *ii*) If dissimilar, are the environmental differences driving the inter-basin pattern of assemblages' functional differentiation?

Material and Methods

Study area. The Tocantins-Araguaia river basins is one of the most important watersheds in the Amazonian province (Ribeiro *et al.*, 1995; Lévêque *et al.*, 2008). The drainage area of the rio Araguaia (hereafter Araguaia basin) and the rio Tocantins (hereafter Tocantins basin) are adjacent in Central Brazil. In this region, they are geographically separated by Serra do Caiapó and Serra dos Pirineus (Tejerina-Garro, 2008) and possess distinct physiographic units along their longitudinal profiles (Ribeiro *et al.*, 1995). Added to these physiographic disparities, rio Araguaia is known as a floodplain river with a low drainage density and it remains connected with its principal tributaries during the wet season, whereas the rio Tocantins is a channelized river with a high drainage density and fewer floodplain lakes (Ribeiro *et al.*, 1995).

Data and sampling protocol. Analyses were performed on data from 25 headwater streams distributed between Araguaia (13) and Tocantins (12) basins (Fig. 1). We considered a stream as a headwater by its location in the river system (1^{st} - 3^{rd} order; Vannote *et al.*, 1980) and drainage area (10<drainage area<1,000km²; Meybeck *et al.*, 1996). We determined stream order using Strahler's modification of Horton's scale (Petts, 1994). We checked streams location and order using a geographical information system map (1:250,000), available in the website of the *Sistema Estadual de Estatística e de Informação Geográfica de Goiás* (SIEG, 2014).

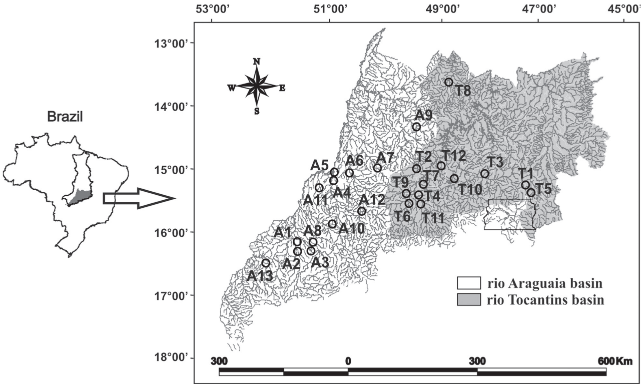

Fig. 1. Locality of streams sampled in the Araguaia (A1-A13) and Tocantins (T1-T12) river basins, Central Brazil. Tocantins-Araguaia basin is represented in the small map of Brazil.

All headwater streams were sampled during dry season - May to September 2008 - when fishes are captured more efficiently (Pease *et al.*, 2012) and the relationship between habitat and fish assemblage structure is stronger (Willis *et al.*, 2005). For each stream, a reach of 50m was defined and fish species were sampled with a seine net (4m x 1,5m x 1cm of mesh between opposing knots), which is an efficient sampling technique when the focus is on ecological patterns of species richness and composition (Medeiros *et al.*, 2010). The sampling effort was standard for all reaches, that is, ten passes along the reach by two persons handling the seine net. All specimens collected were stored in the collection of the Centro de Biologia Aquática Pontifícia Universidade Católica de Goiás for a first triage. After that, fish specimens were sent to the laboratório de Ictiologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul for identification.

Species traits and environmental variables. For all fish species, we collected data for eight functional traits: average body mass, trophic guild, water column position, parental care, foraging locality, substrate preference, foraging method and migration (Table 1 and supplementary material in Table S1). Body mass was calculated as the mean value for all organisms of the species. The substrate preference and the foraging method were obtained from field data. To determine substrate preference all locations where the species was collected were evaluated and the substrate(s) identified. Then, for each species, we calculated their occurrence frequency in each substrate. The substrate preference was the substrate where the species had higher frequency of occurrence. Foraging locality was determined according to streams velocity, and we considered streams with water velocity superior to 20 cm/s as running waters (riffles) while streams under this limit as standing waters, slower pools (see Rezende, 2007). The other functional traits were obtained from specialized literature (Melo, 2011) and an on-line database for fishes (Froese & Pauly, 2014). If information for a species was not found, the data for the genus or family was extrapolated to the species level. If there was only one species in the genus and extrapolation was not possible, we considered species trait as not available (NA).

For each reach, three transversal transects were delimited and used to measure eight environmental variables: altitude (m), channel depth (m), channel width (m), turbidity (NTU), pH, conductivity ($\mu S.cm^{-1}$), dissolved oxygen ($mg.l^{-1}$), and water temperature (°C). Altitude was measured in the first transect with a GPS (Garmin 12) and turbidity was measured in the middle transect with a turbidimeter (LaMotte 2020). All other variables were measured in all transects using: an oximeter (Lutron YK-22DO) for dissolved oxygen and temperature, a conductivity meter (WTW 315i) for conductivity, a measuring rope for channel depth, a rangefinder (Bushnell-Yardage Pro 500) for channel width distance and a pH meter (Lutron PH-208) for pH. For each environmental variable measured in more than one transect, we used in our analyses the mean value of the variable for all transects.

