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Resource partitioning among freshwater congeneric fishes (Loricariidae: *Hypostomus*): trophic, spatial, and temporal dimensions

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ABSTRACT

Resource partitioning is essential for coexistence of phylogenetically related species in altered environments, where changes in biotopes can limit resources and change ecological strategies. We investigated resource partitioning between two congeneric catfishes (*Hypostomus affinis* and *H. luetkeni*) in three niche dimensions (trophic, spatial, and temporal) in a Neotropical reservoir. We tested the hypothesis that the use of different mesohabitats (spatial dimension) is more relevant for the coexistence of species, and that morphological differences between the species confer different advantages in the mesohabitats occupation. We evaluated species morphology, diet composition and abundance along a spatial-temporal gradient. A high dietary overlap and a low temporal variability in species abundance were found, indicating that these two dimensions play a minor role in the species distribution. However, a strong spatial segregation modulated apparently by morphological differences was observed. *Hypostomus luetkeni* has a larger oral disk area, and a flatter body that confer advantages in the occupation of lotics habitats, whereas *H. affinis* has relatively larger fins that provide more efficient displacements in lentic habitats. Spatial partitioning was the main driver modulating mechanism for the coexistence of these species and differences in the occupation of the mesohabitats probably have been amplified in this altered environment.

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Introduction


The term ‘resource partitioning’ was introduced in the 1960s to designate how species differ in the use of resources (Toft 1985; Ross 1986). For fish, these differences are commonly summarized in three main dimensions: (i) food, with species consuming different foods or prey (e.g. Lujan et al. 2011; Nascimento et al. 2020; Galindo et al. 2021), (ii) space, where species use different areas to forage or hunt (e.g. Leitão et al. 2015; Westrelin et al. 2021) and (iii) time, where sympatric species rotate peak foraging times (Ventura et al. 2014; Lear et al. 2021), or change co-occurrence patterns on a diel or seasonal scale (e.g. Echevarría & Rodríguez 2017). Resource partitioning is related to coexistence because interspecific differences in the use of resources (e.g. food, space) decrease the competition from potential competitors, and thus can promote the maintenance of diversity (Walter 1991).

Among phylogenetically related species (i.e. family or genus level) that exhibit similar functional traits, the partitioning of resources is relatively common (e.g. Manna et al. 2020; Galindo et al. 2021), but not a rule (e.g. Syafei et al. 2020). Until recently, it was accepted that the strength of

interspecific competition was driven by phylogenetic relatedness, with closely related species competing more strongly than distantly related species. However, Mahon et al. (2021) in a recent meta-analysis study to investigate the role of phylogenetic relatedness and functional similarity on interspecific competition concluded that functional similarity, not phylogenetic relatedness, predicts the relative strength of competition.

In environments where resources are limited and competition is potentially high, resource partitioning is essential for species coexistence (Schoener 1974). Many studies have indicated the importance of interspecific resource segregation for the maintenance of populations (e.g. Leitão et al. 2015; Manna et al. 2020). Resource segregation also occurs at the intraspecific level, with individuals of the same species consuming different resources, or using different habitats, and being exposed to different predators and parasites (Bolnick et al. 2003). In theory, the increase in intraspecific competition forces a species to expand its niche, while the increase in interspecific competition forces it to reduce it (Connell 1983).

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Loricariidae is one of the most speciose fish families in the Neotropical region (Nelson et al. 2016), with *Hypostomus* being one of its genera with the largest number of species (149 species) and most widely distributed (Weber 2003; Silva et al. 2016; Queiroz et al. 2020). These armored catfish have an essentially benthic habit and are usually found in environments with fast or slow flows, associated with stony and/or sandy bottoms in both deep river channels and/or in small streams (Weber 2003; Casatti et al. 2005; Villares-Junior et al. 2016). *Hypostomus* usually occur in sympatry in environments where more than one species of Loricariidae is present; however, spatial (Casatti et al. 2005; Manna et al. 2020) and food (Delariva & Agostinho 2001; Abilhoa et al. 2016) partitioning have already been reported. In the Guandu and Paraíba do Sul river basins (Southeast Brazil) the occurrence of two species of *Hypostomus* is recognized. *Hypostomus luetkeni* (Steindachner, 1877) (named *H. auroguttatus* in previous studies, e.g. Gomes et al. 2015) and *H. affinis* (Steindachner, 1877) occur in sympatry in natural environments, but exhibit different habitat preferences (Mazzoni et al. 1994). *Hypostomus luetkeni* has preference to lotic sections with rocky substrate, whereas *H. affinis* occupies a broader niche, being present in both lentic and/or rapid sections, on rocky and/or sandy-rocky bottoms (Mazzoni et al. 1994; Gomes et al. 2015).

