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Resource partitioning among syntopic Characidae corroborated by gut content and stable isotope analyses

Karine O. Bonato · Edward D. Burress · Clarice B. Fialho · Jonathan W. Armbruster

Abstract We aim to test the hypothesis that an assemblage of characid fishes coexist by partitioning food resources. We calculated dietary niche overlap of four syntopic species of the Characidae using gut content analysis. Secondly, we used a carbon (^{13}C) and nitrogen (^{15}N) isotope Bayesian mixing model to estimate relative assimilation. All characids consumed large proportions of plant material and aquatic insects; however, Pianka's index indicated low dietary overlap among species throughout most of the sampling period. The low degrees of dietary overlap were due to discrepancies in the relative consumption of Ephemeroptera and aquatic insect remains. Secondly, there was high correspondence between the gut content analyses and isotope mixing model estimates. *Astyanax xiru* and *Bryconamericus iheringii* were the only species that ingested and assimilated large fractions of aquatic plants and algae, respectively. *Astyanax procerus* consumed and assimilated large fractions of terrestrial invertebrates, whereas *Bryconamericus* sp. assimilated mainly aquatic invertebrates. Therefore, we demonstrate that the assimilated nutrients were consistent with the relative consumption of food items. These results are consistent with the hypothesis that this characid assemblage may coexist via resource partitioning.

Keywords Stream fish · Diet · Prey assimilation · Niche overlap

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Introduction

Species of the Characidae (tetras) have highly heterogeneous ecologies due to their high taxonomic diversity (Lima et al., 2003). This family can occupy many trophic niches including piscivory (e.g., *Oligosarcus* spp.), lepidophagy (e.g. *Roeboexodon geryi* Myers, 1960 and *Roeboides bonariensis* (Reinhardt, 1851)), omnivory (e.g. *Astyanax* spp.), and frugivory (e.g. *Piaractus mesopotamicus* (Holmberg, 1887) and *Brycon hilarii* (Valenciennes, 1850)) (Lima et al., 2003; Galetti et al., 2008; Reys et al., 2009; Javonillo et al., 2010; Neves et al., 2015). Therefore, characids

ingest a wide variety of food items, occupy different parts of the food web, and range from generalists to specialists. The characid genera *Astyanax* and *Bryconamericus* are the most speciose genera in the family with species normally occurring in high abundance in rivers and streams. These species, particularly the Neotropical ones, exhibit varied diets and may function as herbivores, omnivores, or meso-predators in the ecosystems they inhabit (Winemiller et al., 2008; Burress et al., 2013). Moreover, they have the ability to change their feeding habits (mainly *Bryconamericus*) in response to variation in prey availability (Abelha et al., 2001; Orciolli & Benne-mann, 2006; Brandão-Gonçalves et al., 2009; Bonato et al., 2012).

According to Gerking (1994), there was resistance to classify fish as herbivorous, because it was believed that an herbivorous diet would prevent proper growth and reproduction. This is a consequence of fish intestines not producing enzymes capable of breaking down plant cells (e.g., cellulose); therefore, fishes need other tools to assist with breakdown of plant materials such as microorganisms that produce nec-essary enzymes, mechanical processing to physically rupture cell walls, and/or longer guts to allow for higher intake of food and to maintain the food in the gut for a longer time to maximize nutrient assimilation (German et al., 2009; Wagner et al., 2009; Pelster et al., 2015). Accordingly, many studies suggest that fishes can assimilate ingested plants and that plants can provide sufficient nutritional value to support proper growth (Hemmi & Jormalainen, 2002; Smit et al., 2006; Clements et al., 2009).

There are several methods to quantify the diets of fishes. Stomach content analysis usually indicates food consumed recently, but not the dietary patterns over time or differential assimilation because of differences among food items associated with detectability, measurability, and digestibility (Bene-ditto et al., 2013; Park et al., 2015). Stable isotope studies may provide evidence about the relative amounts of nutrients derived from plant and animal origins. The stable isotopes of nitrogen (δ^{15}N) and carbon (δ^{13}C) provide powerful tools for estimating trophic positions that integrate the assimilation of energy and carbon flow to consumers in food webs (DeNiro & Epstein, 1981; Post, 2002). This technique is based on the observation that the isotopic ratios of a consumer are dependent upon the ratios of its diet such

that there is a consistent trophic enrichment factor between consumer and diet (Anderson & Cabana, 2007; Di Beneditto et al., 2011, 2012; Compson et al., 2014; Cresson et al., 2016). Stable isotopes of nitrogen (δ^{15}N) can be used to estimate trophic level and relative food assimilation over time, and carbon (δ^{13}C) indicates different sources of carbon (i.e. aquatic or terrestrial) (DeNiro & Epstein, 1978; Peterson & Fry, 1987; Fry, 2008). Thus, gut content and isotope analyses may provide complementary answers about the trophic ecology of species (Genner et al., 1999; Bearhop et al., 2004; Quevedo et al., 2009) and can be used to compare rates of consumption and assimila-tion. Using multiple approaches allows for more robust assertions about the trophic patterns and trophic interactions among species such as coexistence by food niche partitioning.

