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Coexisting small fish species in lotic neotropical environments: evidence of trophic niche differentiation

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Abstract Differences among species and their ecological requirements are considered fundamental in determining the outcome of species interactions as well as in coexistence. Thus, species that co-occurs tends to differ in the use of resources as a way to mitigate the effects of interspecific competition, facilitating interactions between pairs of species. So, this study used a set of seven small-sized characid species with similar morphology and feeding strategies, in order to investigate the hypothesis that the coexistence these species is facilitated by the differential use of food resources. Samplings were conducted in the rivers Verde and São Domingos, Upper Paraná River basin, Brazil, in hydrological periods rainy and dry. The analysis of 1055 stomach contents, by the volumetric method, indicated that the species consumed mainly allochthonous items, such as seeds, terrestrial plants and insects. In addition, they showed inter- and intraspecific differences in the diet composition between hydrological periods, which allowed the identification of items that particularise each species and contribute to the trophic segregation between them. Despite the wide variety of food items used, it was not possible to observe a consistent pattern of widening or narrowing of the food spectrum between hydrological periods, as expected. The trophic niche overlap showed intermediate and low values in both periods. In this sense, resource partitioning among species of small characids, facilitated by exploitation of different preferential resources as well as the intraspecific variation in response to seasonal availability of resources, became evident. The alternation of items and proportions of items in the diet as well as changes in feeding behaviour in opportune moments was probably the key for the coexistence of these species.

Keywords Characidae · Diet overlap · Niche breadth · Resource partitioning · Tropical rivers

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Introduction

Differences between species in their niches, either their requirements, impacts or both, are considered a key pillar for the niche theory (Chase and Leibold 2003). In this aspect, the competition for food resources has been postulated as an important driving factor in the evolution and diversification of species (Hutchinson 1957; MacArthur 1958). In contrast, species coexisting may differ in the use of resources as a means of mitigating the effects of competition (Pianka 1973; Schoener 1974; Svanbäck and Bolnick 2007; Wiens et al. 2010; Wang et al. 2015). Therefore, resource partitioning mechanisms may arise mainly from the similar ecological requirements and/or facilitation interactions between species pairs (Giacomini 2007; McCreadie and Bedwell 2013; Robertson et al. 2014). In this sense, understanding the processes that govern the partition of resources between morphologically similar and coexisting organisms is essential to the foundation of biological studies as well as conservation actions and management of ecosystems (McCreadie and Bedwell 2013; Mise et al. 2013; Swanson et al. 2015; Silva et al. 2016b). In particular, understanding the trophic niche dimension provides important insights into the coexistence of different species in the same community (Stevens 1989; Ward et al. 2006; Wiens et al. 2010; Sá-Oliveira and Isaac 2013; Quirino et al. 2015; Wang et al. 2015; Mateus et al. 2016).

In this sense, to understand the coexistence of species in the same location, the optimal foraging theory (OFT; Stephens and Krebs 1986) suggests that competition leads the species to change their foraging behaviour, broadening or narrowing the diet, depending on biotic conditions, such as competition (Punchard et al. 2000; Gotelli and McCabe 2002; Ward et al. 2006; Araújo et al. 2011) and predation (Englund et al. 2009; Fernandes et al. 2009) or environmental conditions (Peres-Neto 2004; Mouchet et al. 2013). Thus, the level of trophic segregation between sympatric species may vary considerably over time, reflecting food flexibility and seasonal abundance of prey (Roughgarden 1972; Abelha et al. 2001; Silva et al. 2014).

Tropical lotic environments show a pronounced seasonality resulting from the rainfall regime and fluctuations in water level, which cause cyclical changes in river characteristics and affect all the trophic dynamics of ecosystems (Lowe-Mcconnel 1999; Abujanra et al. 2009; Dodds et al. 2015). As a result, these seasonal changes in the hydrological cycle alter the abundance and availability of food resources for fish (Correa and Winemiller 2014; Silva et al. 2014). Thus, the OFT predicts that under abundance of preferred food items, consumers tend to narrow their diets (Stephens and Krebs 1986). On the other hand, during the food shortage period, the generalist feeding activity may be favoured, with expansion of the trophic niche (Roughgarden 1972; Robinson and Wilson 1998). In this way, temporal diet analysis of the species allows strong inferences on the mechanisms underlying the patterns of organisation and coexistence in fish communities (Ward et al. 2006; Mouchet et al. 2013).