In altered environments, such as reservoirs, lotic stretches with rocky substrate are suppressed after the water level rises (Agostinho et al. 2016), and other preserved habitats are usually restricted upstream of the reservoir. The fragmentation of a river by a dam causes, among other effects, losses of physical complexity, changes in the physical-chemical conditions, anoxia in the lower strata of the water column, and, also, impairment of free migration of aquatic organisms (Agostinho et al. 2016). In such a situation, many benthic armored catfish specialized in rapids and rocky substrate can be excised locally (Less et al. 2016), and in the remaining preserved habitats, normally located in the upper zones of the reservoirs, may occur intense competition for space and other resources. Edds et al. (2002) raised fundamental questions: If two closely related species used substantially different resources in the natural (pre-impoundment) environment, would their resource use remain different in the artificially created habitat, or might they converge to a common niche within the new system?

Responses to environmental changes in an impacted basin vary between congeneric *Hypostomus*, with certain species associated with structurally complex and well-preserved environments, whereas others show tolerance to the impacted environments (Silveira et al.

2018). Garavello and Garavello (2004) suggest that *Hypostomus* spp. could benefit from the environmental changes caused by the construction of dams. Their main argument is that the reservoirs decant the organic matter and release clean and clear waters downstream that would then favor the penetration of light and proliferation of algae and peripheral vegetation, which would then be exploited by these species. Santos et al. (2020) present an antagonistic, but not exclusive view, arguing that reservoirs, especially those built in cascades, impair the abundance of detritivorous species due to the loss of nutritional quality resulting from the high sedimentation of nutrients and organic matter. Thus, species of the same genus may respond differently to the damming process and those that previously occurred in sympatry in a natural environment, may tend to be segregated and to rearrange interspecific relationships in a scenario where food and space are limited.

The present study investigated the use of resources at spatial, temporal, and trophic dimensions by two congeneric armored catfish (*H. affinis* and *H. luetkeni*) in an ancient reservoir to detect possible interspecific resource overlapping or partitioning. Our hypothesis was that the use of different mesohabitats (spatial dimension) is more relevant for the coexistence of species, and that morphological differences would confer different advantages in the occupation of mesohabitats. In addition, we expect *H. affinis* to show higher abundance due to its greater reproductive investment (Mazzoni & Caramaschi 1995) and more ability to use lentic habitats (Gomes et al. 2015) compared to *H. luetkeni*.

Materials and methods

Study area

The Lajes Reservoir (Figure 1; 22°42'–22°50'S; 43°53'–44°32'W), State of Rio de Janeiro, Brazil, was formed between 1905 and 1907 and is one of the oldest reservoirs designed for the primary purpose of generating electricity in Brazil (Araújo et al. 2021). The mean inflow of water is 13.7 m³/s⁻¹ of which most of the flow (8.3 m³/s⁻¹) is received by transposition from an inter-basin diversion (From the Paraíba do Sul River basin). Lentic conditions predominate in the longitudinal extent of the reservoir, because of the low connectivity with natural tributaries and the dendritic reservoir morphology, associated to a high retention time (Guedes et al. 2020). The shoreline presents dense vegetation cover of the Atlantic Forest biome in different stages of ecological succession. Water transparency