Here, we evaluated the ecological relationships among four characid species occurring syntopically in Southern Brazil in the Caixões River: *Astyanax procerus* Lucena et al., 2013a; *Astyanax xiru* Lucena et al., 2013b; *Bryconamericus iheringii* (Boulenger, 1887); and *Bryconamericus* sp. More specifically, we focus on potential mechanisms by which they coexist through resource partitioning. Therefore, to under-stand the complex trophic relationships among these four syntopic characid species, the objectives of this study were to (i) evaluate the relative consumption of food items as described by gut contents analyses, (ii) estimate the relative assimilation of those prey items with isotopic analyses, and (iii) assess the existence of resource partitioning among these species based on their diets.

Materials and methods

Sampling

We studied four syntopic species of Characidae in the Caixões River (S29°01′54″/W52°49′25.1″). This stream is located in the Alto Jacuí sub-basin that belongs to the Patos Lagoon drainage in Rio Grande do Sul, Brazil. For gut content analysis, fish were collected in 2012 and 2013 bimonthly. We sampled fish using electrofishing. Fish were euthanized with 10% eugenol (Vidal et al., 2008; Lucena et al., 2013a), fixed in 10% formalin, and then transferred to 70% alcohol for preservation. Fish were identified in the

laboratory with identification keys and voucher specimens were deposited in the fish collection of the Departamento de Zoologia at the Universidade Federal do Rio Grande do Sul (*Astyanax procerus*—UFRGS 19323, *Astyanax xiru*—UFRGS 19326, *Briconamericus iheringii*—UFRGS 19974, *Bryconamericus* sp.—UFRGS 17931).

For isotope analysis, sampling occurred in the same location, but in February 2015 using the same method cited above. Fishes and possible prey items were temporarily stored on ice in the field and later stored in a −80°C freezer in the laboratory. The fishes used for all analyses were representative of adult size classes. Additionally, we manually sampled invertebrates that represent potential prey items, including (i) aquatic insects (Ephemeroptera, Trichoptera, Plecoptera, Lepidoptera larvae, Megaloptera, Coleoptera larvae and adult), (ii) terrestrial insects (Lepidoptera larvae, adult Hemiptera, adult Coleoptera, adult Orthoptera, adult Hymenoptera (i.e., ants and bees), and adult Odonata), (iii) other invertebrates (*Aegla* sp., Oligochaeta, Bivalvia, snail, and Araneae) and (iv) plants (terrestrial leaves, periphyton, Bryophytae and aquatic plants (Podostemaceae)).

Gut contents

Stomachs were dissected and then preserved in 70% alcohol. Stomach contents were identified under optical and stereoscopic microscopes to the lowest taxonomic level possible. Food items were identified using identification keys for invertebrates (Merritt and Cummins 1996; Costa et al., 2006; Mugnai et al., 2010). Food items were then quantified according to the volumetric method (i.e., the total volume of a food item consumed by the fish population given as a percentage of the total volume of all stomach contents (Hyslop, 1980)) using graduated test tubes and a glass counting plate (Hellawell and Abel 1971).

Feeding overlap

We used Pianka's index (Pianka, 1973) to estimate the species' feeding overlap within each sampling month to test the assumptions of niche overlap theory (Pianka, 1974; Ross, 1986). Overlap values range from zero to one, where zero indicates the absence of overlap and one indicates complete overlap. We established three categories to improve understanding

of the overlap results, high overlap is depicted by overlap values >0.6, intermediate overlap by overlap values between 0.4 and 0.6, and low overlap depicted by values <0.4 (Grossman, 1986).

To evaluate the significance of Pianka's index, we used the null model with a RA3 algorithm (Winemiller & Pianka, 1990). We performed 9999 Monte Carlo randomizations that represent a null model that we can compare (mean niche overlap values for all group pairs) with the observed data. In this model, mean overlap values that are significantly lower than those expected by chance might indicate food partitioning; however, values higher than those expected by chance might indicate food sharing (Albrecht & Gotelli, 2001). The observed results were compared with the null model at the significance level $p < 0.05$ to evaluate if the observed pattern differs of the overlap values simulated at random. Both feeding overlap and null model were calculated using the prey volumes (Online Resource 1) and they were computed using R Project for Statistical Computing program (version 3.2.3) in the EcoSimR package (version 0.1.0) (R Core Team, 2016). Pairwise Pianka's niche overlaps were calculated using the 'spaa' R package (Gotelli, 2000; Zhang, 2004).

Stable isotope methods

We dissected a sample of caudal muscle tissue *A. procerus* ($N = 6$; 39.7 ± 7.2 mm), *A. xiru* ($N = 4$; 41.3 ± 8.5 mm; SL), *B. iheringii* ($N = 5$; 58.9 ± 5.1 mm), and *Bryconamericus* sp. ($N = 5$; 61.8 ± 7.0 mm), which were then lyophilized until dry (i.e., asymptotic mass), ground into a homogenous powder and weighed into tin capsules. Invertebrates and basal resources were lyophilized whole and homogenized. Samples were analyzed for ^{15}N and ^{13}C at the University of Georgia stable isotope laboratory (Athens, Georgia, USA). All values are written in delta notation, which represents the deviation of stable isotope ratios ($^{13}C:^{12}C$ and $^{15}N:^{14}N$) from universal standards: PDB limestone (C) and atmospheric nitrogen (N). Lipid content can bias ^{13}C analysis (Post et al., 2007) because lipids are depleted relative to proteins and carbohydrates. However, consumer C:N ratios were less than 3.5 indicating that lipid content was sufficiently low to prevent bias (Post et al., 2007). Furthermore, lipid content (i.e., as estimated from C:N) was similar among consumers

suggesting uniform effects (if any) from lipids, thus limiting potential bias in our analyses.

