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Is coexistence between non-native and native Erythrinidae species mediated by niche differentiation or environmental filtering? A case study in the upper Paraná River floodplain

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The limiting similarity theory predicts that divergence in the functional traits of native and introduced species is an essential component in species establishment, as introduced species must occupy a niche that is unoccupied by resident species. On the other hand, the environmental filtering hypothesis predicts convergence between introduced and native species, as both possess traits that make them adapted to the local abiotic environment. Morphology, spatial co-occurrence, diet, feeding selectivity, and niche breadth and overlap of Erythrinidae were evaluated to detect possible mechanisms acting in the coexistence between non-native and native species. Native (*Hoplias* sp. B and *Hoplias* cf. *malabaricus*) and non-native (*Hoplerythrinus unitaeniatus* and *Hoplias mbigua*) species presented differences in morphological traits, spatial co-occurrence, diet, selectivity, and niche breadth and overlap. The mechanisms mediating species coexistence seem to vary according to species. The absence of spatial and feeding overlap suggests that non-native species *H. unitaeniatus* occupy a different niche than native species, supporting its successful establishment without eliminating the native species. However, low feeding overlap and similar morphologies between non-native and native species of *Hoplias* point to environmental filters; in this case, the non-native *H. mbigua* is able to establish due to similarities in functional traits.

Keywords: Competition, Co-occurrence, Fish feeding, Morphology, Predation.

Teorias sobre nicho ecológico afirmam que divergência em traços funcionais entre espécies nativas e introduzidas são essenciais ao estabelecimento da espécie introduzida, pois estas devem ocupar um nicho não utilizado pelas espécies residentes. Por outro lado, a teoria de filtros ambientais afirma a convergência entre espécies introduzidas e nativas, pois ambas possuem traços funcionais que fazem com que essas espécies estejam mais adaptadas as variáveis ambientais. Foram avaliadas a morfologia, ocorrência espacial, dieta, seletividade alimentar, sobreposição e largura de nicho em Erythrinidae para detectar possíveis mecanismos atuando na coexistência de espécies nativas e não nativas. Espécies nativas (*Hoplias* sp. B e *Hoplias* cf. *malabaricus*) e não nativas (*Hoplerythrinus unitaeniatus* e *Hoplias mbigua*) apresentaram diferenças em todos os atributos testados. Os mecanismos mediando a coexistência de espécies nativas e não nativas parecem variar de acordo com a espécie considerada. A ausência de sobreposição espacial e na dieta sugere que a espécie não nativa *H. unitaeniatus* ocupa um nicho distinto que as espécies nativas, favorecendo seu estabelecimento sem eliminar as espécies nativas, apontando para segregação de nicho. Por outro lado, morfologias similares, porém com diferentes dietas foram observadas para as espécies de *Hoplias*, sugerindo que as espécies coexistem devido à filtros ambientais, assim, neste caso, a espécie não nativa *H. mbigua* é capaz de se estabelecer no novo ambiente devido à similaridades em traços funcionais.

Palavras-chave: Alimentação de peixes, Competição, Co-ocorrência, Morfologia, Predação.

Introduction

Theories about competition and niche segregation predict that species coexistence is achieved through differences in species niches. In this case, when demand for resources exceeds supply, there will be increased competition, and tolerance of interspecific niche overlap will decline (Pianka, 1974, 1981). Therefore, niche differentiation will lead to a reduction in the niche overlap between potential competitors, reducing competition

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and allowing coexistence; in other words, there is limited similarity among coexisting species (MacArthur, 1958; Pianka, 1973, 1974; Schoener, 1974). For species coexisting in the same habitat, niche differences might involve changes in some combination of strategies for habitat use, such as feeding time, energy allocation, and defense (Winemiller *et al.*, 2015), including diet restrictions through feeding selectivity or niche retraction (Correa, Winemiller, 2014). According to the limited similarity theory, differences in resource use are crucial in species coexistence and have likely resulted in the selection for optimal morphologies that reduce competition for resources (De León *et al.*, 2014).

On the other hand, species coexistence can be mediated by environmental filters, as predicted by the niche filtering hypothesis (*sensu* Southwood, 1977). In this case, coexisting species would be more similar to one another than expected by chance due to the abiotic properties of the habitat, which would act as a filter allowing only a narrow spectrum of species to survive (Zobel, 1997). According to this hypothesis, habitat characteristics can be viewed as filters imposed on species gene pools to select traits suited to a particular set of environmental conditions (Diaz *et al.*, 1998), resulting in a higher degree of biological similarity among coexisting species than would be expected by chance (Cornwell *et al.*, 2006; Mouillot *et al.*, 2007). Considering introductions, once species have passed through dispersal and abiotic filters, that is, they were able to arrive at a site, survive and grow under the prevailing conditions, niche-based interactions will have little or no effect on these species interactions (Thompson *et al.*, 2010).

According to the limiting similarity theory, coexisting species are dissimilar due to biotic interactions and are thus complementary, while in the environmental filtering hypothesis, the assembly is more similar due to similar environmental conditions and thus ecologically redundant (Mouillot *et al.*, 2007). The first theory would predict that the divergence in functional traits of native and introduced species is an essential component in species establishment because each niche is occupied by the best competitor species and, as species with high similarity in their biological features are likely to have the same Eltonian niche (Devictor *et al.*, 2010), these species cannot co-occur and have to segregate along temporal, spatial and/or environmental gradients to coexist regionally (Mouchet *et al.*, 2013). On the other hand, the environmental filtering hypothesis predicts convergence between introduced and native species, as both possess traits that make them adapted to the local abiotic environment (Cross *et al.*, 2015) (Tab. 1).