Analyses. Based on the available data, we constructed three matrices for analyses: a presence-absence matrix (species *vs.* site), an environmental matrix (environmental variables *vs.* site) and a functional traits matrix (species *vs.* traits). To test for functional dissimilarities between headwater fish assemblages of both basins, we ran a one-way analysis of similarities (ANOSIM) that is a non-parametric variant of analysis of variance (Clarke, 1993). This statistical method operates directly on a dissimilarity matrix and computes if differences between groups are greater than those within groups (Oksanen *et al.*, 2014). We performed the ANOSIM using a functional dissimilarity matrix among communities that was obtained using a double principal coordinate analysis (DPCoA). It takes into account differences between species to describe the diversity of a community and, then, computes differences between two communities (Pavoine *et al.*, 2004). Since we had qualitative and quantitative traits together in our functional matrix, we used a modification of Gower distance to obtain the dissimilarity matrix (Pavoine *et al.*, 2009). We ran ANOSIM with 999 permutations. All analyses were performed in the R software (R Development Core Team, 2014).

To test for functional traits response to environmental conditions we used a combination of two methods: RLQ (Dolédec *et al.*, 1996) and fourth-corner analysis (Legendre *et al.*, 1997). Both methods are based on the analysis of three matrices: R (environmental characteristics of sampling locations), L (species distribution across sampling locations) and Q (species traits). The RLQ method is a multivariate technique that performs a double inertia analysis of matrices

Table 1. Category and codes by functional trait of fish species sampled in 25 headwater streams of Araguaia and Tocantins river basins.

Trait	Category	Code
Average body mass (g)	Average body mass	ABM
Trophic guild	Algivorous	A
	Omnivorous	O
	Carnivorous	C
	Detritivorous	D
	Invertivorous	I
Parental care	Parental care	Y
	No parental care	N
Water column position	Benthic	BE
	Pelagic	P
	Benthopelagic	BP
Foraging method	Visual feeding	V
	Barbells	B
	Electricity	E
Substrate preference	Sand	S
	Gravel	G
	Rock	R
	Sand/gravel	SG
	Sand/rock	SR
	Gravel/rock	GR
Foraging locality	Lentic	LE
	Lotic	L
Migration	Migratory	M
	Non-migratory	NM

R and Q, assuming that matrix L is the link between environment and species traits (Dolédec *et al.*, 1996). Initially, matrices R and Q are submitted to an ordination method (principal coordinate analysis, PCA) and, then, used to constrain a correspondence analysis of the central matrix L (Dray *et al.*, 2003) followed by a Monte Carlo permutation test (999 iterations with a sequential approach; ter Braak *et al.*, 2012). The analysis produces a matrix that describes traits-environment associations, called fourth-corner matrix, which summarizes the joint structure of the three matrices (Dray *et al.*, 2014). The fourth-corner method also combines matrices R, L and Q into a single matrix describing traits-environment associations (fourth-corner matrix; Legendre *et al.*, 1997). Additionally, this analysis tests the relationship between one trait and one environmental variable at a time, allowing the evaluation of individual trait-environmental relationships. When the evaluated relationship is between two quantitative variables the link is measured by a Pearson correlation, but when the evaluated relationship is between one quantitative and one qualitative variable the link is measured by Pseudo-F or Pearson r (Dray & Legendre, 2008). For fourth-corner analysis, we performed a log-transformation on each environmental variable, excepting for pH, to increase linearity and avoid extreme values, given the different nature and scale of them. RLQ and fourth-corner are complementary methods and their combined use may improve strongly the study of trait-environment associations (Dray *et al.*, 2014). To run RLQ and fourth-corner analyses, we used the package ADE-4 (Dray & Dufour, 2007) implemented in the R software (R Development Core Team, 2014).

Results

We found 62 species occurring in the 25 headwater streams sampled. Forty-nine species were found in the streams of the Araguaia basin, while 37 species were found in those of the Tocantins basin, and 24 species were common to streams of both basins (Table 2). The average species richness for Araguaia basin streams was 9.69, while for the streams of the Tocantins basin was 7.41.

