

# The coexistence of fish species in streams: relationships between assemblage attributes and trophic and environmental variables

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**Abstract** Diet overlap and niche breadth are well-known species traits from trophic ecology that can assist in explaining how species interact and coexist as well as the ecological mechanisms that influence biodiversity. In the present study, we analyzed the relationships between these trophic variables and indicators of resource availability with some attributes of fish assemblages (species richness, Shannon diversity index, evenness, density and individual body size). The physical and chemical characteristics of the biotopes (topography, water quality and conservation of slopes) were examined to identify possible patterns. Monthly sampling using electrofishing was conducted in 2003 along five streams located in the Cuiabá River watershed. The relationships between environmental variables and attributes of fish assemblages

were evaluated using Spearman correlation. Species richness and abundance varied among streams, with higher values (54 and 82 species) found in low-gradient streams that drained small swampy areas discharging in Cuiabá River. Diet overlap showed significant and negative correlations with species richness, the diversity index, abundance, variation in body size and food availability and positive correlations with evenness and niche breadth. Environments that had greater food availability had a reduced variety of food items (smaller amplitude) and distinct values in terms of dietary overlap. Nevertheless, to explain resource partitioning in a fish assemblage (overlap), it is necessary to consider food availability and niche breadth (degree of trophic specialization) beyond the interaction of these variables with species richness and density. In conclusion, high diversity and abundance values were strongly associated with a high degree of trophic specialization (low amplitude of trophic niche) and a small degree of overlap in the diet.

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## Introduction

Freshwater research has historically focused on large rivers due to their great economic importance as

resources for fisheries. Nevertheless, the number of studies on smaller watercourses has recently increased due to their unique biota, higher vulnerability to degradation as a result of anthropogenic activities and their strategic importance as water supplies for urban and rural areas (Luiz et al. 1998). Moreover, strategic planning for the management and conservation of streams requires knowledge of the structure and dynamics of their communities, including the biotic and abiotic interactions that promote species coexistence.

Stream flow pulses caused by precipitation in a watershed cause the displacement of biota and food resources to lower stretches, thereby changing microhabitats, interrupting ongoing succession and promoting the initiation of new succession by recolonization (Gordon 1993). At a regional scale, the pluviometric regime has predictable seasonal characteristics, but the susceptibility of small streams to sudden precipitation events promotes stochastic variation in the amount of water discharge, which influences community structure and reduces the relative importance of biotic interactions. Local variation in water velocity, substrate characteristics, bathymetry, shelter, marginal vegetation and declivity are some of the variables that contribute to habitat heterogeneity in small watercourses. This heterogeneity has been associated with spatial segregation among species, which is further influenced by morphological specializations (Winemiller et al. 2008) that allow species coexistence and diversity maintenance.

The importance of abiotic factors in influencing community assemblages may cause the role of biotic factors to be underestimated, but studies on niche breadth, niche overlap or food resource partitioning among fish species in streams may contribute significantly to a better understanding of how these species are interacting. In addition, such studies can help identify the main dimensions of resources along which species segregate and provide opportunities to test hypotheses related to the control of communities (Ross 1986). The variety of trophic guilds in tropical streams, a peculiarity related to resource partitioning, plays a fundamental role in the organization of communities (Flecker 1992). Therefore, differences among species concerning resource use (food and space) play an essential role in determining coexistence and, consequently, in the maintenance of biological diversity.