In the upper Paraná River floodplain, native and introduced Erythrinidae species coexist. The native *Hoplias* sp. B and *Hoplias* cf. *malabaricus* (Pazza, Júlio-Jr, 2003; Graça, Pavanelli, 2007; Bifi, 2013) currently coexist with *Hoplias mbigua* Azpelicueta, Benítez, Aichino, Mendez, 2015 and *Hoplerythrinus unitaeniatus* (Spix, Agassiz, 1829), which were introduced to this region after the flooding of the geographical barrier of the Sete Quedas Falls to create the Itaipu Reservoir (Júlio-Jr *et al.*, 2009). These are typical carnivorous fish with a preference for lentic environments, which are widely distributed in South American basins (Oyakawa, 2003). Considering that interactions within the same family are stronger (Golani, Galil, 1991; Golani, 1993) and that phylogenetic niche conservatism would predict high similarities in ecological niche use among closely related species, leading to competitive exclusion (Dammhahn *et al.*, 2015), some mechanism must be acting to mediate the coexistence of these species.

Considering the limiting similarity theory, there should exist a mechanism that determines differences in the use of resources, such as space and food. On the other hand, according to the environmental filtering hypothesis, persistence in a particular environment would lead to similar traits among these species, and, consequently, similar resource use. Therefore, the objective of this study was to identify whether such mechanisms are acting as mediators of species coexistence in Erythrinidae in the upper Paraná River floodplain and the mechanism that most contributes to it, based on morphological and ecological traits. If species coexistence is mediated by niche differentiation, niche segregation, in terms of space and food, between native and introduced species with a larger divergence in ecological traits would be expected, while if species coexistence is mediated by environmental filtering, we would expect that species would be more similar in ecological traits.

Tab. 1. Main definitions and assertions of each theory, highlighting differences between them.

Limiting similarity	Niche filtering
Niches of species overlap less than expected by chance (Fowler *et al.*, 2014).	Species niches overlap more than expected by chance (Fowler *et al.*, 2014).
Closely related taxa compete most strongly (MacArthur, Levins, 1967).	Habitat characteristics can be viewed as filters imposed on species gene pools to select traits suited to a particular set of environmental conditions (Díaz *et al.*, 1998).
The coexistence of many species within a community can be due to weak interspecific interactions (Kokkoris *et al.*, 2002).	Large differences among species may actually more often result in exclusion than in coexistence (Herben *et al.,* 2014)
Occurs at only small spatial scales (Takahashi, Tanaka, 2016).	Occurs at any spatial scale (Takahashi, Tanaka, 2016).
Differences among species allow the persistence (Hutchinson 1959; MacArthur, Levins, 1967; MacArthur, 1970).	Similarities among species allow the persistence (Mouillot *et al.*, 2005; Mouchet *et al.,* 2010).

Material and Methods

Sampling. The upper Paraná River floodplain (22°-22°50' S and 53°15'-53°40' W) is located in the lower third of the upper Paraná River and is the only remnant of the upper Paraná River with lotic waters within Brazil. This area is characterized by high biodiversity and endemic fauna, which are highly threatened due to hydrological alterations and species invasions (Agostinho *et al.*, 2005).

Sampling was performed as part of the PELD project (Long Term Research Project - Site 6 - CNPq) in different environments of the floodplain, totaling 36 sampling stations (fig. 1 of Luz-Agostinho *et al.*, 2008). These environments included connected and non-connected lakes, channels, and the main river channel. Fish species were captured quarterly from March 2007 to June 2013 using seine and gill nets of different mesh sizes (2.4 to 16 cm between opposite knots). The gill nets were deployed for a 24-hour period and checked at 8:00 AM, 4:00 PM, and 10:00 PM. All sampled fish were identified, measured, anaesthetized (Benzocaine), and euthanized. The Erythrinidae species were eviscerated, having their stomachs removed and preserved in 10% formalin for later analysis. Species were identified according to Graça, Pavanelli (2007), except the species of *Hoplias*, which were identified according to Bifi (2013). Only adult Erythrinidae were used for the analyses. The adults were selected by the standard length at first gonadal maturation (L50), which corresponds to the length at which 50% of the individuals are able to reproduce; for *H. unitaeniatus*, the L50 is 165 mm for females and 140 mm for males, and for *Hoplias* species, it is 164 mm and 152 mm for females and males, respectively (Suzuki *et al.*, 2004).

Voucher specimens were deposited in the Fish Collection of Nupélia (Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura - UEM/Maringá). *H. mbigua*: NUP 9953, 7589, 3456, 7584, 7582, 7590, 9725, 7592, 10437, 4253, 269; *Hoplias* sp. B: NUP 10439, 12260, 12285, 10438, 10226, 10225, 3040, 6399; *H.* cf. *malabaricus*: NUP 11415, 12257, 265, 9698, 11200, 11132, 7286, 3458, 12291, 1140; *H. unitaeniatus*: NUP 11289, 4160, 9710, 10599, 8635, 8857.

