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## Effects of area and available energy on fish assemblages of tropical streams

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**Abstract.** A central issue in fish community ecology is to understand how the size of the drainage area and the available energy influence fish species diversity and their spatial distribution. In the present study, we tested whether the species–area relationship (represented by drainage area) and species–energy association (represented by algal biomass and organic matter) drive taxonomic and functional richness in a regional scale. The results indicated that fish assemblages of the two tropical neighbouring basins sampled responded differently to the size of drainage area. Whereas taxonomic richness was influenced by the size of the drainage area in Tocantins River basin streams, it was not affected in Araguaia River basin streams. Both taxonomic richness and functional richness of the fish assemblages were affected by available energy in the system. A possible explanation for these different responses is related to local conditions, such as the percentage of natural vegetation cover encountered in each basin.

**Additional keywords:** algal biomass, land use, organic matter, vegetation cover.

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### Introduction

Fish species represent 30% of all known vertebrate species on Earth (Strayer and Dudgeon 2010). Considering the totality of fish species described, ~40% of them are encountered in freshwater ecosystems (Dudgeon *et al.* 2006). With human activities pressuring these systems and leading to unprecedented levels of extinction (Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010), there is an urgent need to provide protection for freshwater habitats. However, the development of conservation actions is directly dependent on our knowledge on how species diversity is distributed along space, and which factors affect this distribution.

In the past decade, the number of studies in the Neotropical region focusing on the distribution patterns of fish species diversity in local and regional scales has increased (Bistoni and Hued 2002; Hoeinghaus *et al.* 2004; Fialho *et al.* 2007; Suárez *et al.* 2011; Santana *et al.* 2014; Carvalho and Tejerina-Garro 2015; Teresa *et al.* 2015). The main results of these studies

have shown that fish species diversity is associated to different factors, such as variation in the longitudinal gradient of streams coupled with environmental variables, stream features (e.g. stream order), position in the river channel and changes from dry to rainy seasons (seasonality) and the degree of deforestation. Despite such recent effort, only few studies have investigated the patterns of fish species distribution at a large scale in the Neotropical region (Suárez *et al.* 2011). This situation concerns freshwater-fish conservation because it has been estimated that more than 4000–6000 species are present in the Neotropical region (Reis *et al.* 2003; Lévêque *et al.* 2008; Albert and Reis 2011).

According to classical studies, the following hypotheses were already proposed to explain gradients in species richness: (1) species–area relationship (MacArthur and Wilson 1967); (2) species–energy relationship (Wright 1983); and (3) historical hypothesis (Whittaker *et al.* 2001). The hypothesis of species–area relationship predicts that larger areas will harbour a higher

number of species than do smaller areas because they are expected to (1) have more habitat heterogeneity and food resources availability (Williamson 1988), (2) reduce the probability of extinction because larger areas have more resources available and tend to support more individuals (MacArthur and Wilson 1967) and (3) present higher speciation rates, given their higher habitat heterogeneity (Losos and Schluter 2000). The species–energy hypothesis predicts that species diversity is a response to energy availability in the system. For example, local and regional fish species diversity may respond to variations in the input of energy along the longitudinal gradient of streams, as proposed by the river-continuum concept (Vannote *et al.* 1980). Finally, the historical hypothesis predicts that species diversity is a consequence of the potential of system recolonisation and the maturation of such systems after glaciation. At the global scale, patterns of riverine fish diversity are explained by two major factors, namely, energy availability and habitat heterogeneity (Guégan *et al.* 1998).

Here, our main goal relies on the study of patterns of taxonomic richness (species richness) and functional richness (species richness by trophic group) of tropical freshwater fish assemblages. We tested whether the species–area relationship (represented by drainage area) and species–energy association (represented by algal biomass and organic matter) drive taxonomic and functional richness of fish assemblages in a regional scale; that is, we expect that both taxonomic and functional richness of fish assemblages will be positively related to the increase of drainage area and available energy in the system.

