

Eco-morphological attributes and feeding habits in coexisting characins

T. PORTELLA*, J. LOBÓN-CERVIÁ†, L. R. MANNA*, H. G. BERGALLO* AND R. MAZZONI*‡

**Departamento de Ecologia, Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro – UERJ, Rua São Francisco Xavier, 524, Maracanã, CEP 20550-13, Rio de Janeiro, RJ, Brazil and †Museo Nacional de Ciencias Naturales (CSIC), C/2, José Gutierrez Abascal, Madrid 28006, Spain*

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The head morphology and feeding habits of pairs of characin species (family Characidae) that coexist in four different coastal rainforest streams were analysed. Coexisting species differed in size, but were very similar in eco-morphological attributes. Gut analyses revealed differences in feeding preferences for each coexisting species, indicating resource partitioning. A pattern of organization in species pairs that was repeated in the four studied streams was noticed. The pattern consisted of one slightly larger species with a feeding preference for items of allochthonous origin and another smaller species with a preference for autochthonous items. The hypothesis that small morphological differences enable the current coexistence of those species pairs was proposed. Furthermore, the results show ecological equivalence among different species in the studied streams.

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Key words: characid species; freshwater fishes; morphology; niche overlap; resource partitioning; streams.

INTRODUCTION

An ecological niche may be defined as an n -dimensional space in which an organism is capable of occurring or as the position of the representatives of a population in a community, which is the result of structural, physiological and behavioural adaptations (Hutchinson, 1957). The niche used by a species may determine community dynamics and vary according to species richness, resource availability and the species' dispersal capacity (Gravel *et al.*, 2006).

A well-known model of community structure predicts that only certain combinations of species can coexist (Chase & Leibold, 2003) and only individuals that differ in critical aspects of their morphology or body size are able to exploit the same specific resources (Winston, 1995). Species that are morphologically similar and inhabit the same area tend to have high competitive potential and reduced densities as a consequence of this competition (MacArthur & Levins, 1967; Peres-Neto, 2004; Van Zwol

‡Author to whom correspondence should be addressed. Tel.: +55 21233405250; email: r.mazzoni@globo.com

et al., 2012). In the context of this potential conflict, the phenomenon of competitive exclusion, as proposed by Hutchinson (1965), may occur. A number of studies, however, have recorded the coexistence of morphologically similar species, supported by resource partitioning, but only as long as the available resources are sufficiently abundant (Hurlbert, 1978; Mazzoni *et al.*, 2012). Resource partitioning may thus be an important mechanism structure by facilitating the coexistence of closely related species (Schoener, 1974; Ross, 1986; Friedman *et al.*, 2016; Silva *et al.*, 2016).

Studies in the Neotropical region have shown that coexisting species that are morphologically similar and phylogenetically closely related tend to feed on distinct food items, thus reducing niche overlap and facilitating coexistence (Brazil-Sousa *et al.*, 2009; Mazzoni *et al.*, 2012). This may be accounted for by the diversity of feeding resources (Pianka, 1974) and, as in the specific case of the present study, by the trophic plasticity of characin fish species (Lowe-McConnell, 1987; Araujo-Lima *et al.*, 1995; Manna *et al.*, 2012). Coexistence may also result in distinct morphological adaptations that reflect different ways of exploiting the available resources (Labropoulou & Eleftheriou, 1997; Russo *et al.*, 2008; Nandi & Saikia, 2015). The Characidae is one of the most diverse groups of Neotropical fishes, with a variety of body forms and behavioural strategies related to the exploitation of different microhabitats and environmental conditions (Manna *et al.*, 2012, 2014; Marques *et al.*, 2014).

Morphology of a fish species may be predictive of its diet (Gatz, 1979; Wikramanayake, 1990; Motta *et al.*, 1995; Winemiller *et al.*, 1995; Piet, 1998; Hugueny & Pouilly, 1999; Xie *et al.*, 2001; Pouilly *et al.*, 2003; Mazzoni *et al.*, 2010b; Ramírez *et al.*, 2015). The trophic ecology of a species may thus reflect not only its feeding strategies, but also its morphology and digestive capacity (Wootton, 1990).

A number of studies have emphasised the relationship between the ecology and morphology of a species (Moyle & Senanayake, 1984; Wikramanayake, 1990; Norton, 1995; Dumay *et al.*, 2004; Laporte *et al.*, 2016; Silva *et al.*, 2016) and that different species with similar morphologies tend to be ecologically equivalent (Loreau, 2004), even when inhabiting distinct environments (Pianka, 1994). Considering this, the following questions were focused in the present study: (1) Do coexisting, closely-related species partition trophic resources? (2) Can the morphological differences that may account for this resource partitioning be identified? (3) If the answer to these two questions is positive, can a general pattern that accounts for the coexistence of these close related characin species in different aquatic habitats be identified? To address these questions, an analysis is made of the morphology and diet of pairs of species of characins (known locally as lambaris) that coexist in four streams of the Serra do Mar region in Rio de Janeiro state, Brazil.