Fish species, especially small-sized species belonging to the family Characidae, are excellent models to assess coexistence patterns. This group is very heterogeneous from a phylogenetic point of view and contributes significantly to the composition of the fish fauna of neotropical rivers, where it is widely distributed (Reis et al. 2003; Langeani et al. 2007; Mirande 2009; Albert and Reis 2011). In lotic environments, small fish preferably inhabit marginal habitats, where they find shelter from predators and favourable conditions for feeding (Lowe-McConnell 1987; Thomaz et al. 2004; Hahn and Fugi 2008). In this context, a growing amount of literature has revealed that small fish species have a high diversity of dietary habits and tactics and can explore the most different tropical environments, such as streams (Casatti et al. 2001; Wolff et al. 2009; Uieda and Pinto 2011; Silva et al. 2012), rivers (Viana et al. 2006; Corrêa et al. 2009) and lakes (Petry et al. 2003; Loureiro-Crippa et al. 2009; Carniatto et al. 2012; Quirino et al. 2015).

Thus, considering that feeding is an essential aspect of the life cycle of an organism (Sih and Christensen 2001), identification and quantification of diet composition are crucial steps to understand the role and interactions of each species in shared environments. For community ecologists, the acquisition of food by forager species plays a key role in determining the dynamics of competition between species (Pianka 1981; Mittelbach and Osenberg 1994), predator–prey interactions (Sih et al. 1985) and indirect interactions with the community (Wilbur and Fauth 1990; Wootton 1992).

In addition, understanding the mechanisms that allow the coexistence of many species with similar ecological requirements in neotropical rivers is still a major challenge in ecological studies (Sá-Oliveira et al. 2014). Therefore, assessing the small fish fauna from the trophic niche perspective is promising. Hence, in this study, we used a set of seven sympatric species of small characins with similar morphology and feeding strategies (Casatti et al. 2001; Mirande 2009; Romero and Casatti 2012), inhabiting two seasonal aquatic lotic environments, the Verde and São Domingos rivers, upper Paraná river Basin, Brazil, to test two general predictions. First, we expected to find differentiation in diet composition between these species, supporting the resource partitioning hypothesis. Secondly, we expected to find a narrow diet breadth during rainy periods. In this case, we assumed one of the premises of optimal foraging theory, which states that individuals would tend to focus their diets on more favourable resources in periods of greater abundance of resources. These predictions are closely related, directly reflecting the degree of overlap of food resources.

Materials and methods

Study area

Sampling was carried out in the Verde River, located in the state of Mato Grosso do Sul, which stands out as an important tributary on the right margin of the upper Paraná River and has its mouth in the reservoir of the hydroelectric power plant Sérgio Motta (Porto Primavera), the state of São Paulo and in its main tributary, the São Domingos River, located on its left margin. The study area (20°40′30.61″S, 53°34′4.91″W) is located in the Brazilian Cerrado, which is characterised by plant species with flowers and fruits influenced by seasonal variations in precipitation and humidity, where there is usually loss of leaves in the dry season and seed dispersal at the beginning of the rainy season (Lenza and Klink 2006; Salazar et al. 2012). The climate and hydrological regime (Fig. 1) are characterised by two distinct seasons: dry winters (April to September) and rainy summers (October to March) (Ribeiro et al. 1998; Pagotto and Souza 2006).

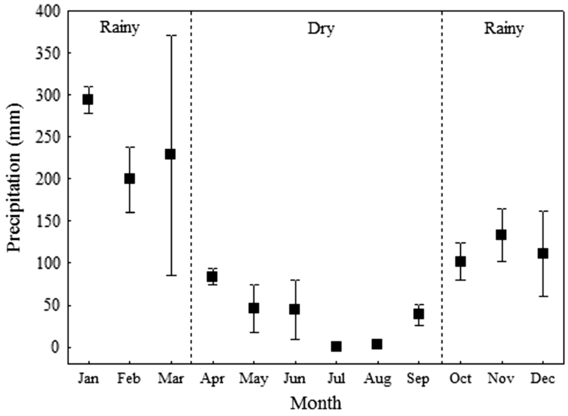

Fig. 1 Mean (*black square*) and standard deviation (*vertical bar*) of monthly variation of rainfall in the Verde River and its tributary, upper Paraná River basin, Brazil, from 2010 to 2012. Data were provided by the Brazilian National Water Agency (ANA) (station of the upper Verde River)

Sampling

Six sampling sites were established, distributed in the Verde River (three sites) and São Domingos River (three sites) (Fig. 2). Fish sampling was performed in the rainy period (December 2010 and January 2011 and December 2011 and January 2012) and in the dry period (from May and August 2011 and 2012), totalling 8 months of collecting. We used the following fishing devices: trawls, cast nets and gillnets with simple mesh sizes of 2.4, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14 and 16 cm and trammel nets (locally known as feiticeiras) with mesh sizes of 6, 7 and 8 cm between non-adjacent knots, with 1.5 m in height and 20 m in length in the Verde River and with 10 m in length in the tributary. After capturing the fish, we anesthetised them with a benzocaine solution (250 mg/l) following the recommendations of the American Veterinary Medical Association (Avma 2001), fixed them in plastic bags containing 10% formaldehyde and placed them in polyethylene containers. In the laboratory, we identified the fish following Graça and Pavanelli (2007), measured (total and standard length in cm) and weighed them (g). Specimens of each species were preserved in 70% alcohol and deposited them in the ichthyological collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia), Universidade Estadual de Maringá.

