A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 104: 179–201 (2025)
DOI: 10.3897/neobiota.104.167161

Research Article

The Small War: Trophic interactions between small-bodied non-native and native characoids in the marginal zones of Neotropical reservoirs

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Abstract

Small-bodied characoids represent a significant portion of Brazil's freshwater fish fauna, yet they remain understudied. In reservoirs, these species are highly abundant, colonise the marginal zone and are important in the aquatic food webs. In the lower Paranapanema River, the neighbouring reservoirs Rosana and Taquaruçu differ in their environmental conditions, but both host native and non-native characoids. This study describes the diet, feeding ecology and interactions of between co-existing native and non-native small-bodied characoids in both reservoirs, as well as their trophic responses to seasonal climatic variations (dry vs. wet season). Samples were collected quarterly between September 2018 and September 2020, with trawls, sieves and cast nets collecting fish in marginal zones and aquatic macrophyte beds. The stomach contents of 416 individuals from seven native and non-native characoids were analysed, with their prey classified into several food categories and resources. In the Rosana Reservoir, both native and non-native characoids were strongly reliant on allochthonous resources and their diet composition showed similar shifts between the wet and dry season. Conversely, in the Taquaruçu Reservoir, the characoids were more reliant on autochthonous resources and showed weak dietary shifts between seasons. Niche breadth and trophic overlap indices indicated diet specialisation and segregation in the characoids of the Rosana Reservoir, while, in Taquaruçu, they overlapped significantly, especially in the dry season. These results reveal considerable differences in the trophic interactions between native and non-native characoids in two Neotropical reservoirs, suggesting high context dependency in the ecological implications of introducing non-native species of these small-bodied fishes.

Key words: Biological invasion, damming, food resources, niche breadth, Paraná River, trophic ecology.

Academic editor: Josie South
Received: 30 July 2025
Accepted: 28 October 2025
Published: 24 November 2025

Citation: Ferraz JD, Casimiro ACR, Garcia DAZ, Vidotto-Magnoni AP, de Magalhães ALB, Tarkan AS, Britton JR, Orsi ML (2025) The Small War: Trophic interactions between small-bodied non-native and native characoids in the marginal zones of Neotropical reservoirs. NeoBiota 104: 179–201. https://doi.org/10.3897/neobiota.104.167161

Introduction

Brazil has numerous hydropower reservoirs, particularly in the southeast and south regions (Agostinho et al. 2016), often arranged in cascading sequences along major river systems (Garcia et al. 2018a). Over time, these artificial ecosystems have simplified fish communities taxonomically and functionally, leading to biotic homogenisation (Vitule et al. 2012; Daga et al. 2020; Ferraz et al. 2021a). Amongst the main drivers of these changes is the establishment and proliferation of non-native fish species, which often outcompete or displace native species, altering trophic dynamics and ecosystem functions (Pelicice and Agostinho 2006; Ganassin et al. 2021). While local environmental factors such as reservoir morphology, flow regime, water retention time and land use also shape fish assemblages (Nogueira et al. 2012; Ferrareze et al. 2014; Koushlesh et al. 2023), non-native species introductions remain one of the most pervasive ecological disturbances in Neotropical reservoirs (Vitule et al. 2012; Daga et al. 2020).

Small-bodied fish species make up the largest portion of the Brazilian ichthyofauna, yet they remain largely "invisible" to the public and are, therefore, highly threatened and poorly studied (Castro and Polaz 2020). Many of these species have adapted to reservoirs through specific reproductive strategies (e.g. short life cycles, high fecundity, non-migratory behaviour and extended spawning events) and plastic feeding habits, including generalist, omnivorous or opportunistic diets (Agostinho et al. 2016). While native small-bodied species are well adapted to fluctuating environmental conditions, non-native species with similar traits can successfully invade and establish populations, often leading to competition for food and habitat (Jarduli et al. 2021; Ferraz et al. 2024). Marginal zones, which provide critical shelter, spawning grounds and feeding areas (Casatti et al. 2003; Pelicice and Agostinho 2006), are particularly vulnerable to invasions. Habitat structure, such as macrophyte beds, driftwood and leaf-littered or rocky substrates, influences species co-existence and trophic interactions (Fonseca et al. 2022; Santiago et al. 2022). However, when non-native species exploit these habitats, they may displace native species, alter resource availability and disrupt natural feeding dynamics.