## Materials and methods

### Study area

The study area is located in the Goiás State, central Brazil. The Tocantins–Araguaia basin is one of the most developed watersheds of the Amazonian province (Ribeiro *et al.* 1995; Lévêque *et al.* 2008). The Tocantins–Araguaia basin has an estimated size of 767 000 km<sup>2</sup> and it presents a mean annual discharge of 11 000 m<sup>3</sup> s<sup>−1</sup> (Costa *et al.* 2003). Our study area is represented by the upper section of the basin that is located in the Goiás State, central Brazil. In this region, the drainage areas of its main tributaries (Tocantins and Araguaia rivers) are geographically separated by mountain chains, such as Serra do Caiapó and Serra dos Pirineus (Tejerina-Garro 2008), and they form two distinct basins, namely, Araguaia River basin (hereafter Araguaia basin) and Tocantins River basin (hereafter Tocantins basin). Both basins have a well-defined dry (May–October) and wet (November–April) season (Albrecht and Pellegrini-Caramaschi 2003; Quesada *et al.* 2004). The original vegetation cover formed mainly by cerrado phytophysognomies was altered by human occupation (mainly agriculture and cattle-ranching activities), which placed the cerrados as the second-most modified Brazilian biome (PMDBBS 2016). However, deforestation is not the same in the two basins because differences in topography differently favour the earlier mentioned activities, that is, the Araguaia basin has plane low-altitude areas favourable to agriculture and cattle-ranching, whereas the Tocantins basin has scarped areas with steep slopes that hamper these activities (de Oliveira 2014), being allied to extended areas for conservation or sustainable use (Galinkin 2003). This situation affects also the riparian vegetation,

**Table 1.** Description of the predominant type of riparian vegetation along the stream bank of stretches sampled in the Araguaia and Tocantins basins

Stream number follows those displayed in Fig. 1

Basin	Stream number	Riparian vegetation by stream bank	
		Right	Left
Araguaia	1	Shrubs	Grasses and shrubs
	2	No vegetation	No vegetation
	3	Shrubs and trees	Shrub
	4	Grasses and shrubs	Grasses and shrubs
	5	No vegetation	No vegetation
	6	No vegetation	No vegetation
	7	Shrubs and trees	Shrubs and trees
	8	No vegetation	No vegetation
	9	Shrubs	Shrubs
	10	No vegetation	No vegetation
	11	Shrubs and trees	Shrubs
Tocantins	12	Shrubs	Shrubs
	13	Shrubs	Shrubs and trees
	14	Shrubs and trees	Shrubs and trees
	15	Shrubs	Shrubs and trees
	16	Shrubs and trees	Shrubs and trees
	17	Grasses	Shrubs
	18	No vegetation	No vegetation
	19	Trees	Trees
	20	Shrubs	Shrubs
	21	Grasses	Grasses

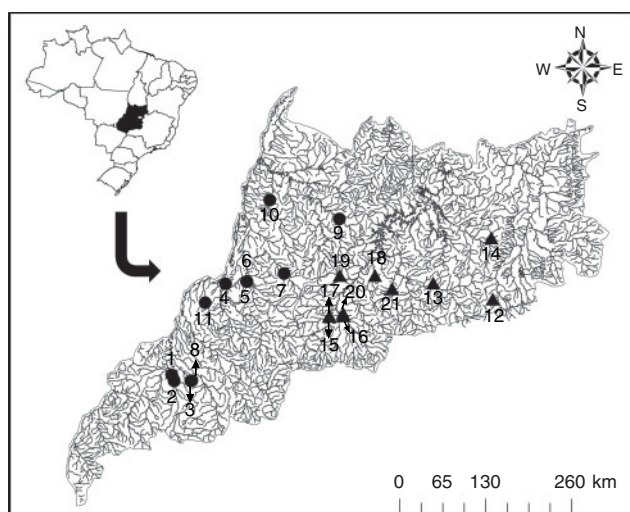
expressed by the absence of this vegetation along many of the stream stretches sampled in the Araguaia basin in relation to those of the Tocantins basin (Table 1).