To estimate the relative assimilation of prey items, we employed the SIAR Bayesian mixing model (Parnell et al., 2010). Potential prey items were partitioned into five functional groups based on their type and origin (aquatic plants, aquatic invertebrates, terrestrial plants, terrestrial invertebrates and algae). We incorporated error associated with (1) fractionation estimates and (2) variation in consumer and source isotope ratios. We used fractionation factors based on generic rates supported by meta-analyses (Post, 2002): 3.54‰ and 0.5‰ for ^{15}N and ^{13}C, respectively. We incorporated error (e.g., SD) associated with these rates as they were reported in Post (2002): 0.98‰ (^{15}N) and 1.3‰ (^{13}C). To prevent erroneously attributing prey items that are not consumed, we utilized a threshold to determine what prey items were included in the models. Any prey items (or functional groups) that represented ≥5% of the gut contents by volume were included for that consumers' model. Therefore, our estimates are not independent assessments of these consumers' diets, but rather estimates of the relative assimilation of known food resources. The model was run for 500,000 generations, with data recorded every 50,000, and 10% burnin.

Results

Gut contents

Collectively, the species fed upon 38 food items (Table 1). The items consumed most by *Astyanax procerus* were Oligochaeta (18%), adult Hymenoptera (18%), terrestrial plants (15%), aquatic plants (15%), and aquatic insects remains (10%). *Astyanax xiru* ingested primarily terrestrial plants (39%), aquatic plants (35%), and Sarcophagidae (14%). *Bryconamericus iheringii* was the only species that ingested detritus (26%) and filamentous algae in high proportions (9%), and also consumed aquatic insect remains (19%) and terrestrial plants (14%). Lastly, *Bryconamericus* sp. consumed mostly aquatic insects such as Ephemeroptera (48%), Trichoptera (11%) and aquatic Lepidoptera larvae (13%) (Table 1).

Feeding overlap

Pianka's index indicated low feeding overlap among the majority of sampling months (Table 2). In December 2012, there was an intermediate overlap and June 2013 was the only month that had a high overlap (Table 2). The higher overlap during these months resulted from sharing of few resources. In December, all four species consumed large proportions of Ephemeroptera (Fig. 1). The overlap among *A. procerus*, *A. xiru,* and *B. iheringii* was also due to higher intake of terrestrial plants, and also between *A. procerus*, *B. iheringii*, and *Bryconamericus* sp., which consumed more aquatic insect remains. Based on pairwise comparisons, the only niche overlaps that were high in December 2012, where those between *B. iheringii* and *A. procerus* and between *Bryconamericus* sp. and *A. xiru*, whereas all other pairwise comparisons exhibited low niche overlap (Table 3). In June 2013 (Fig. 1), *A. xiru* was not sampled. The overlap among *B. iheringii*, *Bryconamericus* sp., and *A. procerus* resulted from the consumption of large proportions of Ephemeroptera and secondary consumption of aquatic insects remains (Fig. 1). Additionally, aquatic Lepidoptera larvae were consumed by both *Bryconamericus* species (Fig. 1). Based on pairwise comparisons, in June 2013, niche overlap was high between *B. iheringii* and *Bryconamericus* sp. as well as between *B. iheringii* and *A. procerus* (Table 3). The only species that exhibited high overlap values in December 2012 and June 2013 were *B. iheringii* and *A. procerus* (Table 3).

Stable isotopes

The four focal characid species were more enriched in ^{15}N ratios than all surveyed prey items (Fig. 2). *Astyanax xiru* and *A. procerus* had similar ^{15}N and ^{13}C ratios, whereas *B. iheringii* was depleted in their ^{13}C ratios, and *Bryconamericus* sp. was enriched in their ^{15}N ratios (Fig. 2). The prey items exhibited diverse isotope ratios and functional groups of these items were generally isotopically distinct (Table 4; Fig. 2). Based on estimates using a dual-isotope SIAR Bayesian mixing model, *Astyanax xiru* assimilated large fractions of terrestrial invertebrates and aquatic plants (Table 4; Fig. 3a). In contrast, *A. procerus* also assimilated large fractions of terrestrial invertebrates, but may also assimilate large fractions of aquatic plants

Table 1 Stomach content analysis (% by volume) for the species of four Characidae species in the Alto Jacuí sub-basin

Origin and trophic categories of items	*Astyanax procerus*	*Astyanax xiru*	*Bryconamericus iheringii*	*Bryconamericus* sp.
Autochthonous				
Aquatic insects				
Chironomidae	*	*	1	3
Simuliidae	*	1	*	6
Psychodidae	–	–	–	*
Empididae	–	–	–	*
Tabanidae	*	–	–	–
Diptera pupae	*	–	*	*
Simuliidae pupae	*	*	–	*
Trichoptera	1	*	2	**11**
Trichoptera pupae	–	–	–	*
Ephemeroptera	3	1	6	**48**
Plecoptera	*	1	2	3
Odonata nymph	2	–	1	1
Aquatic Coleoptera larvae	*	–	1	1
Aquatic Lepidoptera larvae	*	*	1	**13**
Aquatic insects remains	**10**	–	**19**	6
Other aquatic invertebrates				
Nematoda	–	–	–	*
Gastropoda	*	–	*	*
Scale	*	–	*	*
Aquatic plants	**15**	**35**	5	–
Algae				
Diatomacea algae	–	–	2	*
Filamentous algae	1	1	**9**	*
Organic matter				
Undetermined organic matter	2	6	8	*
Vegetal organic matter	1	–	–	1
Animal organic matter	*	–	*	*
Detritus	–	–	**26**	–
Sediment	*	–	1	*
Allochthonous				
Terrestrial insects				
Sarcophagidae larvae	4	**14**	–	–
Adult Diptera	*	–	–	–
Adult Orthoptera	*	–	–	–
Terrestrial adult Hemiptera	*	–	–	–
Adult Hymenoptera	**18**	1	*	*
Adult Coleoptera	1	–	1	1
Adult Lepidoptera	*	–	–	–
Terrestrial insects remains	5	*	*	2
Other terrestrial remains				
Oligochaeta	**18**	–	–	*
Aranae	1	–	–	–
Fur	–	*	–	–