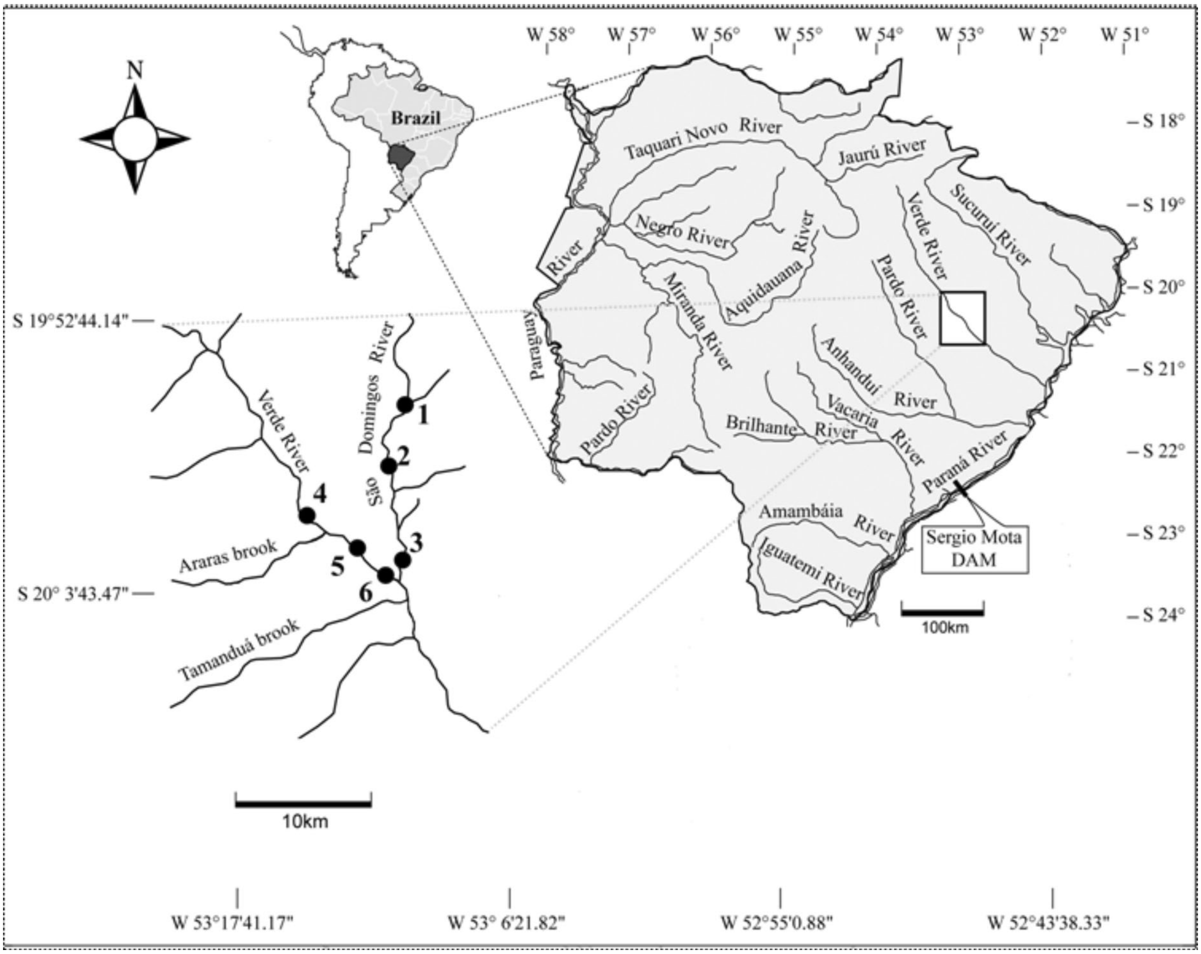

Fig. 2 Study area and sampling sites in the Verde and São Domingos Rivers, Upper Paraná River Basin, Mato Grosso do Sul, Brazil

Diet analysis

Only small-sized species (those in which the adults have a standard length <15 cm), as proposed by Castro et al. (2003) and with the number of stomachs >10 were used in this study. The stomachs analysed were those with a degree of repletion >50% of fullness (for scale, see Zavala-Camin 1996). Stomach contents were examined using an optical microscope and a stereoscope, and the items were quantified according to the volumetric method (Hyslop 1980). The food items were identified using Bicudo and Bicudo (1970) for algae and Mugnai et al. (2010) for invertebrates; When necessary, other specific literatures were used. We also used graduated tubes and a glass counting plate to measure the volume of the items (Hellawell and Abel 1971). The food items were classified according to their origin in autochthonous (originating from the aquatic environment) and allochthonous (originating from the terrestrial environment).