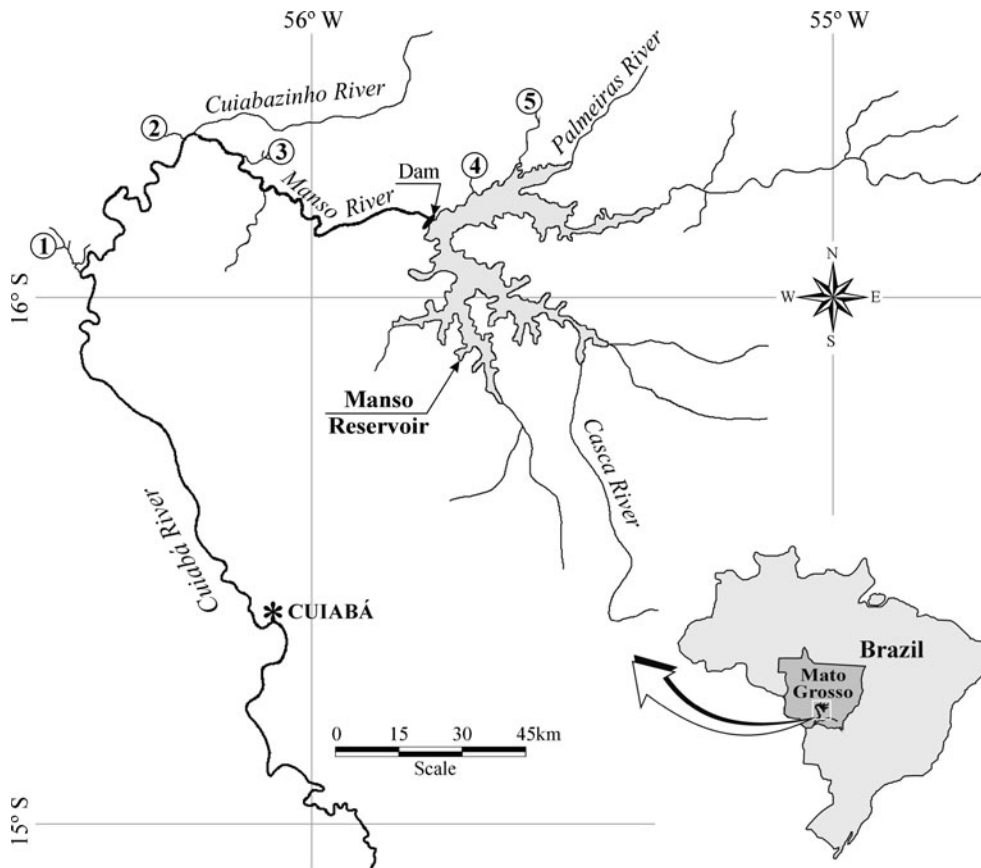
However, there is no agreement about the relationship between community attributes, resource availability and trophic variables with diet overlap and niche breadth. The present study evaluated these relationships based on fish sample data obtained in five streams that presented distinct physical, chemical and biotic characteristics. The objective of the study was to characterize the relationships among the community attributes (species richness, Shannon diversity index, and evenness, abundance and body length) and trophic attributes (food availability, niche breadth and diet overlap). We included a detailed description of these attributes for the studied streams to allow for an improved evaluation of possible relationships between these variables. In addition, these attributes were graphically associated with the characteristics of the streams (physical and chemical) to identify possible trends.

## Materials and methods

### Description of the study area and sampling procedure

We sampled five streams in the Cuiabá River watershed in the State of Mato Grosso, Brazil, above the Pantanal. The streams Imbaúba (14°55'06" S, 56°27'02" W) and Cancela (14°42'30" S, 56°15'51" W) empty directly into the Cuiabá River, whereas Forquilha (14°44'58" S, 56°07'39" W) empties into the Manso River, which, along with the Cuiabazinho River, forms the Cuiabá River. The other two streams, São Joaquim (14°46'54" S, 55°39'59" W) and Lajinha (14°57'18" S, 55°41'15" W), empty into the Manso Reservoir (Fig. 1).

Fish samples were collected by electrofishing from January to December 2003 using a power generator (2.5 KW) coupled to a transformer (1.5 KW, 200, 300 and 500 V, 1 A) and equipped with cables connected to two dip nets with metal rings (cathode and anode, Penczak et al. 1998). For each stream section sampled (each about 40 m in length), the bathymetric profile and water velocity were evaluated at five transects, and the fish captures were performed, starting downstream and moving upstream, using energized dip nets with the lower part of the section blocked with a net (1.0-cm mesh size; Agostinho and Penczak 1995). Sampling could not be conducted in every month among all of the streams because of low water



**Fig. 1** Location of the watershed of the Manso and Cuiabá Rivers, Mato Grosso State, Brazil. The sampled streams included (1) Lajinha; (2) São Joaquim; (3) Forquilha; (4) Cancela; and (5) Imbaúba

conditions. The following streams were not sampled during these months: Imbaúba: January–March, July–October; Cancela: March; Forquilha: July–September; São Joaquim: February–April, and November; and Lajinha: September.