Conversely to the expected, we found functional dissimilarity between fish assemblages of both basins (ANOSIM; R = 0.09, p = 0.03). The results of the RLQ analysis revealed significant relationship between fish species traits and environmental variables (p = 0.01, Monte Carlo permutation test; Table 3) with the first and the second axes accounting for 40.54% and 25. 76% of the total variance, respectively. The RLQ and fourth-corner analysis indicated that the first axis is related to inter-basin dissimilarities that are mainly driven by the environmental variables altitude and water temperature (Figs. 2a-c). Inter-basin dissimilarities are more accentuated for the altitudinal and water temperature gradients. Ten of the 12 streams of the Tocantins basin displayed high altitudinal values (from 534 to 942 m), while 12 of 13 streams of the Araguaia basin low values (218 to 400 m); nine of the 12 streams of the Tocantins basin displayed low water temperature (17.3 to 22.6 ºC), while eigth of 13 streams of the Araguaia basin high water temperature (24.1 to 27.5 ºC). On the other hand, the second axis is related to dissimilarities among streams independently of the basin and mostly driven by turbidity, channel depth and conductivity (Figs. 2a-c).

The five environmental variables influenced principally on six species traits: average body mass, parental care, water column position, foraging locality, substrate preference and migration (Table 3 and Figs. 2c-d). Average body mass is positively correlated to the altitudinal gradient ($p < 0.01$), but it is negatively correlated to channel depth ($p < 0.01$). The presence of fish species displaying parental care is associated to an increase of water turbidity ($p = 0.04$). Fish water column position is influenced by gradients of altitude ($p = 0.04$), turbidity ($p = 0.03$) and conductivity ($p = 0.01$). Benthic species are negatively associated to altitude ($p = 0.01$) and positively to turbidity ($p = 0.01$) and conductivity ($p = 0.02$). Fish species preference for gravel is positively correlated with altitude ($p = 0.01$) while preference for sand/gravel substrate is negatively correlated to this variable ($p = 0.01$). Foraging locality is influenced by conductivity ($p = 0.02$), regardless of category considered. A similar situation is observed for the relationship between migration and water temperature (Table 3).

Table 2. Code and voucher number (MCP = Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul) of species sampled in 25 headwater streams of Araguaia (A) and Tocantins (T) river basins. NA=not available.

Species	Code	Basin		MCP
		A	T	
Aequidens tetramerus (Heckel, 1840)	AEQTET	x	x	45538
Apareiodon sp.	APASP	x		NA
Apareiodon sp. 2	APASP2		x	NA
Aphyocharax sp.	APHSP		x	45592
Apistogramma sp.	APISP		x	45618
Aspidoras sp.	ASPSP	x		45556
Astyanax abramis (Jenyns, 1842)	ASTABR	x		NA
Astyanax fasciatus (Cuvier, 1819)	ASTFAS	x	x	44676
Astyanax sp. 1	ASTSP1	x	x	45522

Species	**Code**	**Basin**		**MCP**
		A	**T**	
Astyanax sp. 2	ASTSP2	x	x	45609
Astyanax sp. 3	ASTSP3	x	x	45520
Bryconamericus sp. 2	BRYSP2		x	45572
Bryconamericus sp. 3	BRYSP3		x	NA
Bryconops caudomaculatus (Günther, 1864)	BRYCAU	x	x	44622
Characidium zebra Eigenmann, 1909	CHAZEB	x	x	45518
Charax gibbosus (Linnaeus, 1758)	CHAGIB	x		45539
Corydoras sp.	CORSP		x	45585
Creagrutus sp.	CRESP	x	x	44603
Curimatella sp.	CURSP	x		45576
Cyphocharax spiluropsis (Eigenmann & Eigenmann, 1889)	CYPSPI	x		45582
Eigenmannia virescens (Valenciennes, 1836)	EIGVIR	x	x	45528
Farlowella amazonum (Günther, 1864)	FARAMA		x	45630
Galeocharax gulo (Cope, 1870)	GALGUL		x	45561
Hemigrammus sp.	HEMSP	x	x	45519
Hoplias malabaricus (Bloch, 1794)	HOPMAL	x	x	44702
Hyphessobrycon sp.	HYPSP	x	x	NA
Hypostomus plecostomus (Linnaeus, 1758)	HYPPLE	x	x	44698
Hypostomus sp. 1	HYPSP1	x		45554
Iguanodectes spilurus (Günther, 1864)	IGUSPI	x		44629
Imparfinis sp.	IMPSP	x	x	45523
Jupiaba polylepis (Günther, 1864)	JUPPOL	x	x	44618
Knodus sp.	KNOSP	x	x	44615
Leporinus friderici (Bloch, 1794)	LEPFRI	x		44608
Loricaria cataphracta (Linnaeus, 1758)	LORCAT	x	x	44700
Moenkhausia collettii (Steindachner, 1882)	MOECOL	x		45534
Moenkhausia dichroura (Kner, 1858)	MOEDIC	x		45524
Moenkhausia lepidura (Kner, 1858)	MOELEP	x	x	44609
Moenkhausia oligolepis (Günther, 1864)	MOEOLI	x	x	44625
Moenkhausia sp. 2	MOESP2	x	x	45535
Moenkhausia sp. 5	MOESP5		x	44660
Odontostilbe sp.	ODOSP		x	44634
Otocinclus tapirape Britto & Moreira, 2002	OTOTAP		x	45623
Pamphorichthys sp.	PAMSP	x	x	45565
Phenacogaster sp.	PHESP	x	x	45537
Pimelodella cristata (Müller & Troschel, 1849)	PIMCRI	x		45529
Pimelodella sp.	PIMSP	x		45584
Poptella longipinnis (Popta, 1901)	POPLON	x	x	44626
Psellogrammus sp.	PSESP		x	44636
Retroculus lapidifer (Castelnau, 1855)	RETLAP	x		44694
Rhamdella sp.	RHASP	x		NA
Rineloricaria sp.	RINSP	x	x	45601
Rineloricaria sp. 2	RINSP2		x	45579
Satanoperca acuticeps (Heckel, 1840)	SATACU	x		45629
Serrapinnus kriegi (Schindler, 1937)	SERKRI	x		NA
Serrapinnus sp.	SERSP	x		44637
Steindachnerina sp.	STESP	x		44617
Steindachnerina sp. 2	STESP2	x		NA
Tetragonopterus argenteus (Cuvier, 1816)	TETARG	x		44638
Tetragonopterus chalceus Spix & Agassiz, 1829	TETCHA	x		44601
Thayeria boehlkei Weitzman, 1957	THABOE	x		45536
Thoracocharax stellatus (Kner, 1858)	THOSTE	x		45527
Trachelyopterus galeatus (Linnaeus, 1766)	TRAGAL	x		45627
Total species richness		49	37	