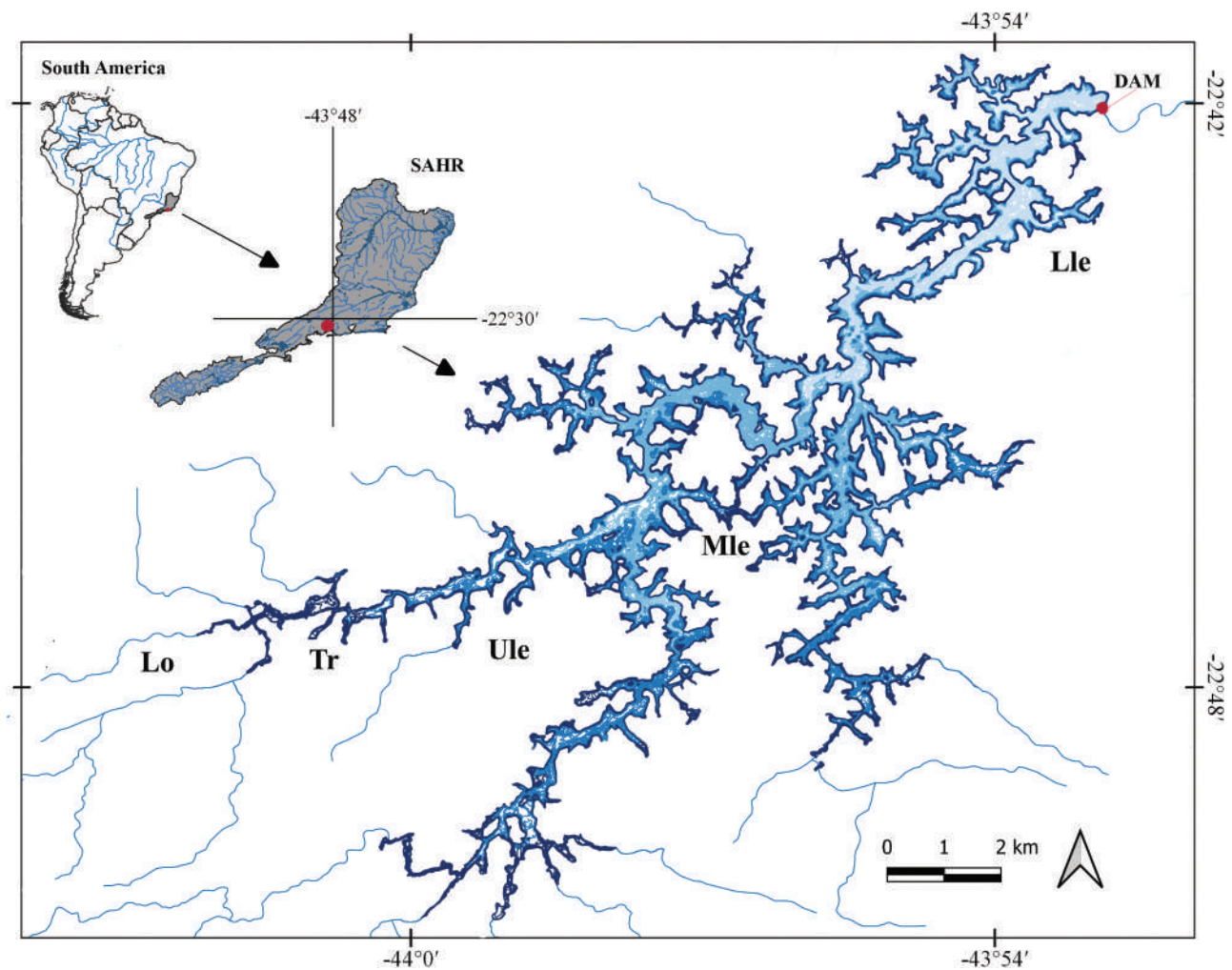


Figure 1. Map of the Lajes Reservoir with indication of the drainage basin and the geographical position in the Southeast Atlantic Hydrographic Region. Longitudinal reservoir zones (Lo, lotic; Tr, transition; Ule, upper lentic; Mle, middle lentic; Lle, lower lentic).

is high and oligo-mesotrophic conditions predominate (Klippel et al. 2020). The climate is seasonal tropical with dry winters and wet summers (Aw), according to the Köppen-Geiger classification.

Fish sampling

Species abundance was registered during monthly standardized samplings, carried out between August 2015 and July 2018 in five longitudinal zones (lotic, transition, upper lentic, middle lentic, lower lentic). Six gill nets (35 × 2.8 m; mesh of 15–110 mm between adjacent knots) were set near the margins at dusk and retrieved the next morning. The sampling unit was defined as the number of individuals collected per 590 m²/14 hours, totaling 180 samples (5 zones × 3 years × 2 seasons × 6 months). The dry season comprises the period between April and September, whereas the rainy season corresponds to the period between October and March. Fish caught alive had the total length (TL)

measured and then were returned alive to the reservoir. Fish caught dead in the gill nets were fixed in 10% formalin, preserved in 70% ethanol and taken to the laboratory for further analysis of diet and morphometry.

Habitat sampling

Water temperature (°C), dissolved oxygen (mg/L) and turbidity (NTU) were measured using a Horiba U-52G multiprobe (Japan. Horiba Ltd.). Depth was measured using a centimeter accurate digital probe (Speedtech model SM-5). The flow (m × s⁻¹) was obtained from a local fluviometric station of the electricity company LIGHT (Code LIGHT-59306000). To qualify and quantify the habitat, underwater videos (~ 20 minutes) recorded on a 200 m² (50 × 4 m) transect area from the shore to the reservoir bed were taken. The videos were made with a small remote operated vehicle (ROV) model Titan Genneino (Shenzen, China) is capable of

operating to a depth of 150 meters and is equipped with a camera attached (1/2.5 inches SONY CMOS, 4k resolution, FOV 160°), operating at a speed of ~0.25 m/s and angled filming of 30° toward the bed. From the videos, the coverage of each item of substrate type (% of rocks, clay, sand, twig,) and aquatic macrophytes was estimated, using a rating protocol of 0–4 corresponding to coverage area: 0 = no coverage (0 m²); 1 = low coverage (1–60 m²); 2 = moderate coverage (60.5–120 m²); 3 = high coverage (120.5–180 m²); 4 = complete coverage (200 m²). The water physico-chemical variables and habitat descriptors were measured in the same places where the fish were sampled, prior to the placement of the gillnets.