Captured fish were anesthetized (benzocaine, 100 mg.l<sup>-1</sup>), preserved in 4% formaldehyde and taken to the laboratories of the Núcleo de Pesquisas em Limnologia, Ictiologia and Aquicultura (Nupélia) at the Universidade Estadual de Maringá, where each fish was measured (total length; cm) and weighed (total weight; g). Next, their stomachs were removed and preserved in 4% formaldehyde until analysis. The stomach contents of 1970 individuals representing 57 species were examined with stereoscopic and optic microscopes, and the food items were identified to the lowest taxonomic level possible based on the literature (Chu 1949; Bicudo and Bicudo 1970; Round 1973; McCafferty 1981; Stehr 1987; Borror and

DeLong 1988; Peres 1988). The voucher specimens of the captured fish are preserved in the Museu de Ictiologia/Nupélia.

Assemblage attributes

Diversity (Shannon index), species richness and evenness for each sample (month and stream) were calculated according to Krebs (1989). Abundance was expressed as the number of fish per 100 m<sup>2</sup>; length was expressed using the median and the coefficient of variation of the total length for every sample.

Trophic attributes

Resource availability, trophic niche breadth and diet overlap among the species present in the samples were calculated from the stomach contents and expressed as the frequency of occurrence (%F; Rosecchi and Nouaze

1987) and the volumetric frequency (%V; Hyslop 1980). To estimate the availability of food resources in every sample (separated by streams), we used the total volume of items consumed for the set of analyzed stomachs. The analysis of stomach contents was restricted to subsamples that were not always proportional to the captures; the volume of food items were then corrected using the proportion of species in the sample, considering only the individuals with food in the stomach (Luz-Agostinho et al. 2006), according to the equation:

$$D = \sum_{n=1}^s \left( \frac{N_i * v_i}{n_i} \right),$$

where  $D$  = availability of items;  $n_i$  = number of analyzed stomachs for species  $i$ ;  $v_i$  = volume of items for species  $i$ ;  $N_i$  = number of stomachs of species  $i$  with food; and  $s$  = number of species.

Niche breadth was calculated using Levins's index (Levins 1968). We standardized the trophic niche values (ranging from 0 to 1) using the Hurlbert formula (1978). To examine the index of diet overlap ( $R_0$ ) among species, we used the Morisita method modified by Horn (1966), calculated with the volume of food items for every sample (pair of species in the same month and stream). The values of overlap were considered biologically relevant when  $R_0 \geq 0.60$  (Sabino and Castro 1990). The value of overlap for each sample was obtained by summing the overlap values of pairs of species with high values ( $>0.60$ ) and dividing by the total number of pairs of species with overlap.

The relationships between diet overlap and assemblage attributes were assessed with Spearman correlations ( $R_s$ ) applied to the data from each sample (month and location). Data values were log-transformed ( $\text{Log}_e$ ) (Myers 1990), and all statistical analyses were performed using Statistica 7 (StatSoft 2005).

## Results

### Streams characteristics

Streams were heterogeneous in all features considered except depth. All streams were very shallow, with depths ranging from 0.2 to 0.3 m. Streams were short

(less than 25 km) and varied in width (7.0 m for São Joaquim and Forquilha; near 2 m for the others). However, velocity was higher for São Joaquim and lower for Forquilha and Lajinha; São Joaquim also had higher discharge and was the largest stream studied (Table 1). The sloped regions adjacent to the sampled areas were mainly pastures (Cancela, São Joaquim and Imbaúba) or fields of other crops (Forquilha). Only Lajinha flowed through the original savanna (Cerrado) vegetation. Floodable areas (várzeas) were present only in Cancela and Ibaúba, whereas shelter was common in Cancela and Lajinha. These two latter streams had a higher degree of preservation than the others (Table 1). Chemical characteristics also varied among the streams. Cancela had higher values of pH and DO than the other streams, while Imbaúba had lower values of these variables and the lowest value for conductivity (Table 1). São Joaquim had the highest conductivity of any stream (Table 1).

### Fish assemblage attributes

Fish assemblage attributes varied greatly among streams (Fig. 2). The Shannon Diversity Index, calculated for every sample, ranged between 1.01 and 5.66, with median values between 2.4 and 3.8; Cancela had the highest values, followed by São Joaquim and Lajinha (Fig. 2b). The high values of diversity recorded in Cancela reflected the high species richness observed in this stream, where at least 33 species per sample were captured, the median value was 40, and the maximum was 59 (Fig. 2a). While Cancela had a high number of species, a few were highly dominant, which is reflected in the lower values of evenness (median=0.2) for this stream (Fig. 2c). São Joaquim, with the second-highest value of the Shannon Index (median=3.3; Fig. 2b), had species richness values ranging from 10 to 21 species (median=16; Fig. 2a) and high evenness values (median=0.5; Fig. 2c) compared to the other streams.