### Sampling protocols

During the dry season (March to September 2008), we sampled 21 watercourses, 11 being located in the Araguaia River basin and 10 in the Tocantins River basin (Fig. 1). All watercourses sampled belong to 1st or 2nd order, according to the classification of Strahler (1957). In each watercourse, we delimited and georeferenced (GPS eTrex, Garmin, USA) a stretch of 50 m. Along the stretch, five transects of 10 m each were demarcated and both biotic (fish) and abiotic (environmental variables) data were collected.

Fish species were collected using a seine net (4 × 1.3 m; 0.1 mm between knots) along the stretch, which was covered 10 times. Fish was fixed with formalin and conserved in containers holding formaldehyde at 20%. In the laboratory of the Centro de Biologia Aquática, PUC Goiás, fish were identified through the use of identification keys (Planquette *et al.* 1996; Santos *et al.* 2004; Melo *et al.* 2005), measured (mm) and weighed (g). Specimens of each species were sent to the Laboratory of Ichthyology of the Pontifícia Universidade Católica do Rio Grande do Sul to confirm identification. The trophic guild of each species was determined according to the online database *FishBase* (R. Froese and D. Pauly, see <http://www.fishbase.org>, accessed 10 September 2015).

For the first, third and fifth transects of each stretch, we used a quadrat (0.5 × 0.5 m) to collect vegetable organic matter (leaves, branches, fruits, seeds; hereafter, organic matter, OM). The OM



**Fig. 1.** Location of the watercourses sampled in the Araguaia (circles) and Tocantins (triangles) River basins in the Goiás State, central Brazil.

was then dried in the laboratory in an oven for 24 h at 105°C, weighed and calcined (furnace) at 550°C, and weighed again (Silva *et al.* 1999). The final OM weight was standardised by dividing it by the quadrat area, and expressed in grams per square metre.

The algal biomass (AB) was determined through the extraction and measurement of the chlorophyll-*a*. For that, at the first and the fifth transects of each stretch, the water along the watercourse bank was pumped during 5 min (water pump, P835, Stihl, Brazil), filtered by a plankton net (20- $\mu$ m mesh) and stored in an amber bottle (1 L) containing 1 mL of magnesium carbonate. In the laboratory, the sample was filtered (Millipore 0.45- $\mu$ m filter, 25-mm diameter), the chlorophyll was extracted with methanol and the concentration determined by a spectrophotometer (Cary, 50 CONC-UV, Varian, USA) following the protocol of Wetzel and Likens (1991). Algal biomass was expressed in milligrams per litre.

The measurements of the drainage area (DA) and the total percentage of vegetation cover (TPVC) of each watercourse were performed in the software ArcGIS (ESRI, USA) using hydrological and land-use maps (scale 1 : 250 000) available on the website of the *Sistema Estadual de Estatística e Informações Geográficas do Estado de Goiás* (SIEG, see <http://www.sieg.go.gov.br/>, accessed 21 October 2015). We measured DA as the area (km<sup>2</sup>) between the headwater of the watercourse and the location of the stretch sampled, respecting the boundaries of the basin. We classified land use into the following five categories: agriculture, urban areas, cerrado *sensu stricto*, forest (cerradão, mataseca, riparian forest, gallery forest) and pasture, all of them measured in square kilometres. We obtained TPVC accordingly to the following formula:

$$\%TPVC = (CA + FA)/DA \times 100$$

where %TPVC is the total percentage of vegetation cover, CA is the total cerrado area, FA is the total forest area and DA is the drainage area.

### Statistical analysis

Separately, we performed two multiple regressions by basin (Araguaia and Tocantins), considering taxonomic richness (S) or functional richness (richness of the trophic guild) as response variables and area (DA) and available energy (AB and OM) as explanatory variables. We tested the principle of normality using a Shapiro–Wilk test and, whenever necessary, we transformed the data with a logarithm ( $\log_{10+1}$ ).

If the multiple regression analysis was statistically significant, we performed an analysis of covariance (ANCOVA) between residuals (dependent variable) and two covariates represented by the basins (Araguaia and Tocantins; categorical predictor variable) and the total percentage of vegetation cover (TPVC; continuous predictor variable). All analyses were performed using the software STATISTICA 8.0 (StatSoft, Brazil).