Morphological analysis. The fish used for morphological analyses were obtained from the Fish Collection of Nupélia and from samples. A total of 90 individuals were measured, with 28 *H. mbigua*, 21 *Hoplias* sp. B, 18 *Hoplias* cf. *malabaricus*, and 23 *H. unitaeniatus*. The standard length ranges of the species were as follows: *H. mbigua* - 170.78 to 287 mm, *Hoplias* sp. B - 160.5 to 347 mm, *H.* cf. *malabaricus* - 175 to 255 mm, and *H. unitaeniatus* - 140 to 248 mm.

Morphological linear measures related to trunk, fins, and head were taken with the aid of a digital caliper (approximation of 0.01 mm); measures greater than 130 mm were taken with a ruler. Measurements of fins and eye areas were obtained from the outline drawings of the structures on plastic sheets, which were subsequently scanned to calculate the internal area using the software AutoCAD (Autodesk, 2013).

A total of 19 ecomorphological indices were calculated from the linear morphometric measurements and the areas to represent the occupation of trophic and spatial niches by species. The use of indices aims to eliminate the effect of individual size, allowing comparisons related only to body shape and its structures (Winemiller, 1991). The following indices were used: compression index (CI), depression index (DI), relative height of body (RHB), compression index of caudal peduncle (CIPd), relative length of caudal peduncle (RLPd), relative height of caudal peduncle (RHPd), relative width of caudal peduncle (RWPd), relative length of head (RLHd), relative height of head (RHHd), relative width of head (RWHd), eye position (EP), relative area of eye (RAE), relative height of dorsal fin (RHD), relative area of dorsal fin (RAD), aspect ratio of caudal fin (ARC), relative height of anal fin (RHA), aspect ratio of anal fin (ARA), aspect ratio of pectoral fin (ARPt), and aspect ratio of pelvic fin (ARPv). More details about the linear and area measures involved in the calculation of morphological proportions, as well as their respective ecological explanations, can be found in Oliveira *et al.* (2010).

To highlight the interspecific morphological patterns, a principal components analysis (PCA) was conducted using the ecomorphological indices. The selection of the axes for interpretation was carried out according to the *broken-stick* model (Jackson, 1993), which creates a null distribution of eigenvalues for comparison with the observed values. After the selection of the axes by the *broken-stick* model, an analysis of variance (ANOVA) was applied, using the axis scores (dependent variable) to identify possible significant morphological segregation among species (categorical variable). Finally, only the selected axes that presented significant results in the ANOVA were retained for interpretation.

Spatial co-occurrence analysis. Null models for species co-occurrence were used to assess whether spatial segregation could be a major driver of species co-existence. Null models are pattern-generating models based on randomized ecological data (Gotelli, McCabe, 2002). This technique allows the comparison of an observed co-occurrence pattern against randomized occurrence data, which represents co-occurrence expected by chance, with no ecological relationship between species. The metric chosen was the C-score (Stone, Roberts, 1990), which represents the average number of checkerboard units in the species matrix. Checkerboard units indicate samples in which species A is present and species B is absent and vice versa (Stone, Roberts, 1990). The observed C-score was compared with C-scores generated by 10,000 randomizations using an algorithm that keeps the row and column sums fixed ("sim 9"; Gotelli, 2000). Statistical differences between the observed and simulated C-scores suggest different patterns of species co-occurrence. Significant negative values mean that species are co-occurring more often than expected by chance, suggesting an aggregation pattern (Stone, Roberts 1992), while significant positive values indicate less species co-occurring than expected by chance, suggesting a segregation pattern (Gotelli, McCabe, 2002). In addition, the total and relative number of occurrences was evaluated for each pair of species to assess which species contributed the most to the observed pattern.

Dietary analysis. To avoid diet variations caused by seasonal changes in the floodplain (dry and flood periods) (Power *et al.*, 1995; Abelha *et al.*, 2001; Luz-Agostinho *et al.*, 2008), diet analyses were performed only for dry periods with river levels below 450 cm for the Baía and Paraná Rivers and 275 cm for the Ivinhema River (Suzuki *et al.*, 2009). This is due to the greatest number of captures occurring in dry periods and because intense and prolonged floods are likely to narrow the niches of these species (Luz-Agostinho *et al.*, 2008), causing the underestimation of niche breadth. The stomach contents were analyzed under stereoscopic microscopes using the volumetric method described by Hyslop (1980) and the contents were identified to the lowest feasible taxonomic level (species, genus, family, or order for fish and usually order for invertebrates). Fish prey was identified according to Graça, Pavanelli (2007) and Ottoni, Costa (2009), measured, and counted. The contribution of each item to the total stomach contents was evaluated as the percentage of the total number of items in all stomach contents (Baker *et al.*, 2014). Partially digested unidentified material and arthropod fragments of unknown origin were excluded from the total. To facilitate statistical analyses, the 45 food types found within the stomach contents were grouped into 36 broad categories. Insects were grouped into only one group, and mollusks and frogs were excluded from the analysis, as they occurred only twice and once, respectively.

For each species, differences in diet among the different river systems of the floodplain (Baía, Ivinhema, and Paraná) were tested through a permutational multivariate analysis of variance (PERMANOVA). As no significant differences among the river systems were found for any of the analyzed species, which means that the species present consistent diets regardless of the river system, the subsequent analysis did not consider different river systems. Differences between the diets of each species were obtained using post hoc PERMANOVA *pairwise* comparisons. The significance level adopted was 0.05; therefore, the probability for *pseudo*-F is higher than that for observed F. The *pseudo*-F value indicates the probability of rejecting the null hypothesis by quantifying the size of the difference among the analyzed samples (Anderson *et al.*, 2008). The original matrix (the volume of each item in the stomach of each captured fish) was transformed into a dissimilarity matrix using the *Bray-Curtis* distance (Bray, Curtis, 1957).