MATERIAL AND METHODS

STUDY AREA

Samples were taken from four coastal streams in three different micro-basins in the Atlantic Rainforest biome of the Brazilian state of Rio de Janeiro (Fig. 1): (1) Rio Perequê-açu (23° 13' 1.73" S; 44° 45' 49.69" W), a third-order stream located in the Bocaina mountain region that flows towards the town of Paraty; (2) Rio Ubatiba (22° 52' 14.73" S; 42° 44' 3.55" W), a third-order stream that flows from the eastern slope of the Serra do Mar mountains to the Maricá Lagoon; (3) Rio Caranguejo

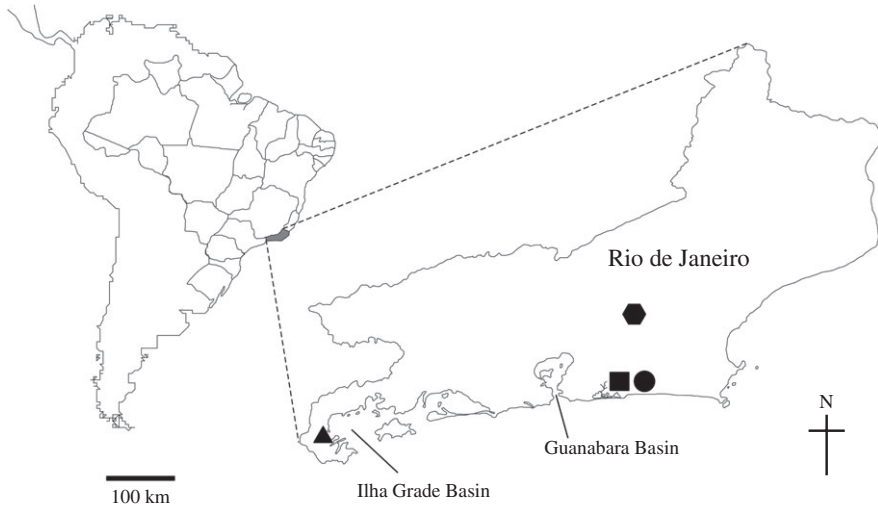


FIG. 1. River system of the state of Rio de Janeiro, Brazil, indicating the appropriate collection points: ▲, Perequê-açu River, Paraty; ■, Ubatiba River, Maricá; ●, Caranguejo River, Maricá; ◆, Guapiaçu River, Cachoeiras de Macacu. Adapted from Pereira *et al.* (2003).

(22° 53' 47.72" S; 42° 42' 50.34" W), a third-order stream that originates on the eastern slope of Serra do Mar and drains into the Guarapina Lagoon; (4) Rio Guapiaçu (22° 26' 4.74" S; 42° 45' 7.47" W), a third-order stream flowing from the Serra dos Órgãos mountains into the Rio Guapimirim, which drains into Guanabara Bay (Pereira *et al.*, 2003).

SAMPLING SCHEDULE

With one exception, sites were selected where the two characin species were the only species known to be present. This removed any possibility of the feeding patterns being confounded by other species. In the one exception (Rio Ubatiba), there was one accompanying species (*Phalloceros harpagos* Lucinda 2008), but it occurred at extremely low densities and the two characin species predominated. All specimens were collected only from the stream sectors where the pairs of characin species under study are syntopic and exploit the same microhabitat. The samples were collected between 2010 and 2012 (IBAMA authorisation no. 16152-1).

For the collection of samples, a 20 m sector of each stream was blocked using a 5 mm-mesh net and specimens were collected using an electrofisher (CA – 1600 W, 220 V, 2–4 A; Mazzoni *et al.*, 2000). Each sector was sampled twice (during the rainy and dry seasons) in order to account for possible seasonal differences in environmental conditions. During each sampling season, 20 specimens of each species were collected. To avoid ontogenetic effects in our analyses, only adult specimens were collected.

The following characin species were studied at the different sites: Rio Perequê-açu, *Hollandichthys multifasciatus* (Eigenmann & Norris 1900) [Fig. 2(a)] (mean \pm s.d., $L_S = 8.27 \pm 0.98$ cm) and *Bryconamericus microcephalus* (Miranda Ribeiro 1908) [Fig. 2(b)] ($L_S = 5.07 \pm 0.51$ cm); Rio Ubatiba, *Astyanax janeiroensis* Eigenmann,