### Results

We found 4093 fish specimens from 5 orders, 15 families and 62 species (Table 2). We collected 56 species from eight trophic guilds and 35 species from six trophic guilds in watercourses of Araguaia and Tocantins River basins respectively (Table 2).

#### *Taxonomic (S) and functional richness (trophic-guild richness)*

The multiple regression analysis indicated that the relationship between the taxonomic or functional richness of fish assemblages and the factor area (DA) and available energy (OM and AB) did not occur in a similar way in the two watercourses grouped by basin (Araguaia and Tocantins).

We did not find significant relationships between taxonomic or functional fish richness and area and available energy in the watercourses of the Araguaia River basin (Table 3). For the Tocantins River basin, we found a positive relationship between taxonomic richness and area and available energy ( $P = 0.007$ ; Table 3), that is, taxonomic richness increased as a function of DA and available energy (OM and AB). When we did not consider the DA, AB was negatively related to taxonomic richness ( $P = 0.023$ ; Table 3), that is, taxonomic richness decreased when AB increased. The functional richness was positively related to OM and AB ( $P = 0.023$ ; Table 3), meaning that, an increase in functional richness was due to an increase in OM and AB (available energy) in the system.

The ANCOVA analysis indicated that the residuals of the significant relationships described above are not related to the covariates considered (basin and TPVC; Table 4), except for the taxonomic richness–available energy relationship, which is related to the TPVC (Table 4). It means that the relationship increases (the residual tends to diminish) when the TPVC increases, independently of the basin (Fig. 2).

### Discussion

Generally, larger areas are expected to harbour a higher number of species; therefore, species richness is expected to grow as the size of an area increases (Arrhenius 1921; MacArthur and Wilson 1967). Evidence of this positive relationship in aquatic systems has been described at smaller (Eadie *et al.* 1986; Chittaro 2002) and larger (Watters 1992; Guégan *et al.* 1998;

**Table 2. Fish species sampled in the watercourses of the Araguaia and Tocantins basins, central Brazil, in the dry season of 2008**  
The trophic guild is indicated for each species.