Data analysis

Diet composition

To test possible significant differences in the dietary composition of the species among the pre-defined groups (species and hydrological periods), PERMANOVA multivariate permutational variance analysis was used through the Bray-Curtis index obtained with 999 random permutations (Anderson 2001). To evaluate the food items that contributed most to the intraspecific dissimilarity between the hydrological periods, we performed a similarity percentage analysis

(SIMPER), using Bray-Curtis dissimilarity (Clarke 1993).

Niche breadth

The test of homogeneity the multivariate dispersion (PERMDISP, Anderson et al. 2008) was used to assess differences in intra- and interspecific niche breadth, between hydrological periods. In our study, the niche breadth was measured through the dispersion of the diet in space. The assumption was that differences in distance between species indicate that some species have more restricted or broader diets than others. By PERMDISP, the distance of the median (i.e. similar to the centroid) of a group defined a priori is calculated, in this case the species/hydrological periods, through a principal coordinate analysis (PCoA). Calculation of the median of the group was performed using the dissimilarity measure of Bray-Curtis, allowing the comparison of the average dissimilarity in *n* individual observations within the group. To test the null hypothesis that the niche breadth did not differ among the groups, a statistical F was calculated to compare the average distance of each sample to the median of the group. Subsequently, the *p* value was obtained through 9999 permutations of the residues of least squares (Anderson 2006). Post hoc pairwise comparisons were made by Tukey's 'Honest Significant Difference' method.

Food overlap

The overlap of the diet was calculated per sample for each species pair that co-occurs in time and space (month and site), based on the volume matrix of the food items. We used the Pianka (1973) food overlap index, described by the equation:

$$O_{jk} = \frac{\sum_i^n P_{ij} \times P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \times \sum_i^n P_{ik}^2}}$$

where O_{jk} = measure of the Pianka niche overlap between the *j* and *k* species; P_{ij} = proportion of a food item *i* in the diet of the species *j*; P_{ik} = proportion of the food item *i* in the diet of the species *k*; *n* = total number of food items. The overlap values ranged from 0 (no overlap) to 1 (full overlay) and were defined at the following levels: low (0–0.39), intermediate (0.4–0.6) and high (0.6–1) (modified from Grossman 1986; Corrêa et al. 2011). A one-way ANOVA was applied to data of trophic niche overlap, considering hydrological period (rainy and dry) as a factor.

The PERMANOVA, SIMPER, PERMDISP, ANOVA and statistical analyses were performed in the program R, using *vegan* and *spaa* packages (Zhang 2013; R Development 2015). The Pianka index of food overlap was calculated using EcoSim® 7.0 (Gotelli and Entsminger 2006). The figures were created in software STATISTICA 7.0. The level of statistical significance adopted for all analyses was $p < 0.05$.

Results

Diet composition

We analysed the stomach contents of 1055 individuals belonging the seven most abundant small-sized fish species (Characidae) (Table 1). The analysed species accounted for 83% of the species recorded (Silva et al. 2016a).

For the set of species, 21 food items were identified. The resources from autochthonous and allochthonous sources were represented by 10 items each, with the most representative allochthonous items in fish diet (Table 2). Significant differences were observed in diet composition between species (PERMANOVA; *pseudo*-F = 56.76, $p < 0.001$) and hydrological periods (*pseudo*-F = 9.88; $p < 0.001$), as well, for interaction between the factors (*pseudo*-F = 17.3; $p < 0.001$).

Astyanax aff. *fasciatus* mainly consumed seeds, Hymenoptera and terrestrial plants in the rainy season; in the dry season, terrestrial plants and Hymenoptera were predominant prey items. In the rainy season, the diet of *Astyanax lacustris* was based on seeds, Hymenoptera and terrestrial plants, while in the dry season, in addition to these items, their diet was supplemented by aquatic plant (Table 2). For *Piabarchus* sp.1, other aquatic invertebrates, Hymenoptera, Isoptera and terrestrial plants, were substantial items in both periods, except Isoptera in the dry season. *Piabarchus stramineus* ingested substantial amounts of Isoptera and other aquatic invertebrates in the rainy season and Hymenoptera, other aquatic invertebrates, Plecoptera and Odonata nymphs in the dry season. The diet of *Moenkhausia* aff. *intermedia* was based on immature Diptera, other aquatic