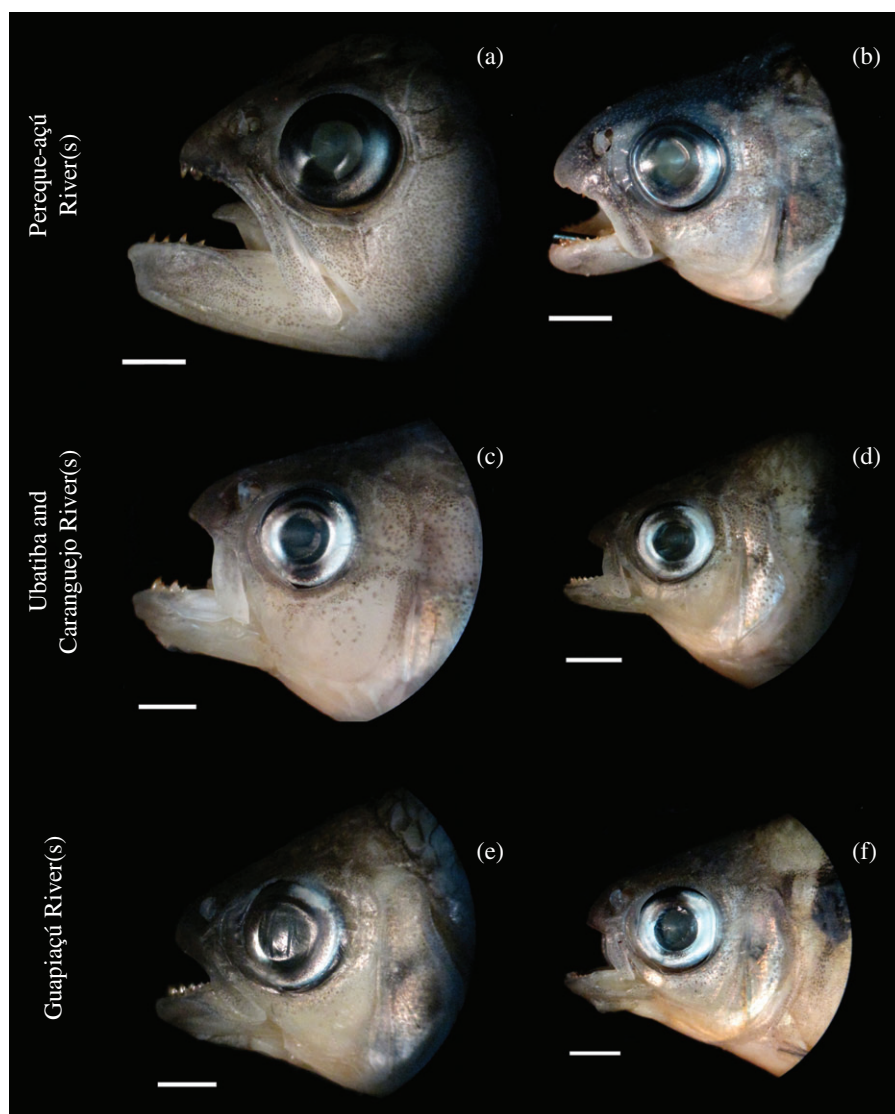


FIG. 2. Feeding apparatus of pairs of Characidae coexisting in each stream studied: Perequê-açu River, (a) *Hollandichthys multifasciatus* and (b) *Bryconamericus microcephalus* (bar length, 5 mm); Ubatiba and Caranguejo Rivers, (c) *Astyanax janeiroensis* and (d) *Astyanax hastatus*; Guapiaçú River, (e) *Astyanax taeniatus* and (f) *Astyanax* sp. Scales bars: 5 mm.

1908 [Fig. 2(c)] ($L_S = 8.32 \pm 1.03$ cm) and *Astyanax hastatus* Myers 1928 [Fig. 2(d)] ($L_S = 4.61 \pm 0.53$ cm); Rio Caranguejo: *A. janeiroensis* (mean $L_S = 6.71 \pm 1.79$ cm) and *A. hastatus* ($L_S = 4.47 \pm 0.51$ cm); Rio Guapiaçú: *Astyanax taeniatus* (Jenyns 1842) [Fig. 2(e)] ($L_S = 8.57 \pm 1.22$ cm) and *Astyanax* sp. [Fig. 2(f)] ($L_S = 5.69 \pm 0.4$ cm).

Following an overdose of anaesthetic, all specimens were fixed in 10% formalin and subsequently preserved in 70% alcohol. Eight morphometric characteristics of

each individual (as proposed by Gatz, 1979) were quantified using callipers and the guts were removed for the subsequent analysis of their contents. The morphometric measurements were transformed into seven eco-morphological indices (Table I), as proposed by Watson & Balon (1984); Hugueny & Pouilly (1999) and Casatti & Castro (2006). The morphological differences between each pair of species were evaluated using a principal component analysis (PC-Ord 4.0; McCune & Mefford, 1999).

The stomach contents were analysed and quantified based on the volumetric (V_O) and frequency of occurrence (F_O) methods (Hyslop, 1980). Food items were identified to the lowest taxonomic level possible. The alimentary index (I_A), proposed by Kawakami & Vazzoler (1980) and adapted by Hahn *et al.* (1997), was calculated by: $I_{Ai} = (F_i V_i) / (\sum F_i V_i) \times 100$, where i is the i th food item, F_i is the frequency of occurrence of the i th item and V_i is the volume of the i th food item, using V_O (the percentage volume) and F_O (the percentage frequency) of each food item.

Niche breadth for each species was calculated based on the F_O values, using the Shannon diversity index: $H' = -\sum p_i (\ln p_i)$, where p_i is the proportion of the i th food item in the diet of the species. Niche overlap was also calculated for each pair of species based on the I_A values, using the simplified Morisita index, proposed by Horn (1966): $C_H = 2 \sum n_i p_{ij} p_{ik} (\sum n_i p_{2ij} + \sum n_i p_{2ik})^{-1}$, where p_{ij} is the proportion of the i th resource in the total diet of the species j , p_{ik} is the proportion of the i th resource in the total diet of the species k and n = total number of resources used (Krebs, 1999). This index varies from 0 to 1 and values above 0.6 are considered to represent significant overlap (Keast, 1978; MacPherson, 1981).

A t -test (Zar, 1999) was used to assess whether there were significant differences between species in the volume of food consumed in each stream. This test was also used to assess the amount of autochthonous (*i.e.* aquatic) *v.* allochthonous (*i.e.* terrestrial) food items consumed in each stream. Finally, a multiple regression analysis was applied (Systat 13; Wilkinson, 2004) on the \log_{10} -transformed values of the volume of food items as the dependent variable and morphological indices [relative mouth width (W_{RM}) and relative eye diameter (D_{RE})] as independent variables. The partial values were used to design two scatterplots related to the dependence between the size of ingested items and the W_{RM} and D_{RE} values recorded for each species.