Table 1 continued

Origin and trophic categories of items	*Astyanax procerus*	*Astyanax xiru*	*Bryconamericus iheringii*	*Bryconamericus* sp.
Terrestrial plants	**15**	**39**	**14**	3
Number of stomach analyzed	66	9	103	156
Variation of size (standard length—mm)	25.00–72.46	28.87–117.92	35.00–74.73	35.00–61.71

The bold values are the most representative items

The asterisk indicates a contribution less than 1%

Table 2 Pianka's index results for observed niche overlap values for four Characidae species and simulated values for the null model

Sampling unit	Observed index	Mean of simulated index	Variance of simulated index	P (observed $\geq$ simulated)
June 2012	0.20	0.11	0.006	0.12
August 2012	0.10	0.09	0.005	0.34
October 2012	0.37	0.15	0.002	0.06
December 2012[a]	0.42	0.19	0.006	0.008
February 2013	0.11	0.11	0.005	0.40
April 2013	0.20	0.17	0.01	0.28
June 2013[a]	0.63	0.22	0.001	0.002

Overlap values range from zero to one to the Pianka's index

[a] Indicate the sampling months with intermediate and high niche overlap

(Table 5; Fig. 3b). *Bryconamericus iheringii* assimilated similar fractions of aquatic invertebrates and algae (Fig. 3c), whereas *Bryconamericus* sp. assimilated primarily aquatic invertebrates and only small fractions of terrestrial invertebrates (Table 5; Fig. 3d). Despite consumption by *A. procerus*, *B. iheringii*, and *Bryconamericus* sp., terrestrial plants are likely not assimilated by these species (Table 5; Fig. 3b, c, d). In contrast, aquatic plants were only consumed by *A. xiru* and are also likely assimilated (Table 5; Fig. 3a).

Discussion

We found that four syntopic characid fishes utilized an array of prey items, including plants and invertebrates as well as autochthonous and allochthonous resources; however, differences in their relative consumption resulted in low degrees of dietary overlap among species. Additionally, we found that invertebrates were often preferentially assimilated, but we also report that some species assimilate large fractions of

plants. Our findings are consistent with the hypothesis that these species may coexist via resource partitioning and also demonstrate the trophic diversity among characid fishes that often dominate Neotropical freshwater ecosystems.

A species niche is often defined as a hypervolume of "n" dimensions, with each dimension representing a condition or resources that allow a species to survive and reproduce (Hutchinson, 1957). Such matrices all change spatially and temporally, and can represent environmental (e.g. temperature, salinity, substrate) and trophic (prey and predators) fields. This study considers only the trophic dimension by quantifying the resources consumed and assimilated by species. Additionally, our results pertain only to the species realized niches within the context of a community in which they co-occur. Stomach contents revealed that *Astyanax procerus* primarily ingested allochthonous items of animal and vegetal origin, whereas *Astyanax xiru* ingested both aquatic and terrestrial plants. The consumption of Sarcophagidae larvae by *A. xiru* may be inadvertent