Morphometry and diet

The morphometry of *H. affinis* (Figure 2A) and *H. luetkeni* (Figure 2B) was evaluated with 13 morphological measurements taken with a digital caliper to the nearest 0.01 mm, using 25 individuals of each species

(Table S1 and Figure S1 in the Supplementary Information). These measures were converted into seven ecomorphological indices (Table S2), which also remove allometric effects (Manna et al. 2020), and are related to the species hydrodynamics, feeding, locomotion and fixation capacity (Gatz 1979; Garavello & Garavello 2004; Leitão et al. 2015).

The diet was analyzed by examination of the contents of the anterior part of the intestine. We removed 1 cm of the first portion of the digestive tract of 10 adult individuals (total length ranging between 26 and 32.5 cm for *H. affinis*; and 22–26.7 cm for *H. luetkeni*) of each species, randomly selected from sampled locations and months. Food items were visualized using an inverted tri-ocular microscope (Model Motic AE31E, at 100x), identified to level of phylum and class (Bicudo & Bicudo 1970). Numerical quantification and frequency of occurrence of the food items (Hyslop 1980), was performed using a Sedgewick-Rafter (SRcc) counting camera. Because the similarity and small size of the food items typical of detritivorous species (Mazzoni



Figure 2. Lateral, dorsal and ventral views of *Hypostomus affinis* (a) and *Hypostomus luetkeni* (b) caught in the Lajes Reservoir, Rio de Janeiro State, Brazil.

et al. 2010; Abilhoa et al. 2016), we chose to arbitrarily analyze 10 fields of 1 mm² to perform the identification and counting of the food items (SRcc).

Data analyses

A two-way ANOVA on aligned ranks transformation (ANOVA ART; function `art` in the `ARTool` package; Kay & Wobbrock 2020) was used for spatial and temporal comparisons and verifying whether species overlap or segregate in spatial (lotic, transition, upper lentic, middle lentic, lower lentic) and/or temporal (seasons: dry and rainy) dimensions. When significant differences were detected, an *a posteriori* Tukey HSD was conducted at the 0.01 confidence level. Fish can exhibit co-occurrence patterns aggregated or segregated according to seasons (e.g. Echevarría & Rodríguez 2017), and therefore, spatiotemporal interactions in species abundance were used in this study as a proxy for temporal partitioning.

The trophic dimension was evaluated using the Feeding Overlap Index (O_{jk}, Pianka 1973). This index was used to assess the diet similarity between the food items of the two species (j,k), according to the following equation: $O_{jk} = \sum p_{ij}p_{ik} / (\sum p_{ij}^2 + \sum p_{ik}^2)^{1/2}$

where p_{ij} = is the numerical percentage of food item i in the species j ; p_{ik} = is the numerical percentage of food item i in the species k . Values range from 0 to 1, with $O_{jk} > 0.6$ indicating high overlap in the diet, 0.4–0.6, intermediate, and < 0.4 , low overlap (Grossman 1986). In addition, differences in diet between species were tested with a permutational multivariate analysis of variance (PERMANOVA). For this analysis, the diet data were previously transformed (square root) and a triangular matrix was constructed using the Euclidean distance. PERMANOVA was applied using the square sum of Type III (partial) with 9999 permutations to calculate the p values.

Principal Component Analysis (PCA) were used separately to (i) identify the main environmental variables (habitat + physicochemical) related to species distribution, and (ii) the main indices related to interspecific morphological variation. Because data have different units of measurements, they were normalized (Legendre & Legendre 2012), i.e. they became dimensionless by subtracting the raw data from the mean and dividing by units of standard deviation, before submit to PCA. The variables with great explanatory power (coefficients > 0.4) were selected in each PCA. Environmental variables and morphological indices with correlations ≥ 0.7 were identified using draftsman's plots, and the covariate with the lowest correlation with the first PCA axis was excluded from the final

analysis (Leathwick et al. 2006). The environmental and morphological variables selected by the PCA were integrated into a redundancy analysis based on a Euclidean distance matrix (dbRDA). The dbRDA was used to assess the importance of ecomorphological indices and environmental variables (predictor variables) on the fish abundance data, which is a proxy of choice of habitat (response variables). Pearson correlations (> 0.4) with the first two dbRDA axes were examined to identify the strength and direction of the morphologic-environmental relationship between congeneric species (Anderson et al. 2008). Multivariate analyses were performed with PRIMER-E v.6.1.13 & PERMANOVA+ 1.0.3 (www.primers-e.com; Anderson et al. 2008), and ANOVA ART was conducted in R environment (R Core Team 2020).