RESULTS

ECO-MORPHOLOGY

The principal component analyses (PCA) indicated a clear pattern of morphological variation between the coexisting species (Fig. 3). The first two PCA axes account for 62.9% of the variation in the data from the Rio Perequê, 69.1% for the Rio Ubatiba, 68.9% for the Rio Caranguejo and 69.7% for the Rio Guapiaçu (Table II). The indices that best distinguish the pairs of species are the relative length of the head (L_{RH}), W_{RM} and D_{RE} (Tables II and III).

DIET

Diets were compared in both the rainy and dry seasons (see Fig. S1, Supporting Information), but as no significant seasonal differences were observed, all subsequent analyses were based on the mean I_{Ai} values for each species and site. The gut content

TABLE I. Eco-morphological indices derived from the different morphometric measurements taken from the specimens of characin captured during the present study of four streams in Rio de Janeiro state, Brazil

Index		Morphometric measure	Interpretation
Relative head length (L_{RH})	=	Head length (L_H) [standard length (L_S)] ⁻¹	Higher values indicate the ability to capture relatively large prey
Relative eye diameter (D_{RE})	=	Eye diameter (L_H) ⁻¹	Higher values indicate the ability to search for small prey
Relative mouth width (W_{RM})	=	Mouth width (W_M)(L_S) ⁻¹	Higher values indicate the ability to capture large items
Relative mouth height (H_{RM})	=	Mouth height (H_M)(L_S) ⁻¹	Higher values indicate the ability to capture large items
Mouth configuration (C_{RM})	=	$H_M (W_M)^{-1}$	Higher values indicate the ability to capture large items
Relative intestine length (L_{RI})	=	Intestine length (L_S) ⁻¹	Higher values indicate a preference for plant items
Relative eye position (P_{RE})	=	Depth of the eye midline (head depth) ⁻¹	Higher values indicate the ability to search for items on the surface

analysis indicates a considerable variety of ingested food items, ranging from 12 to 25 different items per population (Table IV). In the Rio Pereque-açú, *H. multifasciatus* fed mainly on allochthonous arthropods ($I_{Ai} = 63.65\%$), whereas *B. microcephalus* fed on autochthonous arthropods ($I_{Ai} = 88.10\%$) [Fig. 4(a)]. In the Rio Ubatiba, *A. janaeensis* fed predominantly on allochthonous plant matter ($I_{Ai} = 64.5\%$), whereas *A. hastatus* consumed mainly autochthonous arthropods, with an I_{Ai} of 61.52% [Fig. 4(b)]. In the Rio Caranguejo, *A. janaeensis* presents $I_{Ai} = 58.94\%$ for allochthonous arthropods, whereas *A. hastatus* presents $I_{Ai} = 81.99\%$ for algae [Fig. 4(c)]. In the Rio Guapiaçú, *A. taeniatus* returns $I_{Ai} = 57.13\%$ for allochthonous plant matter, while *Astyanax* sp. has $I_{Ai} = 79.61\%$ for autochthonous arthropods [Fig. 4(d)].

Niche breadth is >0.8 ($0.80 < H' < 0.87$) in all the study species, whereas the simplified Morisita overlap index indicates niche overlap of <0.46 ($0.13 < C_H < 0.46$; Table V). A *t*-test indicates significant variation in the volume ($P < 0.05$) of autochthonous and allochthonous items in the diet, except for the Rio Perequê-açú ($P > 0.05$; Table VI). The volume of the different food items ingested by the coexisting species is significantly different ($P < 0.05$) in all streams (Table VI). The multiple regression indicates a significant relationship between the volume of food items and both morphometric variables ($r^2 = 0.286$, $F_{2,161} = 32.196$, $P < 0.001$), with a significant positive relationship ($P < 0.001$) being found with W_{RM} and a negative one ($P < 0.001$) with D_{RE} , i.e. $\log_{10} V_O = 3.314 + 1.891(\log_{10} W_{RM}) - 3.413(\log D_{RE})$ (Fig. 5).