Species	Trophic guild	Basin		Species	Trophic guild	Basin	
		Araguaia	Tocantins			Araguaia	Tocantins
Characiformes				Characiformes (cont.)			
Anostomidae				<i>Steindachnerina</i> sp.	Detritivorous	X	
<i>Leporinus friderici</i>	Omnivorous	X	X	<i>Steindachnerina</i> sp. 2	Detritivorous	X	
Characidae				Erythrinidae			
<i>Astyanax abramis</i>	Omnivorous	X		<i>Hoplerethrinus unitaeniatus</i>	Omnivorous	X	
<i>Astyanax fasciatus</i>	Omnivorous	X	X	<i>Hoplias malabaricus</i>	Piscivorous	X	X
<i>Astyanax</i> sp. 1	Omnivorous	X	X	Parodontidae			
<i>Astyanax</i> sp. 2	Omnivorous	X	X	<i>Apareiodon</i> sp.	Algivorous	X	
<i>Astyanax</i> sp. 3	Omnivorous	X	X	<i>Apareiodon</i> sp. 2	Algivorous		X
<i>Bryconamericus</i> sp. 2	Omnivorous		X	Cyprinodontiformes			
<i>Bryconamericus</i> sp. 3	Omnivorous		X	Poeciliidae			
<i>Bryconops caudomaculatus</i>	Insectivorous	X	X	<i>Pamphorichthys</i> sp.	Invertivore	X	X
<i>Charaxgibbosus</i>	Piscivorous	X		Gymnotiformes			
<i>Creagrutus</i> sp.	Insectivorous	X	X	Sternopygidae			
<i>Galeocharaxgulo</i>	Piscivorous	X		<i>Eigenmannia virescens</i>	Insectivorous	X	X
<i>Hemigrammus</i> sp.	Insectivorous	X	X	Perciformes			
<i>Hyphessobrycon</i> sp.	Insectivorous	X	X	Cichlidae			
<i>Iguanodectes spilurus</i>	Omnivorous	X		<i>Aequidens tetramerus</i>	Omnivorous	X	X
<i>Jupiaba</i> cf. <i>polylepis</i>	Omnivorous	X	X	<i>Apistogramma</i> sp.	Omnivorous	X	X
<i>Knodus</i> sp.	Omnivorous	X	X	<i>Retroculus lapidifer</i>	Insectivorous	X	
<i>Moenkhausia collettii</i>	Omnivorous	X		<i>Satanoperca acuticeps</i>	Omnivorous	X	
<i>Moenkhausia dichoura</i>	Omnivorous	X		Siluriformes			
<i>Moenkhausia lepidura</i>	Omnivorous	X	X	Aspredinidae			
<i>Moenkhausia oligolepis</i>	Omnivorous	X	X	<i>Bunocephalus coracoideus</i>	Insectivorous	X	
<i>Moenkhausia</i> sp. 2	Omnivorous	X	X	Auchenipteridae			
<i>Moenkhausia</i> sp. 5	Omnivorous		X	<i>Trachelyopterus galeatus</i>	Omnivorous	X	
<i>Odontostilbe</i> sp.	Omnivorous		X	Callichthyidae			
<i>Phenacogaster</i> sp.	Insectivorous	X	X	<i>Aspidoras</i> sp.	Invertivore	X	X
<i>Poptella longipinnis</i>	Omnivorous	X	X	<i>Corydoras</i> sp.	Omnivorous	X	X
<i>Psellogrammus</i> sp.	Insectivorous		X	Heptapteridae			
<i>Roeboxodon geryi</i>	Lepidophagus	X		<i>Imparfinis</i> sp.	Invertivore	X	X
<i>Serrapinnus</i> cf. <i>kriege</i>	Omnivorous	X		<i>Pimelodella cristata</i>	Omnivorous	X	
<i>Serrapinnus</i> sp.	Carnivorous	X		<i>Pimelodella</i> sp.	Omnivorous	X	
<i>Tetragonopterus argenteus</i>	Insectivorous	X		<i>Rhamdella</i> sp.	Invertivore	X	
<i>Tetragonopterus chalcus</i>	Omnivorous	X		Loricariidae			
<i>Thayeria boehlkei</i>	Omnivorous	X		<i>Hypostomus plecostomus</i>	Detritivorous	X	X
Ctenoluciidae				<i>Hypostomus</i> sp. 1	Detritivorous	X	X
<i>Boulengerella cuvieri</i>	Piscivorous	X		<i>Loricaria cataphracta</i>	Omnivorous	X	X
Curimatidae				<i>Otocincus tapirape</i>	Algivorous	X	X
<i>Curimatella</i> sp.	Detritivorous	X		<i>Rineloricaria</i> sp.	Algivorous	X	X
<i>Cyphocharax</i> cf. <i>spiluropsis</i>	Detritivorous	X		Trichomycteridae			
				<i>Trichomycterus</i> sp.	Invertivore	X	

Matthews and Robison 1998) spatial scales. In the present study, we demonstrated that patterns of taxonomic and functional richness of fish assemblages of two tropical neighbouring basins (Araguaia and Tocantins) responded differently to the size of the DA. A possible explanation for such differences is related to the percentage of natural cover observed in each basin. The upper section of the Araguaia and Tocantins River basins are both located in the cerrado, a biodiversity hotspot (Mittermeier *et al.* 2004, 2011). This biome is mainly threatened by the conversion of its original vegetation cover into areas for agriculture and cattle ranching (Klink and Machado 2005), implicating habitat loss and fragmentation, which are listed as major threats to fish diversity (Dudgeon *et al.* 2006).

The vegetation cover is not the same in both basins. There are many isolated or continuous areas of savanna shrub and shrub-tree forests in the Tocantins basin, combined with a larger number of protected areas in its north-eastern region than in the Araguaia basin (Galinkin 2003). Streams with a low percentage of natural cover are probably affected by other environmental (e.g. water physicochemical characteristics) and landscape (e.g. presence of a floodplain area) factors than size area, which is the case for Araguaia River basin streams. However, a higher percentage of natural cover could mitigate the effects of agriculture and cattle-ranching, which is the case observed for Tocantins River basin streams, enabling a higher influence of the size of the DA.