Results

Spatial and temporal dimensions

A total of 1092 individuals were collected, being 941 (% $N = 86.1$) specimens of *H. luetkeni* and 151 (% $N = 13.9$) of *H. affinis*. Strong spatial species segregation was observed among the longitudinal zones (Tables 1 and S3). *Hypostomus affinis* occurred in all longitudinal zones always in low densities (Table S3). Significant differences in the abundance of *H. affinis* occurred between the zones (ANOVA ART, $F = 6.28$; $p < 0.001$; Table 1), with pairwise comparisons showing the highest abundances in the middle lentic and the lowest in the lotic zone (Tukey HSD, $F = -4.62$; $p < 0.001$; Table 1). On the other hand, *H. luetkeni* only occurred in the upper zones of the reservoir (lotic, transition and upper lentic), with high densities only in the lotic zone (Table S3). Significant spatial changes in the abundance of *H. luetkeni* (ANOVA ART, $F = 151.1$;

Table 1. Results of two-way ANOVA on aligned ranks transformation (Anova ART) comparing abundance of *H. affinis* and *H. luetkeni* between the longitudinal zones and seasons. *** $p < 0.001$; ** $p < 0.01$.

Source	Zone	Season	Zone × Season
<i>H. affinis</i>	6.28***	4.22	0.77
<i>H. luetkeni</i>	151.1***	1.52	2.04
Tukey HSD		<i>H. affinis</i>	<i>H. luetkeni</i>
Lotic × Lower lentic		-3.08	20.9***
Lotic × Middle lentic		-4.62***	20.9***
Lotic × Transition		-1.4	19.1***
Lotic × Upper lentic		-2.28	20.0***
Lower lentic × Middle lentic		-1.67	0
Lower lentic × Transition		1.81	-2.04
Lower lentic × Upper lentic		0.87	-1.01
Middle lentic × Transition		3.48**	-2.05
Middle lentic × Upper lentic		2.54	-1.01
Transition × Upper lentic		-0.94	1.03

$p < 0.001$; Table 1) were detected in paired comparisons between the lotic and the other zones (Table 1).

In relation to the temporal dimension, no significant differences in fish abundance were observed between the dry and rainy periods (*H. affinis*, $F = 4.22$, $p = 0.15$; *H. luetkeni*, $F = 1.52$, $p = 0.37$).

Diet

The diet analysis indicated the presence of 12 food items (Table S4), with greater relative abundance of Chlorophyceae for *H. affinis*, and of Bacillariophyceae for *H. luetkeni*. Both species showed a high frequency of occurrence (>50%) of inorganic sediments, which came across with the diet. No significant differences were found in the food matrix between the two species according to PERMANOVA (Pseudo- $F = 2.07$; $p = 0.07$). Regardless of the neglected differences in rare food items, the Pianka overlap index indicated high similarity in the diet between the two species (0.79).

Ecomorphology

The first two axes of the PCA explained 66.8% of the total variance in species morphology (Table S5 and Figure 3A). The first axis (PC1 = 36.6% of variance

total) showed differences in the relative sizes of the pectoral (RSPF), pelvic (RSPEF) and caudal (RSCF) fins between the two species, with larger fins to *H. affinis*. The second axis (PC2 = 30.2%) was positively associated with CI and ITS and negatively with RSOD, relating *H. luetkeni* to a larger oral disc area, and *H. affinis* to greater lateral compression (Figure 3A). Three of the seven initial morphometric indices met the criteria (i.e. correlation >0.4; covariance <0.7; Table S5) and were selected for distance-based redundancy analysis (dbRDA).

Environmental conditions

The first two axes of the environmental PCA explained 57.1% of the total variance in the species distribution (Table S6 and Figure 3B). The first axis (44.4%) associated *H. luetkeni* with habitats with greater coverage of rocks and comparatively higher flow, whereas *H. affinis* was associated with clay substrate and low flow. The second axis (PC2 = 12.7%) was related to local environmental variations in dissolved oxygen and turbidity (Figure 3B). Four of the nine initial environmental variables met the criteria (i.e. correlation >0.4; covariance <0.7; Table S6) and were selected for the integrated morphology-habitat model (dbRDA).