Abundance, standardized for 100 m<sup>2</sup> of area, ranged from 5 to 1699 individuals, with higher values in Cancela and Imbaúba (Fig. 2d), which had in common only a moderate current velocity (Table 1). Although variable, the median abundance of the samples was around 700–750 individuals. The median total length values were larger in Forquilha and smaller in Imbaúba and Cancela (Fig. 2e). These last

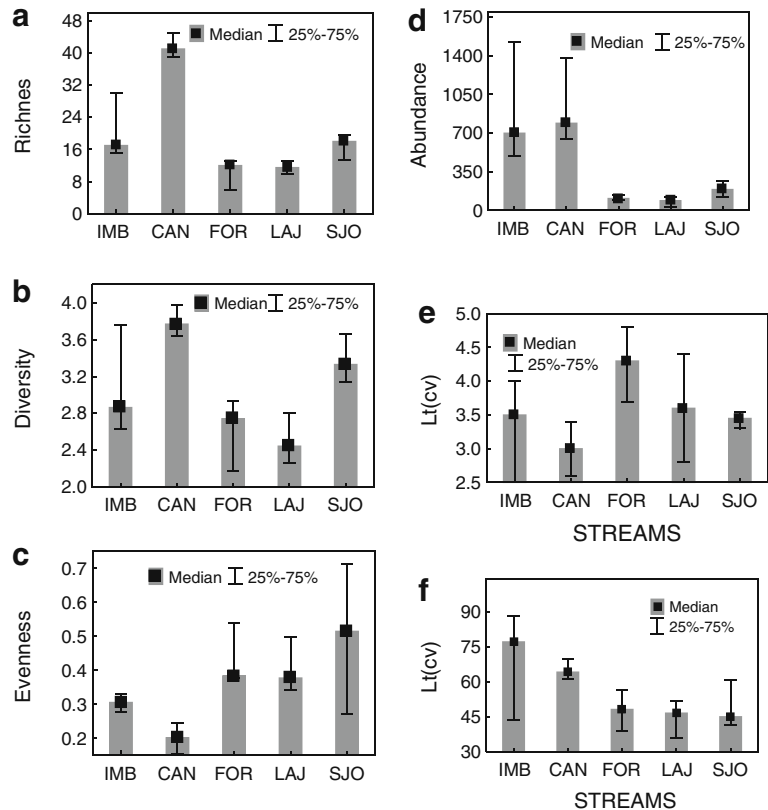
**Table 1** Characterization of the streams studied in the watershed of Manso/Cuiabá River, Mato Grosso State, Brazil. (DO = dissolved oxygen; Mean values ± standard deviation; graduation: + = low, ++ = moderate, +++ = high, ++++ = very high)

Parameters	Stream				
	Imbatuba	Cancela	Forquilha	Lajinha	S. Joaquim
Extension (km)	5	12	8	12	25
Width (m)	1.7±0.43	2.2±0.3	7.0±0.3	2.3±0.3	7.0±0.3
Depth(m)	0.25±0.2	0.2±0.04	0.2±0.04	0.24±0.05	0.3±0.07
Velocity (m. s <sup>-1</sup> )	0.34±0.3	0.34±0.2	0.1±0.1	0.2±0.2	0.6±0.2
Flow (m <sup>3</sup> . s <sup>-1</sup> )	0.2±0.3	0.1±0.1	0.1±0.1	0.1±0.1	1.1±0.6
Slope use	Pasture	Pasture and cultivation <sup>a</sup>	Cultivation <sup>b</sup>	Cerrado vegetation	Pasture
Mouth location	Cuiabá River	Cuiabá River	Manso River	Manso Reservoir	Manso Reservoir
pH	5.7±0.55	7.0±0.3	6.0±0.43	6.5±0.1	6.7±0.26
DO (mg.L <sup>-1</sup> )	3.4±0.9	5.0±1.15	3.9±2.1	3.9±2.6	3.6±1.6
Conductivity (µS.cm <sup>-1</sup> )	41.6±16.7	97.6±25.6	49.33±13.7	141.3±63.6	118.3±38.0
Várzea area	Present	Present	Absent	Absent	Absent
Shelter	++	++++	+	++++	+
Preservation degree	++	++++	++	++++	+