Niche breadth was calculated for each species using Levins' measure (Krebs, 1999), which measures the uniformity of the distribution of items among various food resources. It is given as B = $^1/(\sum_{n=1}^{n} pi^2)$, where *B*=niche breadth, *pi*=the proportion of food item *i,* and *n*=number of stomachs. Possible differences in niche breadth (dependent variable) among species (categorical variable) were tested by an analysis of variance (ANOVA) followed by Tukey's HSD test. Niche overlap among species pairs was quantified using Pianka's (1973) index,

$$O = \sum p_{ij}\, p_{jk} \Big/ \sqrt{\sum p_{ij}^2\, p_{ik}^2}\,,$$

where *O* represents the overlap between a species pair, and p_{ij} and p_{ik} represent the proportion of the i^{th} resource used by the species. This index ranges from 1 to 0, where 1 means complete overlap and 0 no overlap. The significance of the observed mean overlap among species was determined by comparisons against a null model of expected niche overlap when resources are randomly consumed. Simulated diets were generated by a randomization in which the diet breadths were maintained, zero values were reshuffled, and all items had the same probability of being consumed (Gotelli, Graves, 1996).

To determine whether prey size has an influence on species diet rather than taxonomic composition, we performed a feeding selectivity analysis by size range. The data used for the calculations were based on the relative numerical composition of the prey items in the stomach contents of the species and in the environment. For the analysis, the selectivity index E_i proposed by Vanderploeg, Scavia (1979) was used: $Ei = (Wi - n^{-1})\ (Wi + n^{-1})^{-1}$, where *n* is the number of prey types available, and $Wi = ripi^{-1} \sum(ripi^{-1})^{-1}\ ripi^{-1} \sum(ripi^{-1})^{-1}$, where r_i is the percentage of prey item *i* in the diet of the fish, and p_i is the percentage of prey item *i* in the environment. E_i varies from -1 to 1. Negative values indicate avoidance of the prey, positive values indicate active selection, and null values indicate predation by chance. This index assumes that the gut samples and habitat samples accurately reflect the relative abundance of prey consumed and in the environment, respectively (Kohler, Ney, 1982), in this case, the prey size classes. Prey sizes not found in the gut contents during the study were omitted from the analysis, as they were deemed inaccessible to the studied species (Cantanhêde *et al.*, 2009). The data of prey in the stomachs of each individual and in the environment were arbitrarily grouped into eleven classes at 20 mm intervals: 10-29, 30-49, 50-69, 70-89, 90-109, 110-129, 130-149, 150-169, 170-189, 190-209, and 210-230. Environmental data were obtained in the same samples described above, in which each sampled fish was identified and counted as described in the sampling methods.

Due to the great divergence in diet and morphological traits among species, especially those that are non-native (*H. unitaeniatus* and *H. mbigua*), the results are presented by species and not by status (non-native or native). The selectivity test was conducted only for species that mostly prey on fish due to the lack of information on other organisms. Consequently, it was only conducted for *Hoplias* species, as the diet of *H. unitaeniatus* presented a low representation of fish.

The analyses were carried out in R software (R Development Core Team, 2015): null models for species co-occurrence using the package 'EcoSimR' (Gotelli, Entsminger, 2010). PERMANOVA using the package 'vegan' (Oksanen *et al.*, 2015) and Levins' measure with the package 'spaa' (Zhang, 2016). The PERMANOVA pairwise comparison was carried out using the statistical software Primer-E + PERMANOVA (Anderson *et al.*, 2008). Pianka's niche overlap and randomizations were performed in EcoSim 7.71 (Gotelli, Entsminger, 2010). Graphics were generated in the software Statistica 10 (StatSoft Inc, 2011).

Results

Morphological analysis. The ordination (PCA; Fig. 1) revealed three significant axes according to the *broken-stick* criteria (Table 2), but the ANOVA applied to the PCA scores did not present significant values for the second axis ($F_{3,85}$=1.52, p=0.21), so it was not retained for interpretation. In the first PCA axis, differences between *H. unitaeniatus* and the *Hoplias* species were highlighted. Individuals of *H. unitaeniatus* had more negative scores, being characterized by higher values in the aspect ratio of the caudal, anal, pectoral, and pelvic fins. On the other hand, *Hoplias* specimens had positive scores, indicating larger areas of the dorsal fin and eyes, less depressed bodies, and more dorsal eyes than *H. unitaeniatus*. The third PCA axis separated the three species of *Hoplias*. Specimens of *H. mbigua* were characterized by larger dorsal and anal fins, a larger caudal peduncle, and a higher ratio for the pectoral fin than the other two species of *Hoplias*. It was not possible to make a clear distinction between the native species, *Hoplias* sp. B and *H.* cf. *malabaricus*, but both species had longer and deeper heads and more compressed bodies and caudal peduncles than *H. mbigua*. In general, native species (*Hoplias* sp. B and *H.* cf. *malabaricus*) presented similar morphologies, while non-native species (*H. unitaeniatus* and *H. mbigua*) were morphologically distinct from each other and from the native species.