Fig. 1 Observed feeding overlap among characids during the two sampling periods in which niche overlap was intermediate to high based on EcoSimR analysis. The size of the *circles* corresponds to the proportion that each resource represents in their diets. Consumer species codes: *Bryconamericus iheringii* (BI), *Bryconamericus* sp. (BR), *Astyanax xiru* (AX), and *Astyanax procerus* (AP)
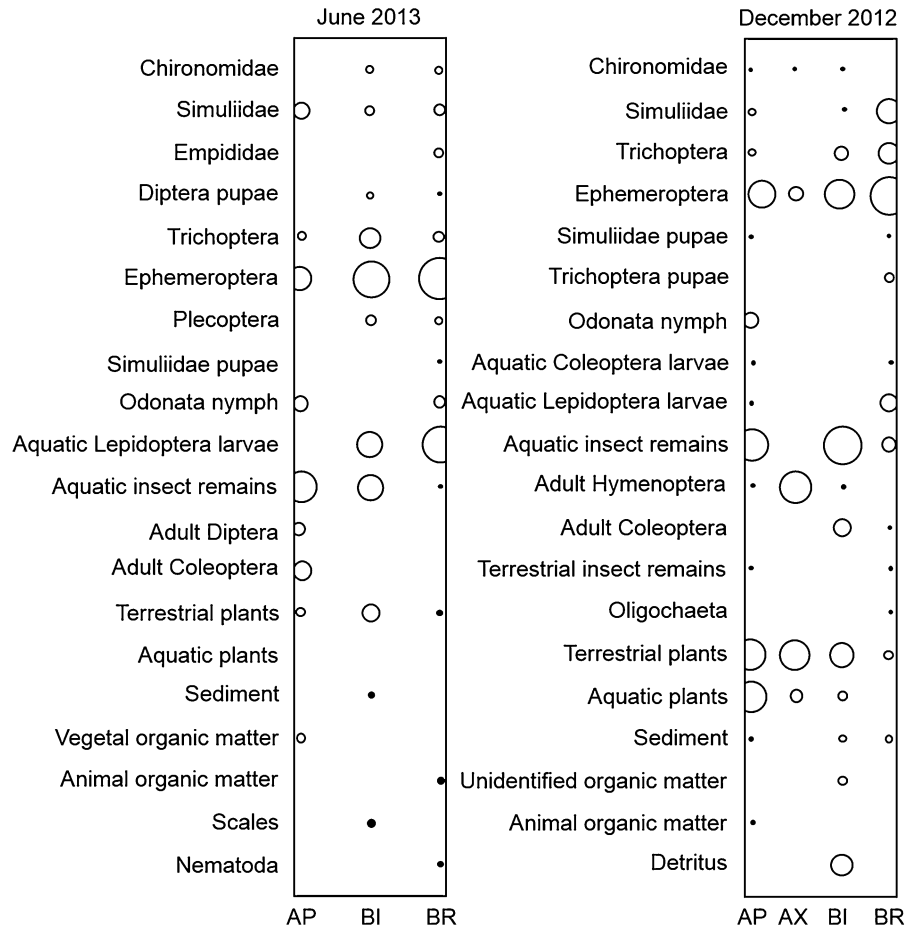
Table 3 Pairwise Pianka's niche overlap between characid species in December 2012 (above diagonal) and June 2013 (below diagonal), in which EcoSimR analysis indicated that niche overlap among species was intermediate to high (Table 2)

	AP	AX	BI	BR
AP		0.389	0.753	0.189
AX	N/A		0.271	0.629
BI	0.619	N/A		0.292
BR	0.407	N/A	0.862	

Species codes: *Astyanax procerus* (AP), *Astyanax xiru* (AX), *Bryconamericus iheringii* (BI), and *Bryconamericus* sp. (BR)

behavior of *Astyanax* species. *Bryconamericus iheringii* fed more from autochthonous items, both of animal and vegetal origin, while *Bryconamericus* sp. consumed primarily aquatic insects. Based on the Pianka's index and the null model results, we confirmed low feeding overlap among these species. The only period of high overlap according to Pianka's index occurred when species consumed large volumes of items such as Ephemeroptera and aquatic insect remains during two sampling months (December 2012 and June 2013).

Aquatic invertebrates (i.e., larval insects) are important food sources for fishes because they often occur in abundance in Neotropical streams (Boulton et al., 2008; Winemiller et al., 2008), including in the Caixões River. In a previous study conducted in the same region as this one, Bonato & Fialho (2014) also found high dietary overlap between *Trichomycterus poikilos* Ferrer & Malabarba, 2013 and *Heptapterus*

because these larvae are necrophagous (Costa et al., 2006), suggesting that the source of the larvae may have been a dead animal body in the stream. This situation demonstrates the opportunistic foraging

Fig. 2 Bi-plot (mean ± SD) depicting the isotopic relationships among *Astyanax procerus*, *Astyanax xiru*, *Bryconamericus iheringii*, and *Brycomamericus* sp. and their potential prey items. Note that some items are shown that were not included in the mixing models (Table 3) because they are not prey items of the characids. For references to color, see the online version
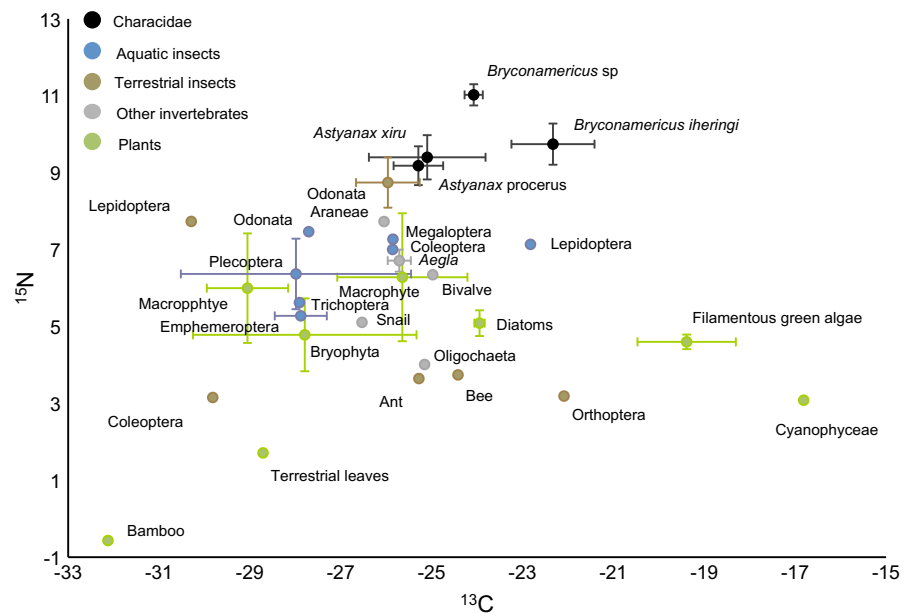