<sup>a</sup> corn and cassava

<sup>b</sup> rice, corn and cassava

**Fig. 2** Spatial variation in the medians of the assemblage attributes: Shannon diversity, abundance (individuals per 100 m<sup>2</sup>), size of individuals (length in mm) and coefficient of variation of length (length (cv)). Streams: *IMB* Imbaúba; *CAN* Cancela; *FOR* Forquilha; *LAJ* Lajinha; and *SJO* São Joaquim. Vertical bars represent the lower (25%) and the upper (75%) quartiles



streams also had higher values for the coefficient of variation of total length (Fig. 2f).

### Trophic attributes

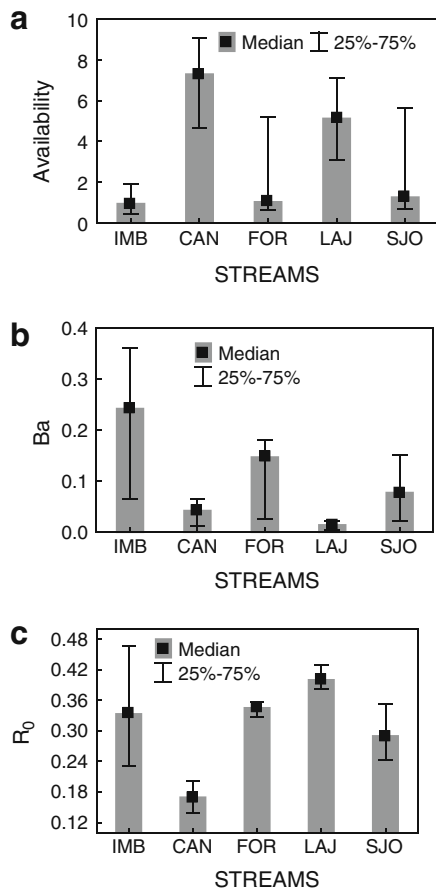
The median of the sum of the estimated values of items mass in the stomachs of fish species in each sample, used as a measure of total food availability, was higher in Cancela and Lajinha (Fig. 3a) than in the other streams. Cancela and Lajinha were similar in length, width, discharge (both low), shelter availability and degree of preservation but differed in the other physical and assemblage attributes (Table 1, Fig. 3a). Nevertheless, the evaluation of niche breadth revealed a less diverse diet in Cancela and Lajinha streams (Fig. 3b), a marked contrast to Imbaúba, which had lower total food availability and a low variety of items in the diet. Finally, diet overlap was greater in Lajinha and Forquilha and lower in São Joaquim and Cancela. The Imbaúba stream had the highest variability in dietary overlap (Fig. 3c).

Correlations between trophic variables and fish assemblage attributes

The correlations between diet overlap, attributes of fish assemblages, food availability and trophic niche breadth were significant and negative for species richness, Shannon diversity index, abundance, the coefficient of variation of total length and food availability (Fig. 4). By contrast, evenness, the median of total length and trophic niche breadth showed significant and positive correlations with niche overlap.

### Discussion

The predominance of small-sized fish observed in the streams from the Cuiabá River watershed is consistent with previous observations in South American streams (Castro 1999; Abes and Agostinho 2001; Lemes and Garutti 2002; Casatti et al. 2001; Oliveira and Bennemann 2005; Abilhoa et al. 2008) and is