**Table 3. Statistics of the multiple linear regression between the taxonomic richness of fish assemblages (S), functional richness and the factors drainage area (DA), algal biomass (AB) and organic matter (OM) of the watercourses sampled and grouped by basin**  
Significant ( $P < 0.05$ )  $P$ -values are in bold

Basin	Richness	Estimate	Factor	
			Area + available energy	Available energy
Araguaia	Taxonomic (S)	$P$	0.618	0.391
		$R^2$	0.213	0.209
	Functional (SGT)		$S = -19.6852 + 1.1964(\text{DA}) - 0.4938(\text{AB}) + 9.3619(\text{OM})$	$S = -18.4216 - 0.5636(\text{AB}) + 9.4468(\text{OM})$
		$P$	0.957	0.862
		$R^2$	0.041	0.036
			$\text{SGT} = 0.8193 - 0.2930(\text{DA}) + 0.1526(\text{AB}) + 0.9597(\text{OM})$	$\text{SGT} = 0.5098 + 0.1697(\text{AB}) + 0.9389(\text{OM})$
Tocantins	Taxonomic (S)	$P$	<b>0.007</b>	<b>0.023</b>
		$R^2$	0.848	0.659
	Functional (SGT)		$S = -19.1060 + 4.2590(\text{DA}) - 3.1201(\text{AB}) + 7.8388(\text{OM})$	$S = -5.6270 - 2.0342(\text{AB})$
		$P$	0.065	<b>0.023</b>
		$R^2$	0.675	0.658
			$\text{SGT} = -8.2386 + 0.5471(\text{DA}) - 0.7609(\text{AB}) + 3.6429(\text{OM})$	$\text{SGT} = -6.5071 - 0.6215(\text{AB}) + 3.2932(\text{OM})$

**Table 4. Statistics of the total percentage of vegetation cover (TPVC, continuous predictor) by basin (categorical predictor) and results of the ANCOVA analysis between the residuals of the significant relationships, resulting from multiple linear regression (dependent variable), and the covariates (basin and TPVC)**

Significant  $P$ -values are in bold ( $P < 0.05$ ). S, taxonomic richness; SGT, functional richness

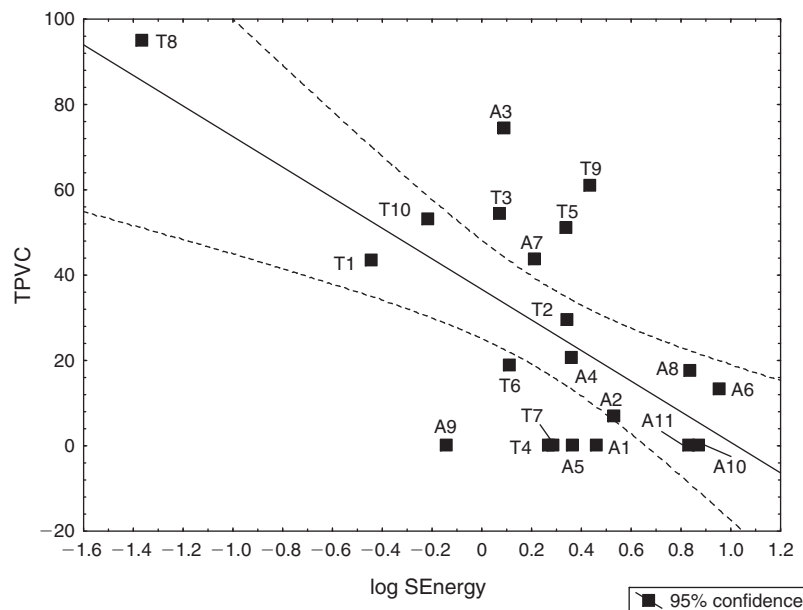
Basin	$n$	TPVC (km <sup>2</sup> )		Covariate	$F_{1,18}$	$P$ -value
		Mean	s.d.	Basin TPVC		
Araguaia	11	16.042	23.575			
Tocantins	10	40.590	29.283			
Residual of the relationship:						
S v. area + available energy				0.089	0.287	3.228
S v. available energy				0.169	<b>0.013</b>	2.057
SGT v. available energy				0.369	0.100	0.850
						0.369