Table 1 Taxonomic position of the species (Reis et al. 2003; Mirande 2009; Koerber et al. 2017), occurrence, number of stomachs analysed and size range of the individuals sampled in the Verde River and its tributary, Upper Paraná River Basin, Brazil, from November 2010 to August 2012

ORDER/family/species	Numerical abundance total	Number of analysed stomachs		Standard length range (cm)	Vouchers specimens
		Rainy period	Dry period		
Characiformes					
Characidae					
Astyanax aff. *fasciatus* (Cuvier, 1819)	2250	107	70	4.7–12.2	NUP 108
Astyanax lacustris (Lütken, 1875)	1294	121	68	3.8–13.0	NUP 6149
Moenkhausia aff. *intermedia* Eigenmann, 1908	1026	99	15	2.1–3.6	NUP 3208
Piabina argentea Reinhardt, 1867	8177	174	137	2.9–6.3	NUP 6209
Piabarchus sp.1	2271	15	24	3–4.3	
Piabarchus stramineus (Eigenmann, 1908)	329	71	78	2.4–5	NUP 55
Serrapinnus notomelas (Eigenmann, 1915)	1395	72	4	2–3.7	NUP 107
Total number	16,742	659	396		

Vouchers specimens = are a representative specimen of the species used in a study

invertebrates, Ephemeroptera and Hymenoptera in the rainy season and Ephemeroptera and immature Diptera in the dry season. In the diet of *Piabina argentea*, seeds were predominant in both periods. *Serrapinus notomelas* ingested larger proportions of algae, detritus and terrestrial plants in the rainy season and mostly aquatic plants in the dry season (Table 2).

The food items that most contributed to the intraspecific differentiation between hydrological periods were seeds for *A.* aff. *fasciatus*, *A. lacustris* and *P. argentea*, other aquatic invertebrates for *Piabarchus* sp.1 and *P. stramineus*; Ephemeroptera for *M.* aff. *intermedia*; aquatic plants for *S. notomelas* (Table 3).

Niche breadth

The species consumed a wide variety of items, which was reflected in intraspecific values in breadth diet (Fig. 3). We did not observe a consistent pattern of expansion or contraction of the food spectrum between hydrological periods (Fig. 3). However, PERMIDISP showed significant differences in trophic niche breadth between species pairs (PERMDISP, $F = 9.69$, $p > 0.001$).

The niche overlap showed overall intermediate and low values (<0.6; Fig. 4). However, there were significant seasonal differences (ANOVA = 3.97, $p < 0.05$), with an increasing trend in overlap in the rainy season, where 55% of the species pairs with niche overlap values above 0.6 were observed. Higher interspecific overlap values were observed for *P. argentea* × *A. lacustris* pairs in the rainy season (seeds partition), *S. notomelas* × *A.* aff. *fasciatus* in the dry season (aquatic plants) and *S. notomelas* × *Piabarchus* sp.1 (aquatic and terrestrial plants) (Fig. 4).

Discussion

Our results show that small characids have a diverse diet, especially composed of allochthonous items whose abundance can be influenced by hydrological seasonality. Allochthonous resources were mainly represented by these items (seeds, plants and terrestrial insects). According to Lenza and Klink (2006) and Salazar et al. (2012), the studied region presents great seasonality in the supply of leaves and seeds. In freshwater lotic environments, allochthonous resources are considered the main food sources for

Table 2 Volume percentage of food items consumed by small-sized fish species, classified by origin in each hydrological period, rainy (*R*) and dry (*D*), in the Verde and São Domingos River, Upper Paraná River Basin, Brazil, from November 2010 to August 2012