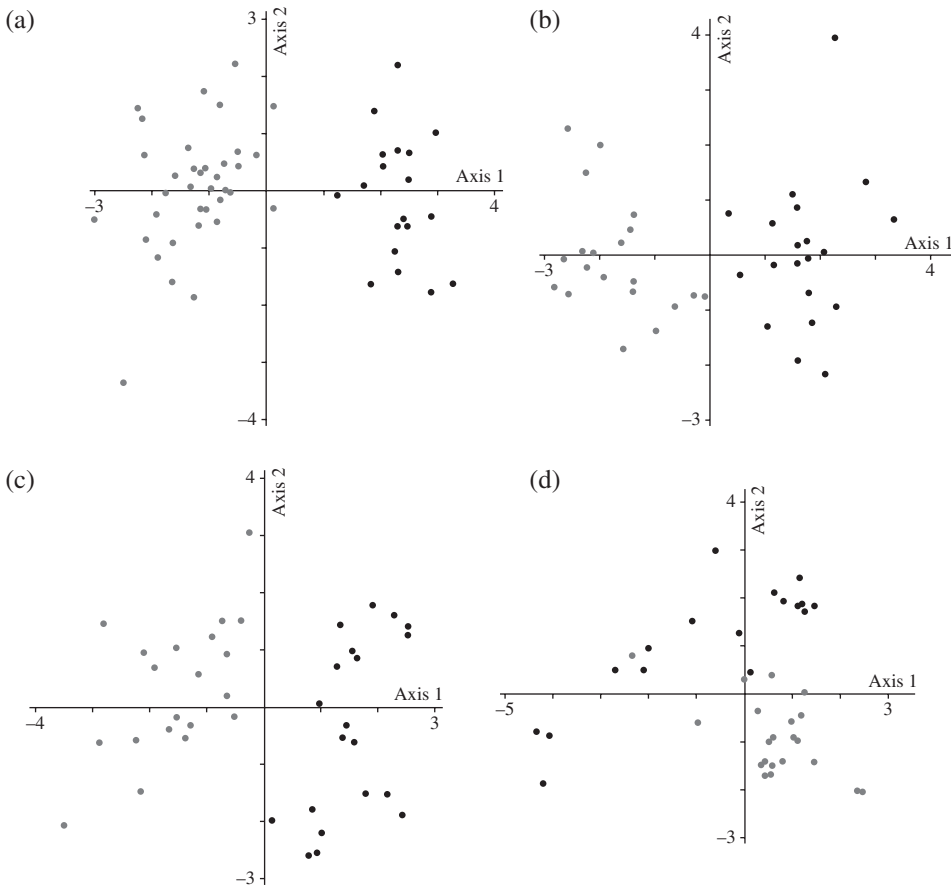


FIG. 3. Principal components analysis using the morphological index based on the oral apparatus for the four sampled sites. (a) Perequê-acú River; ●, *Hollandichthys multifasciatus*; ○, *Bryconamericus microcephalus*. (b) Ubatiba River; ●, *Astyanax janaeirensis*; ○, *Astyanax hastatus*. (c) Caranguejo River; ●, *A. janaeirensis*; ○, *A. hastatus*. (d) Guapiagú River; ●, *Astyanax taeniatus*; ○, *Astyanax* sp.

DISCUSSION

The main goal of eco-morphological studies is to analyse of the relationship between the morphological (phenotype) and ecological (resource use) characteristics of individuals in different populations and communities (Peres-Neto, 1999). In fish studies, the morphology of the head and indices of mouth shape and eye size are commonly used as predictors of trophic ecology (Labropoulou & Eleftheriou, 1997; Kahilainen & Østbye, 2006; Russo *et al.*, 2008; Ramírez *et al.*, 2015).

A similar pattern of morphological differentiation in coexisting characins in all four streams was found. In all cases, one species was slightly larger in size than the other, as confirmed by axis 1 in the PCA (Fig. 3), which accounts for most of the variation in fish size, but not in form. Variation in the size of the mouth (width and height) and eye (orbital diameter) was observed, despite the pronounced morphological similarities between the coexisting species. A similar pattern was found in demersal fishes by

TABLE II. Results of the PCA of the morphometric indices for the pairs of characin species (see Table III) in Rio Perequê-açu, Rio Ubatiba, Rio Caranguejo and Rio Guapiaçu. The eigenvalues for each axis and the percentage of the variance explained by each of PC1 and PC2 are shown

Index	Loading							
	Perequê-açu		Ubatiba		Caranguejo		Guapiaçu	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Relative head length	0.48	0.13	0.48	0.07	0.50	-0.05	-0.49	0.22
Relative eye position	0.18	0.58	0.02	-0.55	0.04	-0.53	-0.35	0.19
Relative mouth width	0.52	-0.09	0.33	0.51	0.44	-0.39	-0.30	0.50
Relative mouth height	0.29	0.46	0.45	-0.09	0.01	-0.67	-0.47	-0.33
Mouth configuration	-0.41	0.41	0.24	-0.65	-0.45	-0.29	-0.18	-0.65
Relative intestine length	-0.23	0.50	-0.42	0.03	-0.27	-0.11	-0.45	-0.27
Relative eye diameter	-0.41	-0.06	-0.46	-0.03	-0.52	-0.12	0.29	-0.24
Variance (%)	46.6	16.3	49.5	19.6	41.4	27.5	40.8	28.9
Eigenvalue	3.3	1.1	3.5	1.4	2.9	1.9	2.9	2.0
Broken-stick eigenvalue	2.6	1.6	2.6	1.6	2.6	1.6	2.6	1.6

Labropoulou & Eleftheriou (1997) and Russo *et al.* (2008). The larger species (*H. multifasciatus*, *A. janeiroensis* and *A. taeniatus*) have relatively larger heads and mouths (L_{RH} and W_{RM}) in comparison with the smaller species (*B. microcephalus*, *A. hastatus* and *Astyanax* sp.), while the smaller species have relatively larger eyes, *i.e.* D_{RE} (Table III). These morphological differences appear to be related to the exploitation of distinct feeding resources (Snowberg *et al.*, 2015), thus facilitating the coexistence of each pair of species. Fishes with larger eyes, that improve visual sensitivity and visual acuity, have been discussed elsewhere (Sibbing & Nagelkerke, 2001; Kassam *et al.*, 2003).