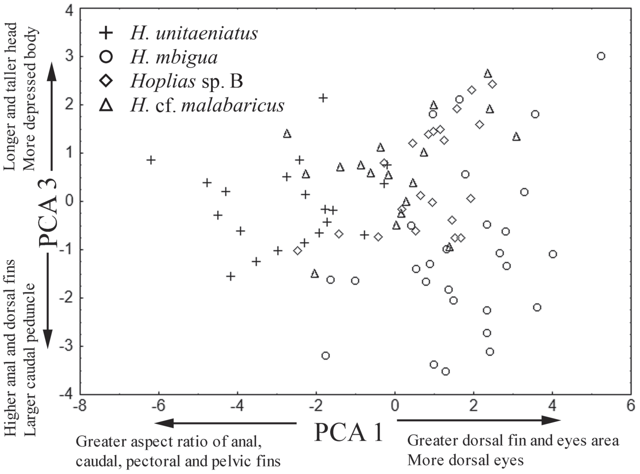

Fig. 1. Distribution of scores of non-native (*H. mbigua* and *H. unitaeniatus*) and native (*Hoplias* sp. B and *H.* cf. *malabaricus*) Erythrinidae species on axes 1 and 3 of the principal components analysis (PCA 1 and PCA 3) applied to the correlation matrix (Pearson) formed by 19 ecomorphological indices.

Tab. 2. Pearson's correlation coefficients (r) obtained among the ecomorphological indices for axes 1 and 3 of the principal components analysis (PCA) applied to the correlation matrix formed by 19 indices describing non-native (*H. mbigua* and *H. unitaeniatus*) and native (*Hoplias* sp. B and *H.* cf. *malabaricus*) Erythrinidae species. At the lower level, the eigenvalues predicted by the *broken-stick* model and the proportions of the accumulated and explained variability are described. The indices with higher correlation values (in bold) were selected for interpretation.

Ecomorphological indices	PCA axes	
	r PC 1	r PC 3
Aspect ratio of anal fin	**-0.32**	-0.15
Aspect ratio of caudal fin	**-0.32**	-0.06
Aspect ratio of pectoral fin	**-0.27**	**-0.20**
Aspect ratio of pelvic fin	**-0.31**	-0.05
Compression index	-0.08	**0.26**
Compression index of caudal peduncle	-0.25	**0.31**
Depression index	**0.23**	0.12
Eye position	**0.28**	-0.14
Relative area of dorsal fin	**0.32**	0.23
Relative area of eye	**0.30**	0.22
Relative height of anal fin	0.12	**-0.34**
Relative height of body	-0.02	**0.38**
Relative height of caudal peduncle	-0.25	-0.14
Relative height of dorsal fin	0.16	**-0.25**
Relative height of head	-0.25	0.07
Relative length of caudal peduncle	-0.07	0.25
Relative length of head	-0.01	**0.34**
Relative width of caudal peduncle	0.17	**-0.29**
Relative width of head	-0.17	0.14
Predicted eigenvalue: *broken-stick*	3.55	2.05
Eigenvalue	5.32	2.20
Explained variability (%)	28.01	11.56
Accumulated variability (%)	28.01	39.56

Spatial co-occurrence analysis. The species co-occurrence pattern had significant positive values for the entire floodplain (C-score=2982, p<0.001), indicating spatial segregation. The same pattern was observed when considering the Baía (C-score=423.17, p<0.001) and Ivinhema systems (C-score=453.50, p<0.001). However, for the Paraná system, a random pattern was observed (C-score=124, p>0.05). Considering each of the species (Table 3), *H. unitaeniatus* had the lowest number of total occurrences, although, when found, the overlap with *Hoplias* species was high. This species was encountered more often in those samples in which *Hoplias* sp. B was also present. *Hoplias mbigua* and *Hoplias* sp. B, which were the most frequent species, had more intense spatial overlap, and both were rarely encountered with *H. unitaeniatus*. For *H.* cf. *malabaricus*, the spatial overlap occurred evenly with *H. mbigua* and *Hoplias* sp. B. However, this was the *Hoplias* species that most spatially overlapped with *H. unitaeniatus*.

Tab. 3. Co-occurrence in terms of number and proportion (in parentheses) of each pair of Erythrinidae species in the upper Paraná River floodplain. Valid comparisons can be made only between the rows of a single column.

Species	*H. unitaeniatus*	*H. mbigua*	*Hoplias* sp. B	*Hoplias* cf. *malabaricus*
		Floodplain		
H. unitaeniatus	63 (100%)	41 (15%)	47 (23%)	38 (29%)
H. mbigua	41 (65%)	271 (100%)	173 (84%)	114 (88%)
Hoplias sp. B	47 (75%)	173 (64%)	206 (100%)	105 (81%)
Hoplias cf. *malabaricus*	38 (60%)	114 (42%)	105 (51%)	129 (100%)
		Baía system		
H. unitaeniatus	33 (100%)	23 (21%)	28 (28%)	19 (30%)
H. mbigua	23 (70%)	109 (100%)	91 (90%)	60 (94%)
Hoplias sp. B	28 (85%)	91 (83%)	101 (100%)	57 (89%)
Hoplias cf. *malabaricus*	19 (58%)	60 (55%)	57 (56%)	64 (100%)
		Ivinhema system		
H. unitaeniatus	23 (100%)	12 (15%)	14 (21%)	14 (32%)
H. mbigua	12 (52%)	80 (100%)	50 (74%)	34 (77%)
Hoplias sp. B	14 (61%)	50 (63%)	68 (100%)	37 (84%)
Hoplias cf. *malabaricus*	14 (61%)	34 (43%)	37 (54%)	44 (100%)
		Paraná system		
H. unitaeniatus	7 (100%)	6 (7%)	5 (14%)	5 (24%)
H. mbigua	6 (86%)	82 (100%)	32 (86%)	20 (95%)
Hoplias sp. B	5 (71%)	32 (39%)	37 (100%)	11 (52%)
Hoplias cf. *malabaricus*	5 (71%)	20 (24%)	11 (30%)	21 (100%)