Species	Af		Al		Mi		Pa		Pi		Ps		Sn	
Items/hydrological periods	R	D	R	D	R	D	R	D	R	D	R	D	R	D
Autochthonous %	17.7	18.1	9.2	26.8	64.3	74.1	20.5	21.2	44.9	39.7	46.7	51.3	51.0	85.2
Ephemeroptera	0.6	0.8	0.3	1.5	**15.3**	**50.3**	2.3	1.0	6.4	8.0	8.3	2.9	0.8	1.9
Odonata nymph	0.7	3.3	1.1	1.5	0.6		0.9	1.8		8.9	5.7	10.7		
Plecoptera	0.3	0.9	0.6	0.7	2.5	0.2	0.6	1.7		4.4	6.2	11.5	0.3	
Immature Coleoptera	*	0.1	0.0	0.1	2.6	0.6	0.7	0.3	0.1	0.6	0.2	0.7		
Immature Diptera	0.1	0.0	0.0	0.0	23.4	**11.6**	0.9	2.1	0.2	0.2	6.1	9.4	1.4	*
Immature Lepidoptera	0.1	0.1	0.3		1.1		0.9	0.1			0.1	0.2		
Other aquatic invertebrates	2.3	0.9	0.7	1.0	**18.2**	9.2	**12.5**	**10.9**	**38.3**	**17.5**	**20.0**	**15.9**	3.9	
Fish	0.1	0.4	0.1	2.1	*	0.0	0.6	0.1		*	*		*	
Algae	5.3	4.6	6.1	7.5	0.6	2.3	0.6			0.2			**44.6**	**13.0**
Aquatic plant	8.3	7.0		**12.5**			0.4	3.1			0.1			**70.4**
Allochthonous %	82.3	81.6	90.8	72.8	35.7	25.9	78.6	77.7	55.1	60.3	53.3	46.9	23.3	14.8
Oligochaeta	1.3		5.7	3.0										
Araneae		0.1	0.1	0.1	0.5	3.5	0.7	0.0			0.0	2.5		*
Orthoptera		0.5	2.4	1.9			0.1	1.2				0.4		
Isoptera	0.5		0.7	2.3	**10.7**		1.4	0.0	**17.1**		**43.1**			
Hemiptera	2.0	1.7	1.0	5.9	1.1	3.9	1.0	0.5	0.1			0.9		
Hymenoptera	**18.8**	**33.4**	**15.6**	10.0	**12.2**	5.9	3.3	3.8	**18.5**	**21.3**	6.2	**26.0**	0.0	
Coleoptera	1.6	4.4	4.2	1.0	1.1	8.3	0.6	1.5		2.7	1.5	9.9		
Terrestrial insect remains	3.4	2.4	1.5	0.4	3.4		1.7	4.1	6.1	6.2	0.7	0.6	0.1	
Seeds	**43.5**	4.0	**46.2**	**31.4**	4.3	0.4	**61.1**	**58.6**	3.4	1.7	0.9	5.1	6.2	
Terrestrial plants	**11.2**	**35.3**	**13.4**	**16.8**	2.6	3.8	**8.7**	**8.1**	9.8	**28.4**	0.9	1.3	**16.9**	**14.8**
Undetermined														
Detritus		0.3		0.4			0.9	1.0				1.8	**25.8**	

Asterisk indicates values below 0.1%. The most consumed food items are in bold

Af = *A.* aff. *fasciatus*, Al = *A. lacustris*, Mi = *M.* aff. *intermedia*, Pa = *P. argentea*, Pi = *Piabarchus* sp.1, Ps = *P. stramineus*, Sn = *S. notomelas*

fish fauna (Nakano and Murakami 2001; Correa et al. 2007; Trevisan and Hepp 2007; Richardson et al. 2010; Marcarelli et al. 2011). This is mainly observed in sites with riparian vegetation as well as deciduous vegetation, where resources are carried to the aquatic environment, resulting in a strong association between the abundance of the allochthonous items and the rainy season (Prejs and Prejs 1987; Nakano and Murakami 2001; Alvim and Peret 2004; Correa et al. 2007; Pinto and Uieda 2007). Due to declining water levels and, consequently, a reduction in foraging areas in the dry period, some allochthonous resources become less abundant. In this scenario, the fish species tend to consume other items, changing their diets to other items available at that particular time (Correa and Winnemiller 2014).

The intraspecific seasonal variation in the diet was demonstrated in our results. The probable variations in the contribution of resources certainly promoted food spectrum changes in species between the hydrological periods. Thus, this allows us to infer that small species examined here have high trophic plasticity, presenting exploratory and diverse feeding tactics, which represents a recurrent pattern found in the literature (Casatti et al. 2001; Cassemiro et al. 2002; Russo et al. 2004; Casatti and Castro 2006; Viana et al. 2006; Ceneviva-

Table 3 Percentage values of the main items that contributed to dissimilarity in the diet of the seven fish species, between rainy and dry hydrological periods. Values obtained through the SIMPER analysis in the Verde and São Domingos River, Upper Paraná River Basin, Brazil, from November 2010 to August 2012

Species/item	Af	Al	Mi	Pa	Pi	Ps	Sn
Percentage contribution of origin							
Ephemeroptera		**24.50**					
Odonata nymph					9.08		
Plecoptera							
Immature Diptera		14.51					
Other aquatic invertebrates	11.61	9.41	**22.20**	**16.13**			
Algae							16.67
Aquatic plant						**39.86**	
Hymenoptera	18.31	11.78			11.62	12.83	
Isoptera						12.00	
Terrestrial plants	18.25	13.99		8.39	16.92		
Seeds	**22.22**	**29.56**		**33.19**			