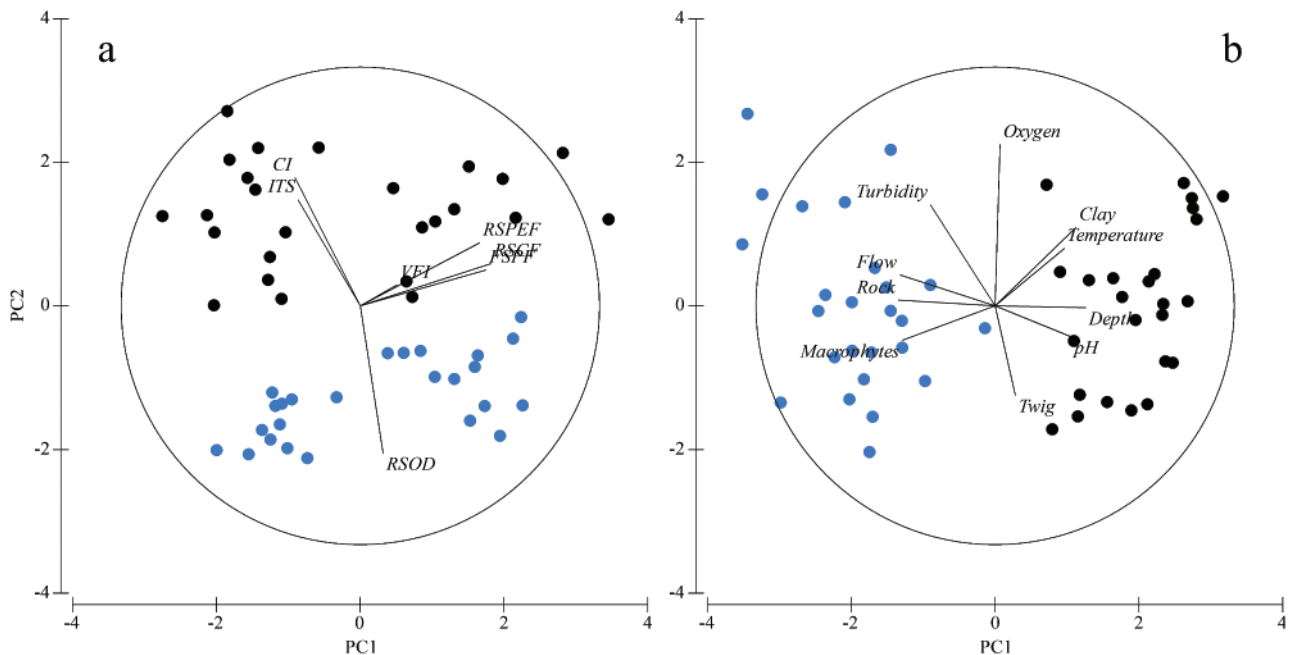


Figure 3. Scatterplot diagram of the first two axes scores from Principal Component Analysis on ecomorphological indices (a) and environmental variables (b) with samples representing *Hypostomus affinis* (black circles) and *Hypostomus luetkeni* (blue circles). RSPF = Relative size of pectoral fin; RSPEF = Relative size of pelvic fin; RSCF = Relative size of the caudal fin; RSOD = Relative size of oral disc; CI = Compression index; VFI = Ventral flattening index; ITS = Index of trunk shape.

Morphology–habitat relationship

A total of 34.5% of the variation in the morphological data was explained by the environmental variables according to the first two axes of dbRDA (Figure 4). The first dbRDA axis (33.3% of total variation) represents the interspecific differences, being positively correlated to the lateral compression index (CI, Pearson correlation (r) = 0.85) and habitats with lesser rock cover and flow, characteristics associated with *H. affinis* (Table 2). On the other hand, *H. luetkeni* was negatively correlated to RDA1, with a strong association with a larger oral disc area (RSOD, r = -0.97), and habitats with rocky substrate (r = -0.91) and comparatively higher flow (r = -0.74). Only 1.2% of the data variation was explained by the second dbRDA

Table 2. Pearson's correlation of habitat-related and ecomorphological indices with the first two axes of dbRDA for the two congeneric species of *Hypostomus* in the Lajes Reservoir. Highly significant correlations in bold.

	Correlation	
	RDA1	RDA2
<i>Environmental</i>		
Rocks	-0.81	-0.10
Flow	-0.74	0.08
Turbidity	-0.33	0.05
Dissolved oxygen	-0.02	0.16
<i>Morphometric indices</i>		
RSCF	-0.09	-0.99
RSOD	-0.97	0.03
CI	0.85	0.27

axis, indicating interspecific differences in the size of the caudal fin (RSCF, r = -0.99 ; Table 2), being greater in *H. affinis*.

Discussion

This study shows a high temporal and trophic overlap, and strong spatial segregation among the two congeneric fish species (Loricariidae: *Hypostomus*), corroborating the main hypothesis. The distribution of *H. affinis* and *H. luetkeni* in the Lajes Reservoir is linked to strong spatial segregation that occurs between the mesohabitats and that does not change over seasons (dry/rainy). *Hypostomus luetkeni* occurred in high abundance only in the lotic zone, associated with mesohabitats with rocky substrate and more hydrodynamic environmental conditions. On the other hand, *H. affinis* always occurred in comparatively lower densities in all mesohabitats, with a greater predominance of unconsolidated substrate (clay). This pattern indicates that the distribution of species in the reservoir reflects in the differentiated use of the mesohabitats and may be modulated by differences in ecomorphological characteristics and environmental tolerances.