Dietary analysis. Species of *Hoplias* had diets dominated by fish, with some participation of insects, crustaceans, and plants, while *H. unitaeniatus* had a diet dominated by aquatic insects (mainly Ephemeroptera), which represented more than 50% of its diet (Table 4). Significant differences in species diets were observed (PERMANOVA: *pseudo*-F_{218}=1.98, p=0.001), and all species revealed significant differences in diet in the pairwise comparison (Table 5). All three *Hoplias* species consumed individuals of the same genus (*Hoplias* spp.). The non-native, *H. mbigua* consumed mainly *Pimelodus* spp. A great participation of *Hoplosternum littorale* and *Gymnotus* spp. was observed in the diets of the natives *Hoplias* sp. B and *H.* cf. *malabaricus*, respectively (Table 4).

Differences in niche breadth among species were observed (ANOVA, $F_{3,15}$=11.82, p<0.001). The non-native *H. unitaeniatus* presented a narrower niche breadth than *Hoplias* sp. B (Tukey's HSD: p=0.02 and p=0.001, respectively), presenting similar niche breadth to that of *H.* cf. *malabaricus* (Tukey's HSD: p=0.99). The non-native *H. mbigua* presented a niche breadth that was distinct from that of *H.* cf. *malabaricus* (Tukey's HSD: p=0.02); however it had a similar niche breadth to that of *Hoplias* sp. B (Tukey's HSD: p=0.37) (Fig. 2). Niche overlap among species was greater than expected under a null model of random consumption of resources (p=0.01). The lowest overlap found was between *H. unitaeniatus* and *H. mbigua*, and the greatest overlap was between *H. mbigua* and *Hoplias* sp. B (Table 4).

The selectivity test showed that the three species of *Hoplias* positively selected small-sized prey, especially those in the interval between 30 and 49 mm, which was one of the most abundant class ranges available in the environment, and avoided prey larger than 150 mm, despite their abundance. *Hoplias* cf. *malabaricus* avoided prey between 10 and 29 mm, the most abundant class range in the environment; this species positively selected prey of 50 to 69 mm (Fig. 3A and 3B). Specimens of *Hoplias* sp. B presented positive selectivity for prey between 90 and 109 mm, while *H.* cf. *malabaricus* negatively selected this interval.

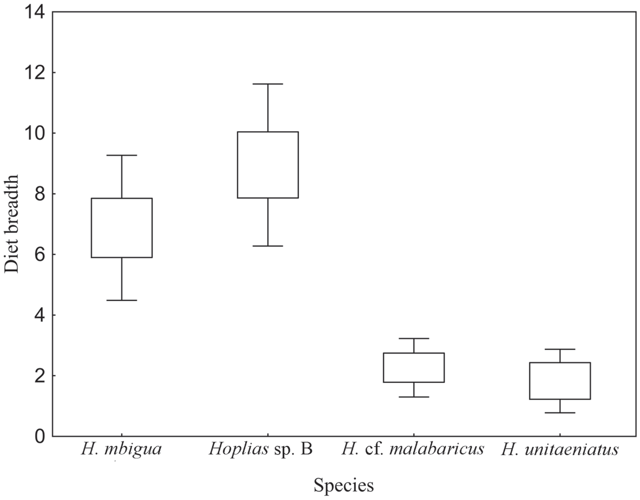

Fig. 2. Mean variation (vertical lines) in diet breadth (boxes) from non-native (*H. mbigua* and *H. unitaeniatus*) and native (*Hoplias* sp. B and *H.* cf. *malabaricus*) Erythrinidae species in the upper Paraná River floodplain based on 36 food categories.

Tab. 4. Diet composition (in volume percentage - %V) of non-native (*H. mbigua* and *H. unitaeniatus*) and native (*Hoplias* sp. B and *H.* cf. *malabaricus*) Erythrinidae species in the upper Paraná River floodplain. Bold values indicate the food resources with the highest %V for each species. ne=number of empty stomachs (excluded from the analyses). na=number of analyzed stomachs. *Minimum and maximum size of analyzed individuals (mm).