Food items that most contributed are in bold

Af = *A.* aff. *fasciatus*, Al = *A. lacustris*, Mi = *M.* aff. *intermedia*, Pa = *P. argentea*, Pi = *Piabarchus* sp.1, Ps = *P. stramineus*, Sn = *S. notomelas*

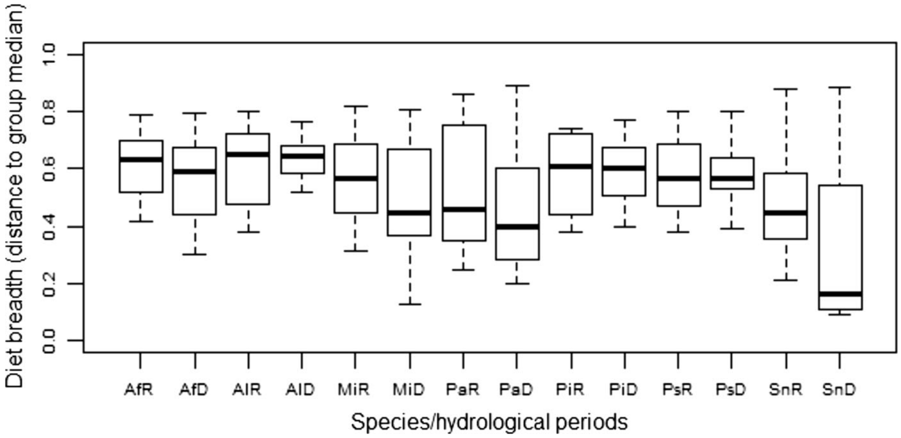

Fig. 3 Variation in diet breadth among seven small-sized fish species based on food items consumed during the hydrological periods rainy (*R*) and dry (*D*) in the Verde and São Domingos River, Upper Paraná River Basin, Brazil, from November 2010 to August 2012. Diet breadth was assessed as species dispersion in diet space using PERMDISP (i.e. greater distance to spatial median indicates larger dispersion and therefore a broader trophic niche). *Box lower* and *upper* endpoints represent the 25th and 75th quartiles, respectively. The *horizontal bar* inside each box represents median diet breadth. Species codes are: Af = *A.* aff. *fasciatus*, Al = *A. lacustris*, Mi = *M.* aff. *intermedia*, Pa = *P. argentea*, Pi = *Piabarchus* sp.1, Ps = *P. stramineus*, Sn = *S. notomelas*

Bastos and Casatti 2007; Wolff et al. 2009; Tófoli et al. 2010; Gandini et al. 2012; Manna et al. 2012, Quirino et al. 2017).

Species with similar morphological characteristics have high competitive potential (Gatz 1979), especially when phylogenetically close, due to what is conceptualised as niche conservatism (Wiens et al. 2010; Wang et al. 2015). Thus, as stated earlier, we expected a high similarity in the diet composition of the species analysed in this study. However, what we have shown is that they segregate from each other in the trophic dimension, supporting our hypothesis of

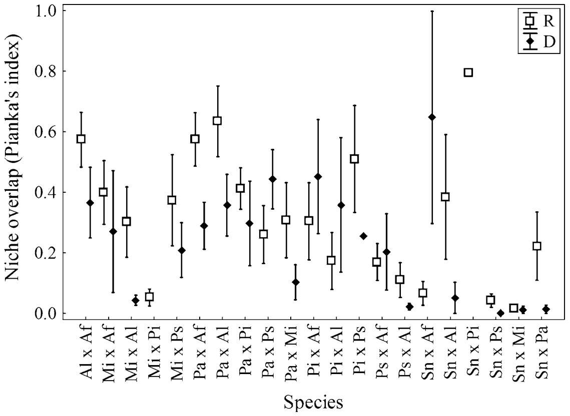

Fig. 4 Diet overlap values (mean ± SE) for species pairs during the hydrological periods rainy (*R*) and dry (*D*) in the Verde and São Domingos River, Upper Paraná River Basin, Brazil, from November 2010 to August 2012. Species codes are: Af = *A.* aff. *fasciatus*, Al = *A. lacustris*, Mi = *M.* aff. *intermedia*, Pa = *P. argentea*, Pi = *Piabarchus* sp.1, Ps = *P. stramineus*, Sn = *S. Notomelas*

differential resource utilisation. According to the intraspecific information of the diet, even if the species consume some items in common, they are ingested in different proportions, as if there were a rotation of consumption of certain items, between the species and between the hydrological periods.

Since food is considered the most important niche dimension in the segregation of fish species (Schoener 1974; Ross 1986; Gerking 1994), sympatric species tend to differ in the use of resources to minimise competition (Wootton 1990). Furthermore, species coexistence depends on different ecological responses to similar ecological processes (Hutchinson 1957). In this way, many species tend to select their diet, sharing food resources (Schoener 1974; Gerking 1994). This mechanism seems to be the key factor for trophic segregation between small fish in the Verde River. This idea becomes even more consistent as the analysed species have very similar morphological characteristics (Casatti et al. 2001; Reis et al. 2003; Romero and Casatti 2012) and are exposed to the same biotic and abiotic conditions.