Table 4 Functional groupings of prey items used in the mixing models to estimate the diets of *Astyanax xiru*, *Astyanax procerus*, *Bryconamericus iheringii*, and *Bryconamericus* sp. Isotopic values are means (±SD)

Source	Specific source (number of samples)	^{15}N	^{13}C	C/N
Aquatic plant	Podostemaceae (2)	6.0 ± 1.4	−20.1 ± 0.9	12.6
Aquatic plant	Podostemaceae (2)	6.3 ± 1.7	−25.7 ± 1.4	10.9
Aquatic plant	Bryophyta (2)	4.8 ± 0.9	−27.8 ± 2.5	14.1
Terrestrial plant	Bamboo (1)	−0.6	−32.1	23.7
Terrestrial plant	Leaves (1)	1.71	−28.7	21.3
Algae	Periphyton (5)	4.6 ± 0.2	−19.4 ± 1.1	9.8
Algae	Periphyton (1)	3.1	−16.8	11.2
Aquatic invertebrate	Ephemeroptera (2)	5.3 ± 0.1	−27.9 ± 0.6	5.4
Aquatic invertebrate	Trichoptera (4)	6.4 ± 0.9	−28.0 ± 2.5	5.5
Aquatic invertebrate	Plecoptera (1)	5.6	−27.9	5.4
Aquatic invertebrate	Odonata (1)	7.5	−27.7	5.1
Aquatic invertebrate	Lepidoptera (1)	7.1	−22.3	5.2
Terrestrial invertebrate	Ant (2)	3.65 ± 0.7	−25.3 ± 0.7	5.6
Terrestrial invertebrate	Bee (1)	3.7	−24.4	5.6
Terrestrial invertebrate	Oligochaeta (1)	4.01	−25.2	5.5

In most cases, multiple individuals were pooled together for each sample

sp. due to consumption of aquatic insects. According to Hardin (1960), ecologically similar species cannot coexist if they use the same resources due to resulting resource-based competition. In response to such competition, species may reduce niche overlap via resource partitioning or exploitation of a novel resource (Pianka, 1974; Ross, 1986; Towsend et al., 2006). Alternatively, if resources are abundant and not limiting, species may coexist despite similar resource use. For example, Guo et al. (2015) demonstrated with
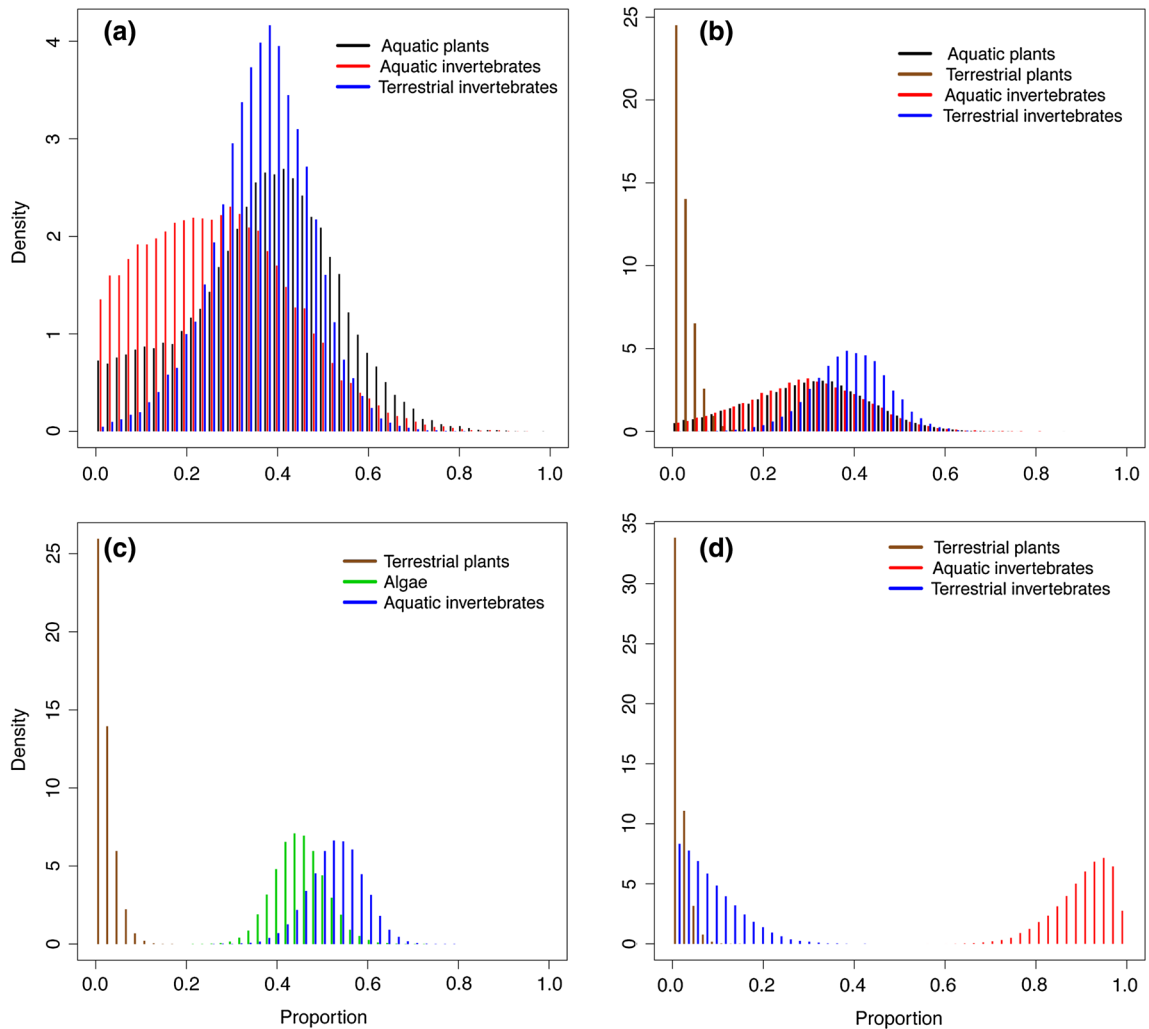
Fig. 3 Density plots depicting the relative isotopic contribution of prey items to *Astyanax xiru* (**a**), *Astyanax procerus* (**b**), *Bryconamericus iheringii* (**c**), and *Bryconamericus* sp. (**d**) as estimated by a SIAR Bayesian mixing model. Note that the *y*-axes are not standardized across panels. For references to color, see the online version