TABLE III. Mean \pm S.D. values of the principal eco-morphological indices (W_{RM} , relative mouth width; L_{RH} , relative head length; D_{RE} , relative eye diameter) used to characterize each fish species in Rio Perequê-açu, Rio Ubatiba, Rio Caranguejo and Rio Guapiaçu

Site	Species	W_{RM}	L_{RH}	D_{RE}	n
Perequê-Açu	<i>Hollandichthys multifasciatus</i>	0.105 \pm 0.009	0.291 \pm 0.011	0.278 \pm 0.027	29
	<i>Bryconamericus microcephalus</i>	0.065 \pm 0.008	0.243 \pm 0.020	0.333 \pm 0.036	37
Ubatiba	<i>Astyanax hastatus</i>	0.071 \pm 0.005	0.242 \pm 0.007	0.365 \pm 0.030	30
	<i>Astyanax janeiroensis</i>	0.079 \pm 0.008	0.270 \pm 0.010	0.276 \pm 0.018	35
Caranguejo	<i>A. hastatus</i>	0.075 \pm 0.007	0.242 \pm 0.011	0.406 \pm 0.039	32
	<i>A. janeiroensis</i>	0.099 \pm 0.011	0.274 \pm 0.012	0.313 \pm 0.033	9
Guapiaçu	<i>Astyanax</i> sp.	0.070 \pm 0.009	0.236 \pm 0.025	0.403 \pm 0.053	41
	<i>Astyanax taeniatus</i>	0.087 \pm 0.004	0.256 \pm 0.023	0.322 \pm 0.028	37

n , sample size.

TABLE IV. Alimentary Index (I_A) recorded for each food item identified in the diet of the characin populations studied (HM, *Hollandichthys multifasciatus*; BM, *Bryconamericus microcephalus*; AJ, *Astyanax janaeensis*; AH, *Astyanax hastatus*; AT, *Astyanax taeniatus*; ASP, *Astyanax* sp.) in Rio Perequê-açu, Rio Ubatiba, Rio Carangueijo and Rio Guapiaçú

Item	Perequê-açu		Ubatiba		Carangueijo		Guapiaçú	
	HM	BM	AJ	AH	AJ	AH	AT	ASP
Autochthonous items								
Plant								
Algae					0.55	66.17	8.19	9.20
Filamentous algae		0.73	0.12	7.58	0.02	21.41	4.81	0.39
Animal								
Acari								
Unidentified		0.05			0.01			
Diptera								
Ceratopogonidae				0.08				0.01
Chironomidae		0.05	0.17	4.59	0.10	0.01		0.01
Psychodidae		0.22		0.02				
Ptychopteridae		0.02						
Simuliidae (pupae)		1.22		1.91		0.15		
Simuliidae		27.50	2.59	8.29	0.01	0.95		0.05
Thaumaleidae		0.01						
Ephemeroptera								
Baetidae		0.33		1.07				
Ephemeridae		0.02						
Leptophlebiidae		0.13						
Unidentified		0.28						
Lepidoptera								
Pyrilidae							1.52	
Odonata								
Anisoptera	0.12				0.13			
Zygoptera		0.01			0.01			
Plecoptera								
Gripopterygiidae		0.08						
Perliidae					0.06		0.00	0.03
Unidentified					0.01			
Trichoptera								
Hydropsychidae				3.02	0.01			
Hydroptilidae		1.03		0.04		0.01		
Leptonema		0.32						
Limnephilidae				0.12				
Xiphocentronidae				1.07				
Unidentified							0.01	0.21
Insect fragment	16.94	51.58	6.43	32.18	0.01	0.49	1.56	80.84
Other								
Decapoda	0.32		0.05				0.04	
Fish larvae			0.05					
Oligochaeta			0.13			0.01		
Oocyte	0.08			0.02				
Scale	0.04	0.01					0.03	0.01

TABLE IV. Continued

Item	Perequê-açu		Ubatiba		Carangueijo		Guapiaçú	
	HM	BM	AJ	AH	AJ	AH	AT	ASP
Allochthonous items								
Plant								
Seed	0.27		64.14	23.31	9.86		0.11	
Plant matter (leaves and twigs)	10.85	1.00	6.24	2.69	43.56	10.43	73.31	7.93
Animal								
Araneae	0.21		0.13		0.09	0.32		0.04
Coleoptera								
Curculionidae (larva)				0.29				
Curculionidae	0.02	0.06						
Dryopidae		0.08						
Elmidae (larva)				0.25				
Elmidae	0.91							
<i>Macrelmis</i> sp.	0.04							
Unidentified larva				1.03				
Unidentified	0.62	0.08			0.38			
Diptera	0.35	1.42			0.03			
Hymenoptera								
Formicidae	37.28	10.85	14.21	0.02	13.18	0.03	0.69	0.28
Vespidae							1.10	
Unidentified							0.01	
Hemiptera								
Cercopidae			0.17					
Unidentified	0.06				0.55			
Neuroptera					0.01			
Orthoptera					9.89			
Arthropod fragment								0.01
Insect fragment	31.88	2.91	5.66	12.41	20.71	0.01	8.62	0.89
Total	16	25	13	20	21	12	13	14

The feeding patterns recorded in the present study reveal similarities and also marked differences in the same species inhabiting different environments. In the Rio Perequê-Açu for example, *H. multifasciatus* is omnivorous, feeding mainly on allochthonous arthropods, as observed in other Atlantic forest streams by Esteves & Lobón-Cerviá (2001) and Abilhoa *et al.* (2009). This indicates an intimate relationship between the fish and the riparian vegetation. In contrast, *B. microcephalus* presents an ample niche breadth in the present study, feeding mainly on autochthonous arthropods, contradicting the findings of Rezende & Mazzoni (2003, 2006), who observed this species feeding predominantly on allochthonous arthropods at other sites in south-eastern Brazil. The coexistence of *B. microcephalus* and *H. multifasciatus* and similar shifts in the composition of their diets were also recorded by Russo *et al.* (2004), suggesting that the trophic plasticity of these characin species is not uncommon in the wild.