Table 3. Results of the RLQ (A) and fourth-corner (B) analyses of environmental variables (variable R) and fish functional traits (variable Q) from 25 headwater streams of Araguaia and Tocantins river basins. Only results with significant values ($p<0.05$; in bold) are displayed.

A)			**Axis 1**			**Axis 2**	
	Eigenvalues		0.331			0.210	
	Covariance		0.575			0.459	
	Monte Carlo test	(1000 iterations)			p = **0.005**		
B)	**Variable R**	**Variable Q**	**Statistic**	**Value**	**p**	**Category of variable Q**	**p**
	Altitude *vs.*	Average body mass	r	0.1326	**0.0166**	-	-
		Trophic guild	F	0.9896	0.2815	-	-
		Parental care	F	2.67574	0.0661	-	-
		Water column position	F	2.58228	**0.0455**	Benthic	**0.0027**
		Foraging method	F	1.69007	0.2336	-	-
		Substrate preference	F	3.0752	**0.0062**	Gravel	**0.0003**
						Sand/Gravel	**0.0042**
		Foraging locality	F	0.0762	0.7502	-	-
		Migration	F	0.8694	0.2901	-	-
	Channel depth *vs.*	Average body mass	r	-0.1385	**0.0078**	-	-
		Trophic guild	F	1.72637	0.0753	-	-
		Parental care	F	1.3814	0.1728	-	-
		Water column position	F	0.3761	0.6265	-	-
		Foraging method	F	1.10694	0.4061	-	-
		Substrate preference	F	0.7968	0.4890	-	-
		Foraging locality	F	2.31319	0.0799	-	-
		Migration	F	2.6192	0.0648	-	-
	Turbidity *vs.*	Average body mass	r	0.0110	0.4273	-	-
		Trophic guild	F	0.3492	0.7755	-	-
		Parental care	F	3.28154	**0.0440**	Yes	**0.0461**
		Water column position	F	2.73296	**0.0374**	Benthic	**0.0004**
		Foraging method	F	3.5812	0.0604	-	-
		Substrate preference	F	1.86394	0.0754	-	-
		Foraging locality	F	0.0425	0.8163	-	-
		Migration	F	1.6774	0.1480	-	-
	Conductivity *vs.*	Average body mass	r	0.0784	0.1032	-	-
		Trophic guild	F	0.4644	0.6604	-	-
		Parental care	F	2.31664	0.0858	-	-
		Water column position	F	3.215	**0.0199**	Benthic	**0.0275**
		Foraging method	F	0.6376	0.5348	-	-
		Substrate preference	F	1.5466	0.1322	-	-
		Foraging locality	F	4.03622	**0.0215**	Lentic	0.3086
						Lotic	0.6216
		Migration	F	1.41625	0.1801	-	-
	Temperature *vs.*	Average body mass	r	-0.0336	0.2979	-	-
		Trophic guild	F	1.28285	0.1727	-	-
		Parental care	F	0.7689	0.3172	-	-
		Water column position	F	1.55591	0.1484	-	-
		Foraging method	F	0.2640	0.7863	-	-
		Substrate preference	F	1.15298	0.2723	-	-
		Foraging locality	F	0.1757	0.6369	-	-
		Migration	F	3.86756	**0.0305**	Migratory	0.6698
						Non-migratory	0.2624