The niche breadth was different between the hydrological periods, however, and does not corroborate with one assumption of the optimal foraging theory, which predicts widening or narrowing of the niche, depending on environmental conditions. Correa and Winemiller (2014), studying Amazonian fish, also described no consistent pattern in niche breadth in response to temporal changes in the quality and availability of food resources, and they suggested that this response to abundant or limited food resources depends on the taxon and ecosystem analysed. This lack of variation in niche breadth relative to seasonality has been reported for various fish species (Ward et al. 2006; Novakowski et al. 2008; Corrêa et al. 2009, 2011; Tófoli et al. 2010; Alves et al. 2011). However, there is no consensus regarding whether the niche is expanded or contracted in the presence of abundant food (Roughgarden 1972; Dyer et al. 2010; Quirino et al. 2017). By means of intraspecific analysis (PERMDISP), we observed that in general, species analysed here, showed high dispersion of food items in diet, regardless of the hydrological period. This supports the hypothesis that species alternate food items and/or their proportions according to preference or availability, but maintain the variety in the diet. According to Sá-Oliveira et al. (2014), wider trophic niches characterise generalist species. In this study, this statement is validated, since the species analysed are identified as typical generalists in the literature (Bennemann et al. 2005; Silva et al. 2012; Moraes et al. 2013; Mise et al. 2013).

The low diet overlap found between most species pairs endorses and confirms the results of niche breadth, where there is no pattern of expansion or contraction of the niche between sampled hydrological periods, although there was an upward trend in the rainy season when seeds and terrestrial insects were probably more available. The importance of fruits and seeds in the fish diet is strongly associated with their availability, as in virtually all ecosystems, fruits and seeds are patchily distributed and seasonally available (Correa et al. 2007), especially in the region studied (Lenza and Klink 2006; Salazar et al. 2012). Although the availability of food resources has not been directly measured in the environment, we rely on the assumption that fish are good samplers of available resources, directly reflecting the resources they can efficiently access (Mérona et al. 2003; Tupinambás et al. 2015). In this sense, the differential exploitation of food resources in the period in which they are more accessible, in this case, in the rainy season, seems to be the key to explain the low diet overlap between most small species analysed. Nevertheless, although some species pairs (e.g. *P. argentea* × *A. lacustris*, *S. notomelas* × *A.* aff. *fasciatus*, *S. notomelas* × *Piabarchus* sp.1) had higher overlap, mainly because of the great consumption of more abundant resources (seeds, aquatic and terrestrial plants), the general trend confirmed was the trophic differentiation, translated into food resource partitioning.

Since Hutchinson (1957), the mechanisms that allow similar species to partition resources and to coexist are questioned. However, it has been observed that in highly diverse assemblages, the species have reduced the realised niche, revealed through the trophic breadth, to prevent the alleged effects of competition (MacArthur 1972; Robertson et al. 2014). Therefore, the results obtained are consistent with the ecological niche theory (reviewed by Chase and Leibold 2003), which focuses on biotic interactions and dynamics of resources for consumers at more local scales. In this case, it is assumed that correlated species that occupy the same environments tend to show partition of resources (Schoener 1974; Wiens et al. 2010). In this sense, the partition of resources has been widely analysed for neotropical fishes in different environments (Hahn et al. 2004; Mérona and Rankin-de-Mérona 2004; Russo et al. 2004; Novakowski et al. 2008; Brasil-Souza et al. 2009; Corrêa et al. 2009, 2011; Alves et al. 2011; Silva et al. 2012, 2016b); it is also supported by our study.

Moreover, it is important to note that for the coexistence of species in natural systems, differences in resource utilisation must be not only food partitioning, but also the way species use these food resources in response to environmental variations (Giacomini 2007). Thus, the spatial differences in food resource utilisation observed by Silva et al. (2014), for the same species, favour the coexistence of small fish species at larger spatial scales.

In this perspective, our findings demonstrate the existence of partition of resources among species of small characids. Thus, the exploitation of different preferred resources by species, either by feeding habit or tactic, and the intraspecific variation in response to seasonal availability of resources might be essential for trophic segregation in these characid species. Possibly, alternation of items and proportions in the diet and variation in foraging behaviour, at favourable periods, may be plausible explanatory mechanisms for the coexistence and high abundance of these species. However, experimental work analysing the diet of fish species (both at an individual and at the community level) is needed to improve our understanding of the different ways of partition resources.

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