Food Resources	non-native		native	
	H. unitaeniatus	*H. mbigua*	*Hoplias* sp. B	*H.* cf. *malabaricus*
	*162 - 215	*142 - 379	*153 - 380	*170 - 385
	(ne=343 na=23)	(ne=1341 na=146)	(ne=1371 na=134)	(ne=473 na=35)
Acestrorhynchus lacustris	-	0.086	0.016	-
Astyanax spp.	-	0.023	0.009	0.021
Bryconamericus spp.	-	0.002	-	-
Cichla kelberi	-	0.065	0.095	-
Cichlasoma paranaense	-	-	0.042	-
Eigenmannia trilineata	-	0.010	0.006	0.004
Geophagus cf. *proximus*	-	0.028	0.021	-
Gymnotus spp.	0.119	0.015	0.036	**0.239**
Hemiodus orthonops	-	0.016	-	-
Hemisorubim platyrhynchos	-	-	0.044	-
Hoplerythrinus unitaeniatus	-	-	0.011	-
Hoplias spp.	-	**0.319**	**0.179**	**0.170**
Hoplosternum littorale	-	0.020	**0.170**	-
Hyphessobrycon eques	-	0.001	0.001	-
Hypostomus spp.	-	-	0.013	0.001
Laetacara araguaiae	-	-	-	-
Leporinus spp.	-	0.056	0.086	**0.277**
Loricariichthys spp.	-	-	0.006	0.119
Moenkhausia spp.	0.018	0.006	0.014	-
Oxydoras eigenmanni	-	0.004	0.019	0.013
Parauchenipterus galeatus	-	-	0.024	-
Pimelodella spp.	-	-	0.002	-
Pimelodus spp.	-	**0.157**	0.039	0.081
Plagioscion squamosissimus	-	-	0.048	-
Porotergus ellisi	-	-	-	0.013
Psellogrammus kennedyi	-	-	0.011	-
Rhamphichthys hahni	-	0.013	0.018	-
Roeboides descalvadensis	-	0.016	0.019	-
Satanoperca pappaterra	-	0.018	-	-
Schizodon borellii	-	0.003	0.028	-
Serrapinus spp.	0.006	0.005	0.019	0.001
Serrasalmus marginatus	-	0.088	0.004	-
Steindachnerina spp.	-	0.032	-	-
Decapoda	0.101	0.010	0.003	0.002
Insects	**0.555**	0.001	-	0.001
Plants	0.202	0.006	0.017	0.059

Tab. 5. PERMANOVA (t - *pairwise* comparison) post hoc test results applied to species diet and Pianka's niche overlap (*O*) between non-native (*H. mbigua* and *H. unitaeniatus*) and native (*Hoplias* sp. B and *H.* cf. *malabaricus*) Erythrinidae species in the upper Paraná River floodplain. *Considered significant.

Species Pairs	Permanova		Niche Overlap	
	t	p	*O*	p
H. mbigua x Hoplias sp. B	1.22	0.012	0.69	<0.001
H. mbigua x H. cf. *malabaricus*	1.2	0.015	0.51	<0.002
H. mbigua x H. unitaeniatus	1.79	0.001	0.02	<0.003
Hoplias sp. B x *H.* cf. *malabaricus*	1.14	0.05*	0.52	<0.004
Hoplias sp. B x *H. unitaeniatus*	1.71	0.001	0.05	<0.005
H. cf. *malabaricus* x *H. unitaeniatus*	1.31	0.028	0.15	<0.006

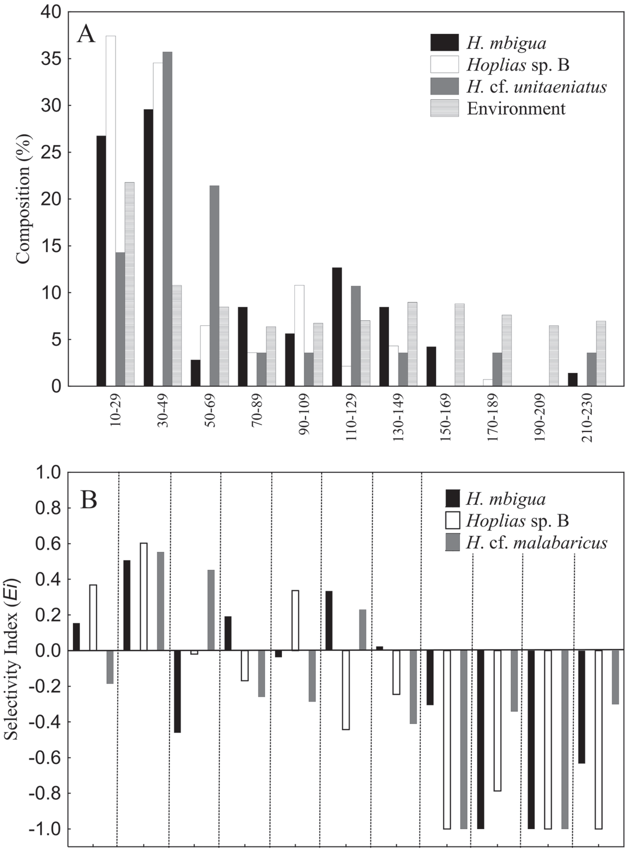

Fig. 3. A- Relative composition of prey species sizes in the diets of non-native (*H. mbigua*) and native (*Hoplias* sp. B and *H.* cf. *malabaricus*) Erythrinidae species in the upper Paraná River floodplain and relative abundance in the environment during the sampling period in the upper Paraná River floodplain. B - Feeding selectivity (E_i) of *H. mbigua* (non-native), *Hoplias* sp. B and *H.* cf. *malabaricus* (native) for different prey size classes (mm). The non-native *H. unitaeniatus* is not present due to the low representation of fish in its diet.