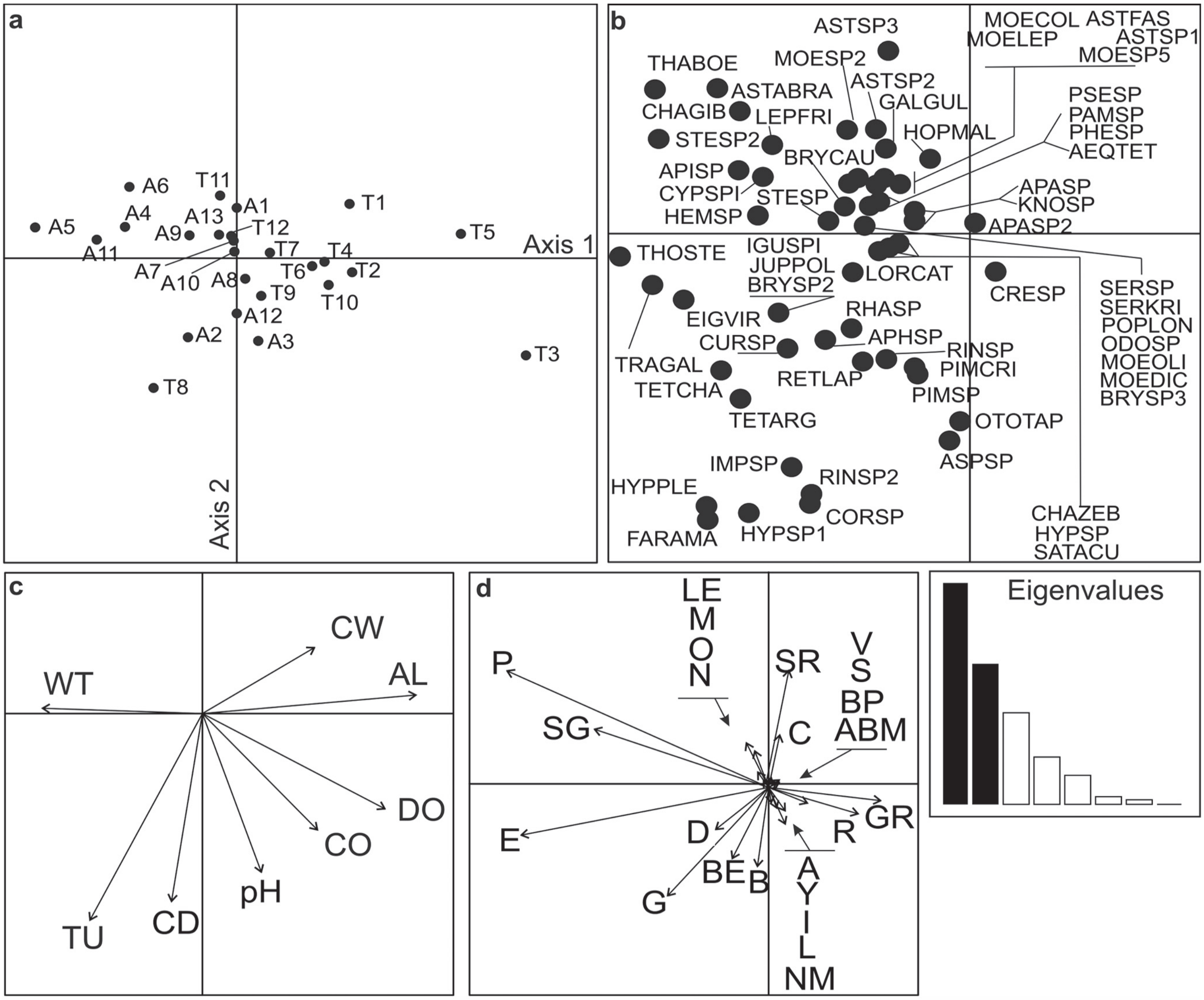

Fig. 2. Ordination of sampling stations (a), species (b), environmental variables (c) and functional traits (d) resulting of the RLQ analysis. In (a) the letter preceding numbers indicates the river basin (A=Araguaia; T=Tocantins). In (c) AL=altitude; CO=conductivity; CD=channel depth; CW=channel width; DO=dissolved oxygen; TU=turbidity; WT=water temperature. Consult Tables 1 and 2 for codes used in (d) and (b), respectively. The eigenvalues of the axes are displayed in the smallest box with the first two axes featured in black.