Ecomorphological analyzes indicated interspecific differences in fitness and performance optimization in the different mesohabitats. *Hypostomus luetkeni* presents a more depressed lateral body, which guarantees greater ability to stay in position in hydrodynamic

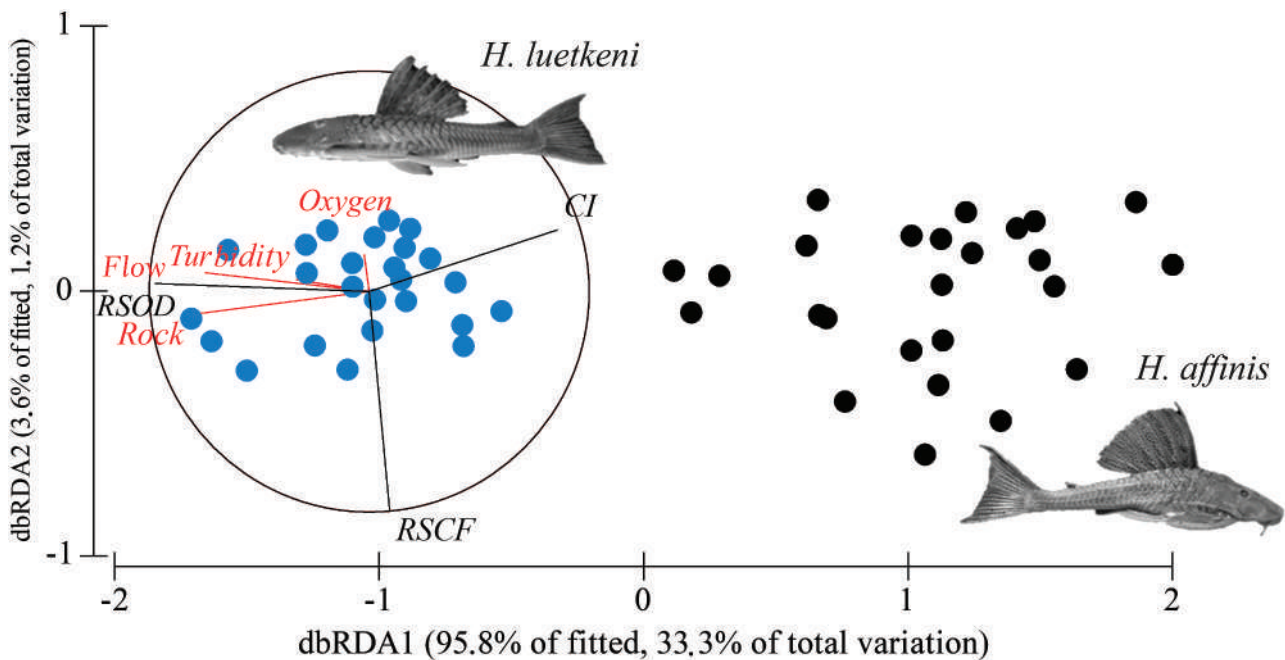


Figure 4. Scatterplot diagram of the two first axes from Distance-based Redundancy Analysis (dbRDA) on the selected environmental and ecomorphological variables of *Hypostomus affinis* (black circles) and *Hypostomus luetkeni* (blue circles). Codes for ecomorphological indices according to Figure 3.

environments (Garavello & Garavello 2004; Casatti et al. 2005), in addition to a larger relative oral disk area, which guarantees a better ability to fix to the substrate (Buck & Sazima 1995). On the other hand, *H. affinis* presents a comparatively higher lateral compression and a comparatively smaller oral disk area, characteristics that are better adapted to the lentic environment and less effective in fixing to the substrate. In addition, *H. affinis* has relatively larger fins that provide more efficient displacements and greater dispersion in the predominant lentic habitats.

Spatial segregation between these two species, however, is not a rule. Mazzoni et al. (1994) indicate that *H. affinis* and *H. luetkeni* occur in sympatry in rivers and streams, highlighting, however, a clear preference of *H. luetkeni* to lotic stretches with rocky substrate, whereas *H. affinis* have a wider spatial distribution occupying lentic or rapid sections, on rocky or sandy-rocky bottoms. The relative sympatric distribution in natural environments and the strong segregation observed in the Lajes Reservoir is an indication that the innate differences in ecomorphological characteristics and in environmental tolerances between these species could be determinant for spatial segregation as reported by Edds et al. (2002). Interspecific differences in resource use can result from interactive segregation, with one species limiting use of resources by another (Nilsson 1967). These differences could be accentuated in altered environments, such as reservoirs, where habitat availability may be more limited, and changes in biotopes may limit resources and lead to changes in species ecological strategies (Maddock et al. 2001; Amundsen et al. 2004; Santos et al. 2010; Pennock et al. 2021).