Discussion

Comparing with other species of the fish assemblage, the Erythrinidae species presents a similar morphology and ecological aspects due to phylogenetic conservatism (Gross *et al.,* 2013). In this sense, non-native species should present adaptations that enable their establishment through niche segregation and/or environmental filtering, as they would have to survive under different abiotic conditions and interspecific interactions. Analyzing at a fine scale, the native and non-native species could be discriminated to a certain level based on morphological traits. This was observed in the native species (*Hoplias* sp. B and *H.* cf. *malabaricus*), as they presented similar morphologies, highlighted by the overlapping scores observed in the PCA, while the two non-native species (*H. unitaeniatus* and *H. mbigua*) presented morphologies that were distinct from each other and from the native species. Considering *H. unitaeniatus*, the morphological differences might lead to niche differentiation, and they should be more important for the coexistence of natives and this introduced species than environmental filtering, especially when considering that all native species presented significant differences in spatial distribution patterns and in their diets compared with such species. The segregation pattern observed allows for the occupation of different microhabitats among these species. This suggests that, at different levels, the species do not occupy the same microhabitat, a fact that would decrease any potential competition that could exclude any of them. The only exception was in the Paraná system, but this could be attributed to the fact that this is the system with the lowest abundances of fish (Fernandes *et al.,* 2009), decreasing any potential competition even further.

Considering diets, the non-native *H. unitaeniatus* presented a narrow niche breadth, with a diet dominated by insects (mainly Ephemeroptera) and small contributions of fish, and showed extremely low values of diet overlap with the native species. The low participation of fish in the diet of this species, allowing it to be classified as insectivorous, goes against previous observations of this species that classified it as a piscivore in the same studied area (Hahn *et al.,* 2002). The low niche overlap is one of the mechanisms facilitating coexistence among this non-native species and the native Erythrinidae, as it suggests reduced competition if spatial and feeding resources were limited. Increased ecological interactions with native species could lead to such temporal differences; however, any explanations on this subject would be based on speculation, and further studies are needed to draw more consistent conclusions. Nevertheless, the low captures of *H. unitaeniatus* must be noted, as this was the species with the lowest number of captures during the study period (326 individuals).

The non-native species *H. mbigua* was distinguished from the native species by the width and height of the head. The higher values presented by the native species are an indication that they are able to ingest larger prey than the non-native *H. mbigua*. Still, the native species presented a greater dorsal area and lower eyes than the non-native *H. mbigua*, implying that the native species occupy more benthic positions in the water column. The differences in the diets of the native species (*Hoplias* sp. B and *H.* cf. *malabaricus*) compared to the non-native *H. mbigua* can be explained spatially. Despite their segregated occurrences, when occurring in the same microhabitat, differences in ecomorphological attributes suggest different foraging locations. The fact that the native species have similar morphologies but different diets suggests that dietary differences between these species are caused by other factors besides morphology. The preference for smaller prey might be associated with gape size, prey handling time, risk of predation, and energy gain (Nilsson, Bronmark, 2000). Moreover, larger prey species possess greater escape capacities and are more difficult to handle than smaller prey (Baras *et al.,* 2010). This distinction in prey size preference among these species may occur to reduce potential competition caused mainly, but not exclusively, by morphological similarities.

Even with differences in diet composition with the native species, the non-native *H. mbigua*, presented higher values of diet overlap with the native species. This degree of overlap might be related to the opportunistic behavior of these species, given their capacity to change their diet composition according to prey availability or due to biotic interactions, such as competition and predation (Pompeu, Godinho, 2001; Carvalho *et al.,* 2002). In fact, *H. mbigua*, as other species of *Hoplias*, presented high feeding plasticity, defined by a varied diet composed of crustaceans, insects, and plants, in addition to a frog (*Trachycephalus typhonius* - Strictar-Pereira, Oda, 2012). Additionally, *H. mbigua* was morphologically distinct in terms of attributes related to swimming and feeding, such as having a larger area of the dorsal fin, which allows this species to achieve higher speeds and perform more stable movements (Gosline, 1971) than the native species (*Hoplias* sp. B and *H.* cf. *malabaricus*). This fact is reflected in its diet, as this was the only species to consume individuals of *Serrasalmus marginatus* and *Acestrorhynchus lacustris*, species that present high swimming capacity (Breda *et al.,* 2005; Teixeira, Bennemann, 2007), considering that both species are predators that capture their prey through active swimming. *Hoplias* species are sedentary, territorial, and solitary predators, inhabiting macrophyte-covered areas and using ambush feeding strategies (Almeida *et al.,* 1997; Luz-Agostinho *et al.,* 2008; Petry *et al.,* 2010). The great participation of congeneric species (*Hoplias* spp.) in the *H. mbigua* diet may be related to this high degree of territorialism; this species presented a large overlap with the native species, and the consumption of congeneric species is noted as a possible mechanism that could facilitate its establishment in the floodplain (Strictar-Pereira *et al.,* 2015). In addition to the tendency for competition, due to their morphological similarities, the two species possess similar abundances in the floodplain, with the presence of the non-native species not eliminating or even reducing the abundance of the native species (Hauser, Benedito, 2012).

Considering only the limiting similarity theory and the environmental filtering hypothesis, it can be concluded that different mechanisms act in mediating the coexistence of native and non-native Erythrinidae species. For non-native *H. unitaeniatus*, which presented an extremely different diet and morphology from the native species, niche partitioning (limiting similarity) seems to be the major mechanism mediating species coexistence. On the other hand, for the non-native *H. mbigua*, which presented similar morphology to that of the native species, environmental filtering seems to be mediating the coexistence among species. These observations emphasize that different mechanisms can be acting in allowing species establishment, persistence and interactions with native species, even for closely related species and similar periods of introduction. This highlights that species introductions are unpredictable, as several simultaneous factors can be acting in mediating species establishment and interactions with other species.

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