Discussion

Despite the growing interest on the determinants of fish assemblages' functional structure, most studies in large scale still focus their attention on the determinants of species richness (Hoeinghaus *et al.*, 2007) and, particularly in tropical rivers, functional traits composition of fish assemblages remains poorly known (Pease *et al.*, 2012). Our results revealed dissimilarities between fish assemblages' functional structure of the two neighboring basins considered (Araguaia and Tocantins) driven by altitudinal and water temperature gradients. In this study, the altitude increases from east (Araguaia basin streams) to west (Tocantins basin streams) and is accompanied by a decrease in water temperature. A similar trend was observed in temperate streams, but involving latitudinal gradients and other variables than altitude and water temperature (Oliveira *et al.*, 2012). These authors suggest that this trend corresponds to different forms of ecosystem functioning, ranging from warm water and lower altitudinal systems (in our study represented by Araguaia basin streams) to colder and high altitudinal systems (Tocantins basin streams). Schleuter *et al.* (2012) also observed differences between fish assemblages' functional structure of neighboring basins separated by mountain chains, as is the case of the Araguaia and Tocantins. Rahel & Hubert (1991) pointed out that transition in biological communities due to thermal conditions is expected in mountainous regions, where water temperature decreases as altitude increases.

Several studies pointed out the importance of abiotic factors in shaping fish assemblages' structure (Poff & Allan, 1995; Peres-Neto, 2004; Hoeinghaus *et al.*, 2007). Species occurrence in headwater streams are directly influenced by water velocity and stream depth (Mendonça *et al.*, 2005, Súarez *et al.*, 2007), whereas the functional structure of headwater streams are driven by factors such as turbidity and dissolved oxygen coupled with channel depth and water velocity (Carvalho & Tejerina-Garro, 2015). Our results revealed that dissimilarities among the functional structure of headwater streams fish assemblages within the basins are mainly determined by channel depth, turbidity and conductivity. Channel depth is often suggested as a reasonable indicator for habitat structural complexity (Súarez *et al.*, 2007), which may increase species traits diversity (Willis *et al.*, 2005). Then, an increase of channel depth from one headwater stream to another may implicate in the addition of species with new and distinct traits in the fish assemblages. Turbidity and conductivity may limit species occurrence in local fish assemblages. For example, the species of catfish *Aspidoras fuscoguttatus* Nijssen & Isbrücker, 1976 was already found in association with high levels of water turbidity (Araújo & Garutti, 2003) that may affect its diet (Casatti *et al.*, 2009). In our sampled streams, a species of the same genus (*Aspidoras* sp.) is also related to streams of high conductivity.

Altitude is related to the regional topography and it influences functional traits composition of fish assemblages at both regional (Oliveira *et al.*, 2012) and local scales (Bistoni & Hued, 2002; Pouilly *et al.*, 2006). Our results provided evidence that altitude affects three functional traits of headwater fish species in different manners: body mass (positively), water column position (negatively to benthic species) and substrate preference (negatively to species with gravel and sand/gravel preference). Schlosser (1990) points out that fish body size (mass) tends to increase towards downstream reaches, whereas we found an opposite trend. This result suggests that changes of stream altitude (from 1st to 3rd order) are not enough to influence on body mass giving a direction. However, contrasting these headwater streams to those streams of downstream areas (>3rd order) may reveal the expected trend mentioned by Schlosser (1990).

In temperate regions, and considering a broad longitudinal gradient, benthic species tends to be absent in headwater streams (1st - 3rd order) and present in streams of higher order (>4th) as a result of biotic zonation (Rahel & Hubert, 1991). Contrary, in tropical regions, Mazzoni & Lobón-Cerviá (2000) observed that the number of benthic species increases upstream, concluding that they did not show a longitudinal-related distributional pattern but varied inversely with channel depth. These authors suggest that this is a result of patchy availability of resources along the stream and, in this case, it is predominant over longitudinal distribution. This seems to explain our results, that is benthic species of the Araguaia and Tocantins streams do not follow a longitudinal-related distributional trend but are influenced by resources availability. Within a drainage basin, the slope and the transport of materials decreases accordingly to the altitude, thus in lower altitudes, for example 3rd order in our study, the transport of materials is lower than upstream favoring the deposition of gravel and/or sand (Suguio & Bigarela, 1990). Gravel favors the presence of benthic algal/detritivorous species (Mazzoni & Lobón-Cerviá, 2000), such as the siluriforms *Hypostomus plecostomus*, *Farlowella amazonum*, *Corydoras* sp. in our study. These fishes have streamlined or flattened bodies with hooks or sucker structures for clinging (Moyle & Cech, Jr. 1996) that allows inhabiting this kind of habitat.