Table 5 Mean (95% C.I.) assimilation (%) of generalized groups of prey items by four characid species: *Astyanax procerus*, *Astyanax xiru*, *Bryconamericus iheringii*, and *Bryconamericus* sp. as estimated by a dual-isotope Bayesian SIAR mixing model

Prey item	Consumer			
	A. procerus	*A. xiru*	*B. iheringii*	*Bryconamericus* sp.
Aquatic invertebrates	1 (0–90)	12 (2–32)	75 (63–86)	73 (60–88)
Terrestrial invertebrates	37 (0–100)	57 (42–91)		21 (12–32)
Aquatic plants	47 (0–100)	31 (38–79)		
Terrestrial plants	14 (0–77)		2 (1–5)	5 (2–12)
Algae			23 (14–33)	

their results that even with a high overlap, two invasive gobies coexisted at similar abundances in Lake Erhai in China because the species had access to sufficiently many food resources that prevented the development of competitive interactions. The processes that led to the observed scenario, in which there seems to be low degrees of dietary overlap among characids in the Caixões River, may have been shaped for a long time during their coevolution. Oftentimes, present day patterns among species may be due to negative interactions from past competition that selected for accommodative processes such as resource partitioning (i.e., "the ghost of competition past"; Connell, 1980) (Bonato & Fialho, 2014; Frehse et al., 2015). Although, we do not have information about resource availability, our results are consistent with predictions associated with the rise of resource partitioning in response to periods of resource-based competition (Pianka, 1974; Connell, 1980). Furthermore, ecologically- and phylogenetically-similar species are predicted to exhibit some degree of ecological differentiation to facilitate their coexistence (Hutchinson, 1957).

Ecological differentiation can involve activity patterns, reproductive season, habitat, and diet (MacArthur, 1958). The feeding specialization exhibited by the two *Astyanax* species in which they largely consume plants may prevent dietary overlap with *Bryconamericus*. Guo et al. (2015) emphasizes that specialization in food resources are often crucial to enhance coexistence by reducing interspecific competition. Another mechanism that allows the co-occurrence of different species would be the use of different habitats for feeding. *Astyanax* are species that forage in the water column and from the water surface, whereas *Bryconamericus* are benthic and thus forage primarily from the substrate (Casatti, 2002; Orciolli & Bennemann, 2006; Peretti & Andrian, 2008). Also, morphology is a factor that may prevent or reduce dietary niche overlap between species (Skúlason & Smith; 1995; Rezende et al., 2013; Song & Kim, 2014; Abilhoa et al., 2016). Traits such as head shape, mouth angle, and gill morphology are closely associated with the trophic characteristics of fishes (Gerking, 1994). Additionally, tooth morphology, number, and diversity are associated with the type of foods consumed by fishes and may permit the exploitation of different trophic roles (Géry, 1977; Burress, 2016). Features such as mouth position may be important for dietary

patterns among characids (Bonato et al., 2017). For example, *Astyanax* has terminal jaws and *B. iheringii* has sub-terminal jaws, which may reflect where fishes feed in the water column (Burress et al., 2016a).

The four characid species were most enriched in ^{15}N ratios than all surveyed prey items, which is indicative of being consumers (Post, 2002). *Bryconamericus iheringii* assimilated primarily aquatic invertebrates and secondarily algae. The carbon assimilated by this species is likely derived from algae because the species were depleted in ^{13}C ratios, which are more similar to that of algae than the other species. *Bryconamericus iheringii* may graze algae from rocky surfaces. Brito et al. (2006) also classified *B. microcephalus* as a secondary consumer, whereas Neres-Lima et al. (2016) classified the same species as omnivorous based on their isotopic relationship with algae, indicating the potential importance of this resource. However, Rodrigues et al. (2013) observed that *B. iheringii* was the most enriched species in both $\delta^{13}C$ and $\delta^{15}N$ and classified the species in the second trophic level and isotopically associated them with zooplankton. According to Burress et al. (2013), *Bryconamericus iheringii* in the Cuareim River had similar $\delta^{15}N$ as *Astyanax*, but had $\delta^{13}C$ more similar to that of aquatic macrophytes. In this study, *Bryconamericus* sp. were the most enriched in ^{15}N ratios, which resulted in estimates that they primarily assimilate aquatic invertebrates followed by terrestrial invertebrates. Based on these results, the gut content data were corroborated despite the fact that gut content analyses did not show the high use of terrestrial insects by *Bryconamericus* sp. Previously, *Bryconamericus* species have been classified in many trophic guilds because they ingest many types of prey, including algae and detritus in degraded environments (Orciolli & Bennemann, 2006; Brandão-Gonçalves et al., 2009; Mazzoni & Rezende, 2009; Bonato et al., 2012). The highly variable trophic roles of *B. iheringii* across ecosystems may indicate their trophic plasticity in response to different environmental conditions (Vitule et al., 2013; Vidal et al., 2014). Such trophic plasticity may also explain their high abundance in the Caixões River.