The abundance between species in the different mesohabitats was also contrasting and apparently counter-intuitive. *Hypostomus luetkeni* occurred in high abundance only in the lotic zone, while *H. affinis* always occurred in low densities in all mesohabitats. *Hypostomus affinis* and *H. luetkeni* had different strategies, with *H. affinis* maximizing reproduction investment to compensate high mortality maintaining a large non-specialized population, whereas *H. luetkeni* minimizes reproductive effort, maintaining small population and high physiological condition with a small mortality rate (Mazzoni & Caramaschi 1995). Gomes et al. (2015) reported that *H. auroguttatus* (= *H. luetkeni*) is predominant in the middle reaches of the Paraíba do Sul River but occurs in low abundance in reservoirs compared with the congeneric *H. affinis*. Carvalho and Araújo (2020) observed an increase in *H. affinis* densities after the construction of a small power plant dams for

hydroelectric purposes. In the Lajes Reservoir, the lentic zones occupy a large longitudinal extension reflecting the long retention time, dendritic reservoir morphology and the absence of large natural tributaries, while the flow and rocky substrate areas are spatially restricted (Guedes et al. 2020). Consequently, our expectations were that *H. affinis* would reach greater abundance due to the greater potential area of distribution in the reservoir, as suggested by Gomes et al. (2015) and for presenting a greater reproductive investment, as suggested Mazzoni and Caramaschi (1995).

A positive relationship between the distribution of a species and its abundance is one of the best-documented standards in ecology (Brown 1984; Borregaard & Rahbek 2010). The results of the present study, however, do not corroborate the expectation of positive relationship between distribution and abundance because *H. affinis* is widely distributed and occurs in densities much lower than *H. luetkeni* whose distribution is restricted to the lotic zone of the reservoir. The low abundance of *H. affinis* in the lentic areas of the Lajes Reservoir may be associated with the greater depths of the lentic areas and the anoxic conditions of the lower extracts of the water column, factors that limit the distribution of species without pre-adaptation to these stressful conditions (Fernando & Holčík 1991; Agostinho et al. 2007). In addition, *Hypostomus affinis* must face competition for space and food with *Loricariichthys castaneus* (Castelnau, 1855), another benthic Loricariidae species associated to lentic areas and tolerant to anoxic conditions, which is the most abundant fish species in the Lajes Reservoir (Ferreira et al. 2013; Guedes et al. 2020). Duarte et al. (2011) noted that *H. affinis* alters some reproductive tactics (e.g. decreasing the size of oocytes and increasing fecundity) to withstand low environmental complexity and succeed in the Lajes Reservoir. These tactics, however, do not seem to result in greater abundances, and it is therefore possible that the discrepancies between abundances between *H. affinis* and *H. luetkeni* are related (but not limited) to environmental factors.

Hypostomus affinis and *H. luetkeni* showed benthic habits with an essentially detritivorous/periphytic diet and a high food overlap. Distinct mesohabitats could suggest different diets; however, this has not been observed to *Hypostomus* congeneric species in the Atlantic streams by Casatti et al. (2005) and in the present study in the Lajes Reservoir. A high overlap of food niche and similarity in the diet were also observed in syntopic species of *Hypostomus* in natural environments, such as in the Atlantic Forest river

(Abilhoa et al. 2016; Villares-Junior et al. 2016) and in artificial environments, such as an Amazon reservoir (Oliveira & Isaac 2013). In general, species of *Hypostomus* forage banks of periphyton that grow on both consolidated and unconsolidated substrates, ingesting a large amount of inorganic material, debris and other unselected items together with organic matter that favor food overlap (Mazzoni et al. 2010; Abilhoa et al. 2016; Manna et al. 2020). Delariva and Agostinho (2001) indicated, however, that species of *Hypostomus* may also partition the food resources. The marked spatial segregation together with a high food overlap between the two species observed in this study suggest that the species select similar food items in the different mesohabitats, and the food resources were spatially dispersed in the environment.

The Lajes Reservoir is one of the oldest reservoirs built in South America, with more than 115 years of operation. The current scenario of the fish assemblage is relatively stable and reflects consolidated effects of environmental filters and apparently established ecological interactions (Guedes et al. 2020). In this landscape, the results of this study revealed a high temporal and trophic overlap, strong spatial segregation, morphological differences translated into different hydrodynamic aptitudes and marked and unexpected differences in the distribution and abundance of these two congeneric armored catfishes. The demonstration of the strength of interspecific competition for the observed patterns, however, requires further evidence and specific further studies. Finally, this study showed that spatial partitioning is a main modulating mechanism for the coexistence of these congeneric species of *Hypostomus*, and that innate differences in habitat occupation have been magnified in altered environments.

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Credit authorship contribution statement

D. L. P. Ferreira: Conceptualization, Investigation, Formal analysis, Writing - original draft; **G. H. S. Guedes and L.G. Silva:** Conceptualization, Investigation, Writing - original draft, Formal analysis; **F. G. Araújo:** Conceptualization, Writing - original draft.

Compliance with ethical standards


This study was authorized by the Ethics Council of Animal Use (CEUA/ICBS/UFRRJ) through Permission 12179 (CEUA 03/2017), and the Brazilian Environmental Agency (SISBIO/IBAMA/ICMBio- Permit no. 10707).

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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