In the Rio Ubatiba, *A. janeiroensis* is omnivorous with a marked preference for allochthonous plant matter (seeds, leaves and twigs). This contrasts with Mazzoni *et al.*

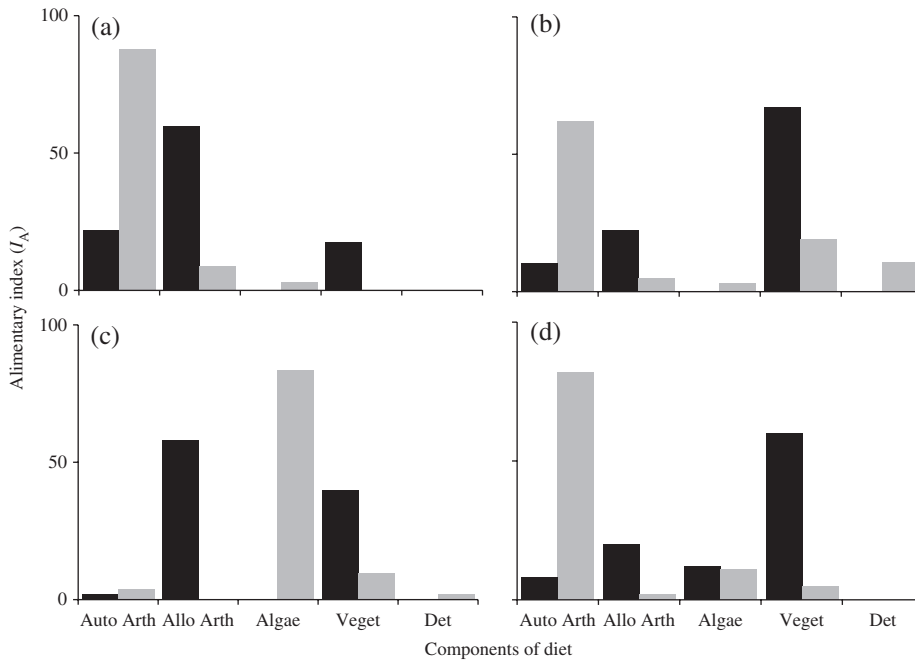


FIG. 4. Alimentary index (I_A) of (a) Perequê-acú River, ■, *Hollandichthys multifasciatus* and ■, *Bryconamericus microcephalus*; (b) Ubatiba River, ■, *Astyanax janeiroensis* and ■, *Astyanax hastatus*; (c) Caranguejo River, ■, *A. janeiroensis* and ■, *A. hastatus*; (d) Guapiaçú River, ■, *Astyanax taeniatus* and ■, *Astyanax sp.* Auto, autochthonous; Allo, allochthonous; Arth, arthropods; Veget, vegetables; Det, detritus.

(2010a), who recorded a diet based on autochthonous plants (mainly algae) for this species. This difference may be accounted for by the presence of a forest canopy at the study site (pers. obs.), which would probably reduce primary productivity and the availability of algae (Sinéan *et al.*, 2012). *Astyanax hastatus* has an ample, omnivorous diet with a preference for autochthonous arthropods, as reported by Mazzoni & Rezende (2003). In the Rio Caranguejo, *A. janeiroensis* and *A. hastatus* are both omnivorous, with different diets from those recorded in the Rio Ubatiba, with *A. janeiroensis* feeding mainly on allochthonous arthropods and *A. hastatus* on algae. These differences may be explained by environmental factors, *i.e.* the absence of a canopy and the presence of shrubby vegetation (pers. obs.). These findings emphasize the capacity of these species to respond to resource availability (Manna *et al.*, 2012). Finally, in Rio Guapiaçú, *A. taeniatus* has an omnivorous diet based on allochthonous plants, as reported by Manna *et al.* (2012) for a nearby stream in the Serra do Mar mountain range.

The estimates of niche breadth indicate that all the study species are generalist feeders with high trophic plasticity, which is typical of characin species (Lowe-McConnell, 1987; Araujo-Lima *et al.*, 1995; Esteves & Aranha, 1999; Abelha *et al.*, 2001; Kido, 2001; Manna *et al.*, 2012). This suggests a high degree of overlap in the feeding niche, although only a few items were consumed very frequently, which may account for the reduced overlap recorded at each site (Table V). This would permit coexistence without any negative effects for either species, as proposed by Pianka (1973) and Hurlbert (1978). In fact, slight morphological variations were detected that would have an

TABLE V. Niche breadth (H'), number of frequently used items ($N\%$) and the niche overlap index (C_H) recorded for the pairs of characin species analyzed (HM, *Hollandichthys multifasciatus*; BM, *Bryconamericus microcephalus*; AJ, *Astyanax janiroensis*; AH, *Astyanax hastatus*; AT, *Astyanax taeniatus*; ASP, *Astyanax* sp.) in Rio Perequê-açu, Rio Ubatiba, Rio Carangueijo and Rio Guapiaçu

Stream	Species	H'	$N\%$	C_H
Perequê-açu	HM	0.84	5	0.43
	BM	0.86	5	
Ubatiba	AJ	0.86	6	0.46
	AH	0.87	9	
Carangueijo	AJ	0.84	6	0.13
	AH	0.81	6	
Guapiaçu	AT	0.82	6	0.13
	ASP	0.82	5	

effect on the trophic ecology of each pair of species. This would facilitate coexistence, as suggested by Labropoulou & Eleftheriou (1997); Russo *et al.* (2008) and Ramírez *et al.* (2015) and corroborates the hypothesis presented in this study that morphological differences may account for this resource partitioning.