We observed that *Astyanax xiru* and *A. procerus* had similar ^{15}N and ^{13}C ratios associated with assimilation of large fractions of terrestrial invertebrates and aquatic plants. Therefore, we concluded that *A. procerus* assimilates both animal and plant resources. Animal resources also appear to be

assimilated by *A. xiru*, although the volumetric contribution of these resources is lower. There are no published ecological data on either *Astyanax* species because they were recently described (Lucena et al., 2013b). However, in the upper Uruguay River basin, Neves & Delariva (in preparation) found that the diet of *A. xiru* was more than 75% terrestrial plants and seeds. Mont'Alverne et al. (2016), using isotopic signatures, also found herbivorous (*Astyanax jacuhiensis* (Cope, 1894)) and omnivorous (*A. fasciatus* (Cuvier, 1819), *A. eigenmaniorum* (Cope, 1894)) characid species in Patos Lagoon. In contrast, *Astyanax* species (*Astyanax* spp., *A. alburnus* (Hensel, 1870) (now is *Diapoma alburnus*), *A. bimaculatus* (Linnaeus, 1758), *A. eigenmaniorum* and *A. fasciatus*) occupied intermediary trophic positions in the freshwater part of Patos Lagoon (Garcia et al., 2007). According to previous studies, isotopic signatures indicate that macrophytes are an important resource for *Astyanax* species in the freshwater part of lagoons (Garcia et al., 2006, 2007; Rodrigues et al., 2013) and stream ecosystems (Burress et al., 2013). Likewise, plants were a very important item for the *Astyanax* in the Caixões River. Here, we found that despite that *A. procerus*, *B. iheringii*, and *Bryconamericus* sp. consumed fractions of terrestrial plants, they did not assimilate nutrients from them. Therefore, perhaps these items were consumed by chance, probably during the ingestion of benthic prey. In contrast, *A. xiru* appears to assimilate the large fractions of aquatic plants that they consume. Either *A. xiru* is the only species capable of assimilating plant-derived nutrients or aquatic plants are more easily assimilated than terrestrial plants. The latter hypothesis is consistent with the C/N ratios of the two plant sources (Table 3) such that terrestrial-derived plants may be poorer quality food resources that are more difficult to digest (Whitledge & Rabeni, 1997; Roth et al., 2006).

Fishes that consume primarily plants are expected to supplement their diets with animal resources to meet nutritional needs for proper development, especially because these species do not have anatomical modification such as long intestines to maximize absorption of nutrient-poor vegetal resources (Horn, 1989; Horn & Messer, 1992). Based on gut content analyses, the ingested volume of terrestrial invertebrates by *A. xiru* was low; however, these items may represent a large proportion of their assimilated nutrients. Similarly, Raubenheimer et al. (2005) showed that complementary feeding may occur in a temperate girellid species such that algae is the primary source of energy but that animal matter is the primary source of protein. In a review about nutrition ecology of marine herbivores, Clements et al. (2009) commented that isotopes from high protein resources such as animals are incorporated; however, carbohydrates from a low protein source such as algae or seagrasses are catabolized directly for energy. Thus, estimates of assimilation are currently limited by large discrepancies in protein content of food items, particularly for herbivores and omnivores that consume a wide variety of food items. However, the depleted C/N ratios observed suggest that biases introduced from lipid content are low (Post et al., 2007). Therefore, it may be more likely that δ^{13}C and δ^{15}N are not assimilated equally which is an assumption of the dual-isotope mixing models (Hopkins & Ferguson, 2012). Indeed, δ^{13}C and δ^{15}N appear to be assimilated independently by some stream fishes such that they preferentially assimilate large fractions of δ^{15}N from invertebrates, even if they represent a small proportion of their diets (Burress et al., 2016b). Regardless, we demonstrate that both plant and invertebrate resources are important food resources for *Astyanax* populations.

We verified the existence of resource partitioning by Characidae populations that may allow their coexistence via reduced competition among species (Hardin, 1960; Connell, 1980). Alternatively, these patterns may be related to differences in morphology or the high abundance of resources in Neotropical streams. Based on stomach content and isotopic data, we demonstrated that characids generally assimilate prey items consistent with their consumption, except that aquatic plants may be more easily assimilated than terrestrial plants. Furthermore, our results indicated that the diets of omnivorous/herbivorous species were complemented with animal matter, which was highly assimilated relative to the proportions consumed. Therefore, the physiological capacity to preferentially assimilate limited nutrients may allow species to satisfy their nutrient and metabolic demands while partitioning their resources and thereby facilitate coexistence among these species.

Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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