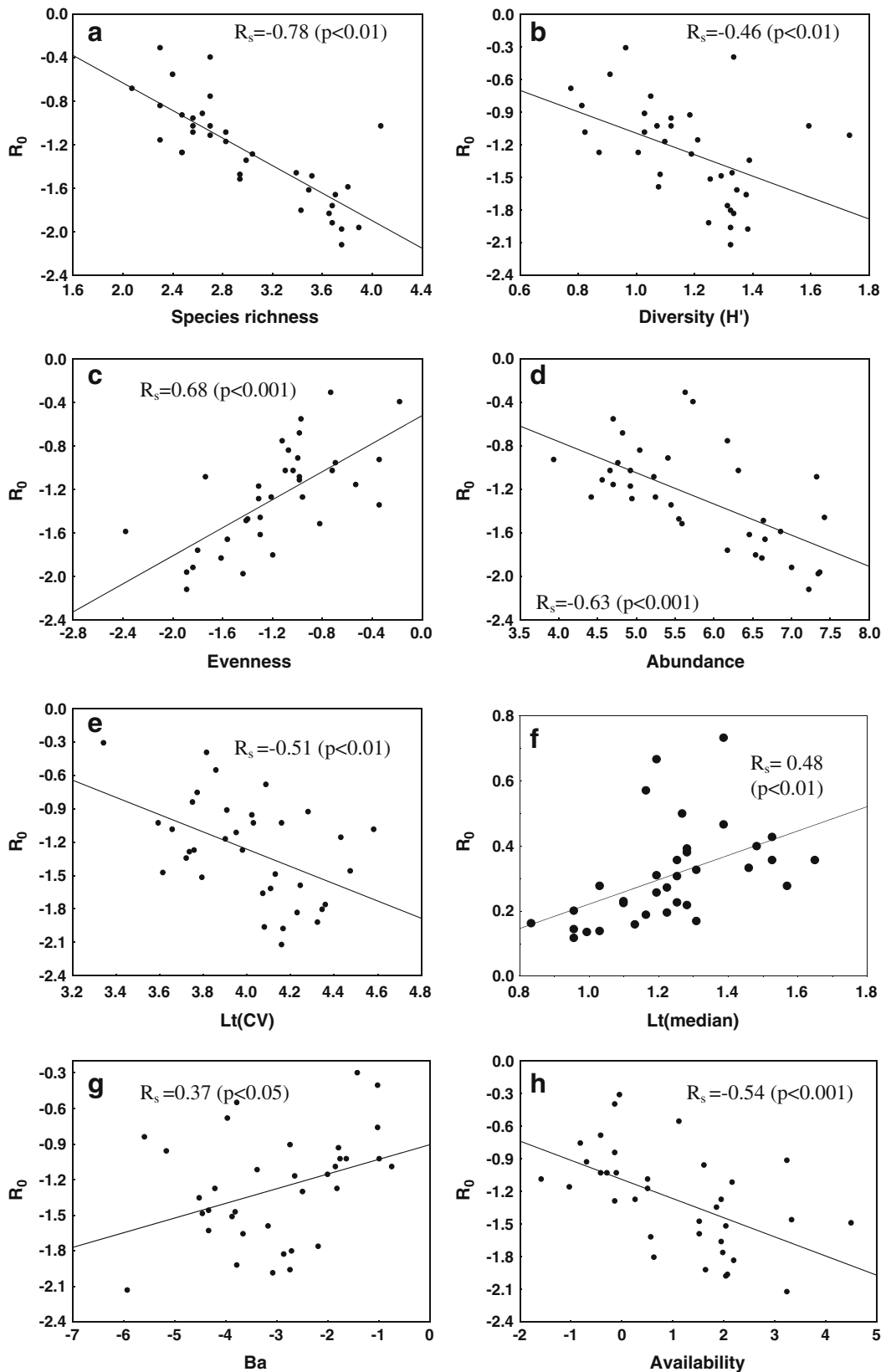
**Fig. 3** Spatial variation in the medians of the sampling values of resource availability (ml), niche breadth (Ba), and diet overlap ( $R_0$ ). Streams: *IMB* Imbaúba; *CAN* Cancela; *FOR* Forquilha; *LAJ* Lajinha; and *SJO* São Joaquim. Vertical bars represent the lower (25%) and the upper (75%) quartiles

considered a characteristic pattern for these environments. Species richness is an attribute that varies quite a lot among streams, with remarkable gradients, and is probably due to the variety of habitats (Garutti 1988; Reyes-Gavilán et al. 1996; Abes and Agostinho 2001; Oliveira and Bennemann 2005). In a review of species richness in tropical streams throughout the world, Winemiller et al. (2008) recorded values of 4–83 species per stream; about 80% of the environments contained between 10 and 30 species and only two had values higher than 40. The number of species identified in the present study was comparatively higher because we only sampled a stretch of 40 m at each stream during one year, and we obtained species richness values of 24 and 82 species in Lajinha and Cancela streams, respectively. Additional studies in

the latter stream (2000–2004; Mendes et al. 2008) found 104 species, which is a remarkable result due to its small length (12 km). This total represents one quarter of the total number of species found in the entire Palearctic biogeographic region (Matthews 1998).