The results of the alimentary indices and niche overlap analyses indicate that the use of distinct resources and the feeding strategies of coexisting species enhance resource partitioning. The trophic generalism displayed by characin species (Lowe-McConnell, 1987; Araujo-Lima *et al.*, 1995; Esteves & Aranha, 1999; Abelha *et al.*, 2001; Kido,

TABLE VI. t and P values for the comparison of the volumes of allochthonous v. autochthonous items in the diets of the pairs of species studied (see Table V) in Rio Perequê-açu, Rio Ubatiba, Rio Carangueijo and Rio Guapiaçu

Site		Allochthonous	t	P	Autochthonous
Perequê-açu	n	65			130
	\bar{x}	2.428			2.061
	S.D.	1.603			1.377
			1.660	>0.05	
Ubatiba	n	61			102
	\bar{x}	2.036			0.689
	S.D.	1.670			1.475
			5.369	<0.001	
Carangueijo	n	78			111
	\bar{x}	2.452			0.835
	S.D.	1.549			1.515
			7.157	<0.001	
Guapiaçu	n	49			67
	\bar{x}	1.881			1.001
	S.D.	2.066			1.954
			2.338	<0.05	

n , number.

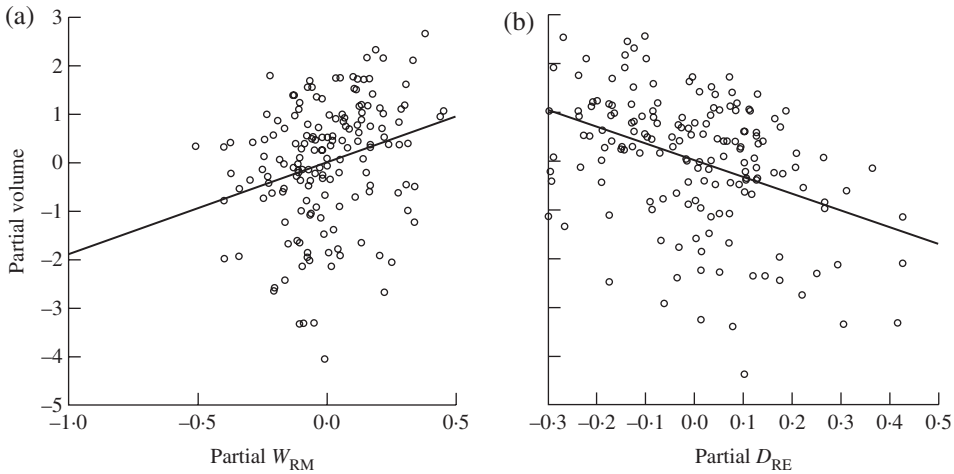


FIG. 5. Scatterplot representing the partial results of the multiple regression between the \log_{10} volume (V) and (a) \log_{10} relative mouth width (W_{RM}) ($P < 0.001$) and (b) \log_{10} relative eye diameter (D_{RE}) ($P < 0.001$). The multiple regression: $\log_{10} V = 3.314 + 1.891(\log_{10} W_{RM}) - 3.413(\log_{10} D_{RE})$, $r^2 = 0.286$, $F_{2,161} = 32.196$, $P < 0.001$.

2001; Manna *et al.*, 2012; Ferreira *et al.*, 2012) associated with resource partitioning and morphometric variations presumably underpin the potential for the coexistence of the characin species observed in the present study.

Major similarities in the morphological and trophic patterns of the coexisting characin species were also observed between the four study streams. This suggests an eco-morphological model based on pairs of species. Each pair includes one species with higher L_{RH} and W_{RM} and a feeding preference for larger allochthonous items and a second species with relatively larger eyes and a preference for smaller, autochthonous items (Table III and Fig. 5).

Many studies have indicated that ingestion of larger food items (in the present study the allochthonous items) may be limited by the mouth width (Wootton, 1990; Abelha *et al.*, 2001; Dufech *et al.*, 2003; Nandi & Saikia, 2015), whereas it has been proposed that larger eyes may facilitate the search for smaller items (in this case, autochthonous) (Sibbing & Nagelkerke, 2001; Kassam *et al.*, 2003). These studies were corroborated by the present study, based on the items gathered in the stomach-content and multiple regression analyses. It was also demonstrated that specimens with a higher W_{RM} ingest larger food items and that specimens with a higher D_{RE} ingest smaller food items.

Non-coexisting species share high similarity regarding both morphology and diet, which may be indicative of ecological equivalence of closely related but spatially distant species (Pianka, 1994; Loreau, 2004; Friedman *et al.*, 2016). Therefore, following the four locations sampled here, it is possible to conclude that the coexistence of these closely related characins is controlled by the availability and choice of food resources. Differences in the morphological design of each species are probably the responsible for these choices resulting in low niche overlap and resource partitioning.

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Supporting Information

Supporting Information may be found in the online version of this paper:

FIG. S1. Alimentay Index (I_A) recorded at Rio Perequê-Açu for (a) *Hollandichthys multifasciatus* and (b) *Bryconamericus microcephalus*; at Rio Ubatiba for (c) *Astyanax janaeirensis* and (d) *Astyanax hastatus*; at Rio Carangueijo for (e) *A. janaeirensis* and (f) *A. hastatus*; and for Rio Guapiaçu for (g) *Astyanax taeniatus* and (h) *Astyanax* sp. ■, Rainy season; □, dry season.

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