Moreover, removal of natural cover, including riparian vegetation, may influence the occurrence of species, because it hampers the input of allochthonous nutrients in the freshwater system (Vannote *et al.* 1980). This fact can partially explain the results found for the Araguaia River and in an opposite manner in the Tocantins basin (increase of taxonomic and functional richness along with the OM). However, the vegetal cover in the Tocantins basin is not continuous, but interspersed with areas where the riparian vegetation is absent. This situation favours the entry of luminosity into the water column, promoting the rise of algae (Giller and Malmqvist 2000) and, consequently, the primary productivity in the aquatic system measured by the chlorophyll-*a* (Barroso and Littlepage 1998), as was observed in the present study. Thus, the positive relationship between available energy and taxonomic and functional richness in Tocantins streams indicated that the input of nutrients into the system by the vegetation cover is capable of increasing the number of species and the number of species with different trophic habits in the system, but only when AB and OM are evaluated together. When these two components are evaluated

separately, it is observed that an increase in AB has negative effects on taxonomic richness. This result suggests that the fish–AB relationship observed in the Tocantins basin works similarly to the eutrophication phenomenon on fish diversity; that is, it causes changes to the fish assemblage composition or displacement, or elimination of fish populations (Lévêque *et al.* 2008).

An additional explanation for the different relationships of the fish assemblages from the two basins with area and available energy is the basin interconnection. In the present study, this was represented by the interconnection between the ‘Vereda Grande’ stream (Tocantins basin) and ‘Brejinho’ stream (Paraná basin; Pavanelli and Britski 1999). These authors stated that this interconnection allows the exchange of fish species between these basins; thus, it influences on taxonomic and functional richness, both of which were measured in the present study.

The mentioned differences can be also related to regional and local characteristics of the habitat, such as the physico-chemical characteristics of the water. The Araguaia is classified as a clear-water river and the Tocantins as a white-water one (Rios-Villamizar *et al.* 2014). The type of water results from basin geochemistry that influences the isotopic composition of basal production (Jepsen and Winemiller 2007) and, in consequence, the type of available energy for aquatic biota including fish assemblages. Additionally, the Araguaia basin includes a floodplain that provides a greater number of shelters and food for fishes (Agostinho and Zalewski 1995; Junk 1997), increasing taxonomic fish richness (Tanaka *et al.* 2015) and the diversity of morphological, physiological and ethological attributes of species (Junk *et al.* 1989; Lowe-McConnell 1999). This could explain the elevated number of species observed in this basin in relation to Tocantins basin. However, some limitations of the present study are necessary to consider; one is related to the number of sampling points and the second to the period of sampling (low-water period). We believe that the sampling effort in the present study was appropriate to give us a first draft of these relationships in regions with little knowledge, and a good first look on how these relationships are structured in regional scales. However, increasing the number of unities and



**Fig. 2.** Relation between the log of the residual of the taxonomic species–available energy relationship (log SEnergy) and the total percentage of the vegetation cover (TPVC) of the watercourses sampled (black squares). A, Araguaia; T, Tocantins.

the sampling effort for both dry and wet seasons in future studies may provide a better picture of the relationships between fish assemblages and area and fish assemblages and energy across space and time.

Understanding how the size of the DA and the available energy may affect fish species and their spatial distribution is a cornerstone to fish community ecology. Here, we showed that fish assemblages of two tropical neighbouring basins responded differently to the size of the DA and, this fact may be a consequence of the presence or absence of natural vegetation cover around streams. In other words, impacts caused by human population, as a result of agriculture and cattle-ranching, on natural vegetation cover near streams may affect species occurrence. Moreover, we demonstrated that both taxonomic richness and functional richness of these fish assemblages were affected by available energy in the system, which may also be influenced by the degree of natural vegetation cover near streams. Considering that area and available-energy effects are directly dependent on the presence or absence of natural vegetation cover, it is important to develop conservation actions to protect this highly endangered hotspot.

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