Significant correlations have been observed between species richness and stream depth (Pouilly 1993) or width (Winemiller et al. 2008). In the present study, the mean depths of the studied streams were similar (0.2–0.3 m), and the stream widths (1.7–7.0 m) did not explain the differences in species richness between streams. Cancela, among the most narrow and shallow of the streams, had the highest species richness (median=40), while Forquilha, with a greater width, had the lowest species richness (10). The low declivity of Cancela, a stream that meanders through swampy areas from its headwaters in the Serra da Cancela to the mouth of the Cuiabá River, seems to be the most parsimonious explanation for this high level of species richness. The Imbaúba, a tributary of Cuiabá River with “várzea” areas, also had high species richness (54 species) but with higher variation among samples. Streams such as this have lower current velocity, abundant pools and riffles, “várzea” areas, rich organic sediments, abundant autochthonous and allochthonous resources and a more seasonal flow pattern, ensuring higher availability of food and habitat (Winemiller et al. 2008). By contrast, the greater width, depth and flow of São Joaquim may be related to its lower species dominance and to its relatively high value of diversity (although it is actually a moderate number of species considering the pattern of the region). The high species richness observed in Cancela is probably associated with the degree of preservation of the vegetation, which offers a diversity of food, shelter and refuge (Suarez and Petrer 2006). Nevertheless, similar conditions of marginal vegetation preservation and shelter availability were also present at Lajinha Stream, which had low species richness.

The higher density of fish in Cancela and Imbaúba streams, direct tributaries of Cuiabá River with similar hydrological and bathymetric features, may be due to the fact that they drain “várzea” areas that, as previously mentioned, are characteristic of rivers with a high availability of resources and, therefore, biogenic capacity (Lowe-McConnell 1999). This fact seems to be sufficient to cause an underestimation of the remark-





**Fig. 4** Diagrams of dispersion between values ( $\text{Log}_e$ ) of diet overlap and the fish assemblage attributes (species richness, diversity, evenness, abundance, individual size— $L_t$  (median) and the coefficient of variation— $L_t$  (CV)), trophic niche breadth (Ba) and food availability of the samples obtained in the streams from the watershed of the Manso/Cuiabá River, Mato Grosso State, Brazil ( $R_s$  = Spearman Rank Correlation;  $p$  = probability to obtain a higher  $R_s$ )

able differences observed in the physical and chemical characteristics of the water, the stream length, the degree of preservation and shelter availability. However, it is important to consider that the other streams are tributaries of smaller rivers or of the reservoir.

The availability of food resources, inferred from the quantity of items in the fish stomachs, was higher in the streams with a greater degree of preservation of the riparian vegetation and a higher availability of shelter (Cancela and Lajinha). Except for flow and length, these streams had low similarity in relation to the other physical and chemical features, indicating the importance of preserving riparian vegetation, which influences the availability of shelter and food resource for fish assemblages. This interaction between the conditions of the slopes and food availability was expected, at least concerning allochthonous sources (Sabino and Castro 1990; Henry et al. 1994; Lowe-McConnell 1999). The input of allochthonous material includes fruits, seeds and terrestrial insects that are either directly consumed by the ichthyofauna or that contribute particulate organic carbon (POC) for invertebrates and detritivorous fish (Russo et al. 2002). These items are abundant in these environments, given the greater relationships of the aquatic environment with the slopes (Agostinho et al. 2007). Several authors have reported diet predominantly based on items from allochthonous sources in fish assemblages of streams (Knöppel 1970; Lowe-McConnell 1975; Soares 1979; Oliveira and Bennemann 2005). On the other hand, other authors argue that autochthonous items are more important in these environments, especially aquatic insects and other aquatic invertebrates (Casatti 1970; Sabino and Zuanon 1998; Esteves and Lobón-Cerviá 2001; Russo et al. 2002; Fogaça et al. 2003; Abilhoa et al. 2008), which depend on allochthonous inputs (Esteves and Aranha 1999). However, the food chains in upper and narrow stretches of preserved streams have a stronger dependence on allochthonous sources than those without the protection provided by riparian vegetation or in wider stretches. Furthermore, frequent

and sudden pulses, common in streams, have a remarkable carrier effect of the available food (Power et al. 1988), which needs to be balanced by a constant external input. Oliveira and Bennemann (2005) verified that in the best-preserved stretches of streams, there is greater consumption of food from allochthonous sources.