The relationship between fish body size and channel depth is expected to be positively correlated and represented by small fish occupying shallow waters and large fish deeper waters (Vannote *et al.*, 1980; Schlosser, 1987, 1991). This pattern seems to reduce the predation risk for both small and large fishes (Harvey & Stewart, 1991) but fish with small body sizes are not exclusive of shallow waters and are also encountered in deeper waters (Angermeier & Karr, 1983; Harvey & Stewart, 1991; Stewart *et al.*, 2002). Channel depth is a reasonable indicator for habitat structural complexity (Súarez *et al.*, 2007), then, deeper streams should have more microhabitats for hiding and escaping from predators (Willis *et al.*, 2005). Furthermore, these microhabitats can be explored by species with different morphologies and physiologies that reduce competition and facilitate species coexistence (Hugueny, 1990). The presence of fishes with lower body mass (small fish) in streams with higher levels of channel depth in our study area may reflects reduced levels of predation and/or competition (Angermeier & Karr, 1983) due to habitat structural complexity of deeper waters. Therefore, survival of small fishes would increase in streams of high channel depth explaining the trend found in this study.

Turbidity is often a consequence of suspended sediments in the water column which influences on light availability and sensory adaption of fish (visually or not oriented) to visibility of prey (Rodriguez & Lewis, Jr., 1997, Tejerina-Garro *et al.*; 1998) and consequently on the fish assemblage of lotic environments (Fialho *et al.*, 2008). This can explain the relationship of elevated water turbidity and non-visually oriented benthic species as the siluriforms (*e.g.*, *Hypostomus plecostomus*, *Imparfinis* sp., *Corydoras* sp.) observed in our study. On the other hand, excess of suspended sediment can promote bed sedimentation resulting in reduced egg and fry survivorship (Soulsby *et al.*, 2001; Walters *et al.*, 2003). In this case, parental care can increase egg survival as seems to be the case of the catfish *Otocinclus tapirapae* (Loricariidae), whose males may present different types of parental care (Blumer, 1982). Since turbidity may increase the levels of water conductivity (Esteves, 1988), we believe that the relationship between benthic species and conductivity is a consequence of their presence in turbid waters, as mentioned above.

One trait related to life history of some tropical fish is seasonal migration (Winemiller, 1989; Winemiller & Jepsen, 1998), which takes place before onset of the rainy season (Sivasundar *et al*., 2001). Tropical seasonality is characterized by alternance of low and high waters that is accompanied by changes of water physicochemical characteristics such as water temperature (Tockner *et al*., 2000). Thus, water temperature along with other variables is an environmental stimulus that directs or regulates fish migration (Northcote, 1984). This can explain the influence of water temperature on migratory habits found in this study.

In a regional scale, our findings are important for the development of future conservation strategies in these systems. If headwater streams fish assemblages of the Araguaia and Tocantins basins differ in species traits composition, conservation strategies should focus their attention on areas that are capable of representing species and functional traits of both basins. Otherwise, they might fail in protecting the diversity of species functional traits of these basins. In this scale, some attention should be given for the following species functional traits: body mass, water column position, preference for substrate and migratory habits. These traits were the most influenced by gradients of altitude and water temperature that drive dissimilarities between both basins. In a local scale, we showed that functional differences among headwater streams were driven mainly by channel depth, turbidity and conductivity. Such environmental drivers influenced fish body mass, presence or absence of species with (or without) parental care, water column position and foraging locality. Local management for the protection of headwater stream fish assemblages should consider these species-traits relationships.

Understanding species-traits relationships is a primordial step for unrevealing how communities (or assemblages) are structured and which factors are responsible for such organization. This study is an attempt to unveil the functional patterns of fish assemblages in a tropical region that continues to be poorly known but severely threatened. Focus on new species traits and environmental drivers should enhance our future knowledge on the functional structure of these systems.

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Table S1. Functional traits of species sampled in headwater streams of the Araguaia and Tocantins river basins.