Streams with a greater availability of food resources (Cancela and Lajinha) were also those that had lower median niche breadth by sample, indicating a higher degree of feeding specialization within those fish assemblages. Larger trophic niche breadth was found in streams with moderately degraded riparian vegetation with lower mean values of pH, conductivity and oxygen, in addition to a scarcity of food resources (Imbaúba and Forquilha). According to Lowe-McConnell (1999), riparian vegetation allows the use of other resources such as fruits, leaves and flowers as well as other terrestrial invertebrates that fall into the water (Castro 1999). With these other food sources, feeding specialization seems to be more important, although it may fluctuate seasonally (Lowe-McConnell 1999).

Diet overlap, a common occurrence in fish assemblages (Ross 1986), was less intense in Cancela where we observed low values of species richness, abundance and food availability. With its well-preserved riparian vegetation and high availability of shelter, this stream had greater pH values and dissolved oxygen levels. Meanwhile, none of those factors separately explained the variation in the degree of diet overlap among the streams. The other streams presented higher values of diet overlap, and physical and chemical conditions were quite heterogeneous. However, greater values of overlap occurred in environments where the resource availability and trophic niche breadth were similar (Cancela and Lajinha). The different composition of the assemblage from these streams probably explains these variations, mainly the overlap. Approximately 75% of the species recorded in Cancela were not observed in Lajinha, and the similarity in relation to abundance (the sum of the lowest abundances from each species) was only 10%. Nevertheless, the combination of the high number of species, high abundance, greater feeding specialization (smaller niche breadth) and conditions of high availability seem to be more decisive for the reduction in diet overlap.

The correlations between the community attributes, niche breadth and food availability with diet overlap was negative and significant for most of the streams. Thus, the overlap in the diet examined for each sample was negatively associated with the Shannon diversity index, species richness, dominance (inverse of evenness), fish abundance, fish size coefficient of variation (CV) and food availability, increasing only with fish size and niche breadth (increase in the participation of generalist species). On the other hand, Winemiller (1989) suggests that, in general, diet overlap is greater in species-rich systems. Lawlor (1980) and Matthews (1998) state that when the resource is scarce, the species need to converge toward a nearly identical use as well; consequently, a high degree of overlap is observed. Similarly, Zaret and Rand (1971) related resource availability and diet overlap but achieved a distinct conclusion. These authors reported that when resources are reduced, overlap is at a minimum, e.g., it is at low values during the dry period and high values during the flood, when the food input is greater. This suggests that this subject should be approached by considering the interactions between these variables. Thus, the results obtained for the fish assemblage of Lajinha, compared to those from Cancela, indicate that food availability and niche breadth, separately, do not explain the values of diet overlap. The influence of these variables will depend on species richness and abundance. With high values of these attributes, the overlap will be low (Cancela) or, on the contrary, high (Lajinha).

Species segregation into different microhabitats, differences in the feeding period and the specific feeding tactics used help to minimize the overlap among species with similar diets (Sabino and Castro 1990; Aranha et al. 1998; Casatti and Castro 1998; Sabino and Zuanon 1998). Segregation into different microhabitats may be determined by preferences in relation to substrate, water velocity and depth, among other variables (Herder and Freyhof 2006), or even by the presence of competitors or predators. In relation to foraging, a high degree of variation in foraging strategies may differentiate feeding patterns. According to Werner and Gilliam (1984), from an ecological and evolutionary perspective, the body size of individuals is one of the most important assemblage attributes and is an efficient way to avoid direct overlap in the use of resources. In the present study,

we verified that only variation in body size led to a reduction in overlap because samples with larger individuals also showed greater concordance in the identity of consumed food items.

In conclusion, a large number of fish species, similar to that observed in large watersheds, and a high fish abundance can be recorded in small Cerrado streams (<12 km in length). These findings may have been influenced by the fact that our study streams were direct tributaries of larger rivers, had low slopes, were meandering and had some “várzea” zones. Apparently, there is a strong association between high values of Shannon diversity index and abundance, a high level of trophic specialization (smaller trophic niche breadth) and low feeding overlap in fish assemblages from the Neotropical region.

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