Species	Average body mass (g)	Trophic guild	Parental care	Water column position	Foraging method	Substrate preference	Foraging locality	Migration
Aequidens tetramerus	2.06	Omnivorous	yes	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Apareiodon sp.	0.7	Algivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Apareiodon sp. 2	3.88	Algivorous	no	Benthopelagic	Visual Feeding	Rock	Lentic	Non-migratory
Aphyocharax sp.	0.27	Invertivorous	no	Benthopelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Apistogramma sp.	0.48	Omnivorous	yes	Benthopelagic	Visual Feeding	Sand/gravel	Lentic	Non-migratory
Aspidoras sp.	0.65	Invertivorous	yes	Benthic	Barbells	Rock	Lotic	Non-migratory
Astyanax abramis	5.91	Omnivorous	no	Benthopelagic	Visual Feeding	Sand/gravel	Lentic	Migratory
Astyanax fasciatus	6.32	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Astyanax sp. 1	1.08	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Astyanax sp. 2	1.28	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Migratory
Astyanax sp. 3	5.07	Omnivorous	no	Benthopelagic	Visual Feeding	Sand/rock	Lentic	Migratory
Bryconamericus sp. 2	0.51	Omnivorous	no	Benthopelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Bryconamericus sp. 3	0.36	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Bryconops caudomaculatus	1.28	Invertivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Characidium zebra	0.77	Invertivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Charax gibbosus	1.49	Carnivorous	no	Benthopelagic	Visual Feeding	Sand/gravel	Lentic	Non-migratory
Corydoras sp.	0.61	Invertivorous	yes	Benthic	Barbells	Gravel	Lotic	Non-migratory
Creagrutus sp.	0.91	Invertivorous	no	Benthopelagic	Visual Feeding	Gravel/rock	Lotic	Non-migratory
Curimatella sp.	3.8	Detritivorous	no	Benthopelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Cyphocharax spiluropsis	0.82	Detritivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Migratory
Eigenmannia virescens	1.28	Invertivorous	no	Benthopelagic	Electricity	Sand	Lotic	Non-migratory
Farlowella amazonum	0.32	Detritivorous	yes	Benthic	Barbells	Gravel	Lotic	Non-migratory
Galeocharax gulo	2.19	Carnivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Hemigrammus sp.	0.64	Invertivorous	no	Benthopelagic	Visual Feeding	Sand/gravel	Lotic	Non-migratory
Hoplias malabaricus	22.69	Carnivorous	yes	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Hyphessobrycon sp.	0.35	Invertivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Hypostomus plecostomus	6.34	Detritivorous	yes	Benthic	Barbells	Gravel	Lotic	Non-migratory
Hypostomus sp. 1	4.68	Detritivorous	yes	Benthic	Barbells	Gravel	Lotic	Non-migratory
Iguanodectes spilurus	1.4	Omnivorous	no	Benthopelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Imparfinis sp.	0.63	Invertivorous	no	Benthic	Barbells	Gravel	Lotic	Non-migratory
Jupiaba polylepis	0.55	Omnivorous	no	Benthopelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Knodus sp.	0.53	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Leporinus friderici	4.88	Carnivorous	yes	Benthopelagic	Visual Feeding	Sand/gravel	Lotic	Migratory
Loricaria cataphracta	2.04	Omnivorous	yes	Benthopelagic	Barbells	Sand	Lentic	Non-migratory
Moenkhausia collettii	0.94	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Moenkhausia dichroura	0.61	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Moenkhausia lepidura	0.85	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Moenkhausia oligolepis	1.07	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Moenkhausia sp. 2	1.12	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Migratory
Moenkhausia sp. 5	2.35	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Odontostilbe sp.	0.47	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Otocinclus tapirape	0.2	Algivorous	yes	Benthic	Barbells	Gravel/rock	Lotic	Non-migratory
Pamphorichthys sp.	0.24	Invertivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Phenacogaster sp.	0.23	Invertivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Pimelodella cristata	1.76	Omnivorous	no	Benthic	Barbells	Gravel/rock	Lotic	Non-migratory
Pimelodella sp.	6.23	Omnivorous	no	Benthic	Barbells	Rock	Lotic	Non-migratory
Poptella longipinnis	0.99	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Psellogrammus sp.	1.26	Invertivorous	no	Benthopelagic	Visual Feeding	Sand	Lentic	Non-migratory
Retroculus lapidifer	16.32	Invertivorous	yes	Benthopelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Rhamdella sp.	0.3	Invertivorous	no	Benthic	Barbells	Sand	Lentic	Non-migratory
Rineloricaria sp.	1.65	Algivorous	yes	Benthic	Barbells	Sand	Lentic	Non-migratory
Rineloricaria sp. 2	1.18	Algivorous	yes	Benthic	Barbells	Gravel	Lotic	Non-migratory
Satanoperca acuticeps	3.51	Omnivorous	yes	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Serrapinnus kriege	0.28	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Serrapinnus sp.	0.21	Omnivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Non-migratory
Steindachnerina sp.	2.15	Detritivorous	no	Benthopelagic	Visual Feeding	Sand	Lotic	Migratory
Steindachnerina sp. 2	1.49	Detritivorous	no	Benthopelagic	Visual Feeding	Sand/gravel	Lentic	Migratory
Tetragonopterus argenteus	3.24	Invertivorous	no	Benthic	Visual Feeding	Gravel	Lotic	Non-migratory
Tetragonopterus chalceus	1.44	Omnivorous	no	Benthic	Visual Feeding	Gravel	Lotic	Non-migratory
Thayeria boehlkei	0.36	Omnivorous	no	Pelagic	Visual Feeding	Sand	Lentic	Non-migratory
Thoracocharax stellatus	1.72	Invertivorous	no	Pelagic	Visual Feeding	Gravel	Lotic	Non-migratory
Trachelyopterus galeatus	9.9	Omnivorous	no	Benthic	Barbells	Sand/gravel	Lentic	Non-migratory