Although small-bodied species are generalists capable of colonising reservoirs (Agostinho et al. 2016), their diets are influenced by seasonal variations in prey availability (Quirino et al. 2015, 2017). Consequently, diet composition shift throughout the year (Neves et al. 2018; Fonseca et al. 2022; Santiago et al. 2022) is driven by environmental conditions and resource availability (Vidotto-Magnoni and Carvalho 2009; Bennemann et al. 2011). The presence of non-native species further complicates these dynamics by intensifying resource competition, forcing native species to broaden or specialise their dietary niches (Barros et al. 2017; Sánchez-Hernández et al. 2017). Understanding how non-native and native small-bodied fish interact in reservoir ecosystems is essential for predicting potential ecological consequences, particularly in regions facing increasing biological invasions.

The Paranapanema River, one of the main tributaries of the Upper Paraná River (Sampaio 1944), has been heavily fragmented by 11 cascading reservoirs (Garcia et al. 2018a). Its course is divided into three main sections: Upper, Middle and Lower Paranapanema (Sampaio 1944). The construction of the Rosana Reservoir (Lower stretch) in 1986 created a 190 km stretch with diverse habitats including marginal lagoons, forested margins and numerous tributaries. However, this stretch was further fragmented in 1991 by the Taquaruçu Dam (Casimiro et al. 2017). Although Rosana and Taquaruçu Reservoirs are part of the Paranapanema cascade (Garcia et al. 2018b) and share the same climatic conditions (Alvares et al. 2013; Terassi et al. 2018), their distinct habitat structures may lead to different fish community responses.

Rosana Reservoir features marginal lagoons with macrophytes beds and forested surroundings (Cassatti et al. 2003; Pelicice and Agostinho 2006) and receives inflow from important tributaries (Agostinho et al. 2007). These habitats provide abundant food resources for small-bodied fishes and are closely linked to seasonal variations, being strongly influenced by rainfall, flooding and temperature (Quirino et al. 2015; Fonseca et al. 2022; Santiago et al. 2022). In contrast, Taquaruçu Reservoir lacks marginal lagoons and forested margins and has few, human-impacted tributaries, offering fewer food resources for marginal-zone species even under seasonal wet-dry variation (Vidotto-Magnoni et al. 2015; Garcia et al. 2018b).

Given the increasing prevalence of non-native fish in Neotropical reservoirs, this study aims to: (i) examine the diet and feeding ecology of small-bodied species, with a focus on interactions between native and non-native species across reservoir and seasons (wet vs. dry) and (ii) compare feeding patterns to assess how habitat conditions influence trophic dynamics. We posit that: (i) in Rosana Reservoir, where habitat complexity and food resource availability are high, native species will display narrower dietary niches and lower overlap with non-native species, maintaining stronger seasonal responses in prey selection and (ii) in Taquaruçu Reservoir, where the habitat complexity is lower and resources are scarcer, both native and non-native species will exhibit broader dietary niches and higher diet overlap, with weaker seasonal variation in diet. By highlighting trophic interactions between native and non-native small-bodied fish, our study provides insight into the ecological consequences of species introductions in reservoir ecosystems and contributes to a better understanding of food web alterations in fragmented Neotropical rivers.

Materials and methods

Study area

The Paranapanema River rises in the Atlantic Plateau, in the Municipality of Capão Bonito, State of São Paulo (SP) (Sampaio 1944). As one of the main left-bank tributaries of the Upper Paraná River Basin, it flows for 930 km, with 330 km of its main channel forming the borders between south-eastern SP and northern Paraná (PR) (Maack 1981). The Lower Paranapanema River begins downstream of Salto Grande Falls, which is now submerged by the Salto Grande Reservoir. From there, it flows to a series of reservoirs, including Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu and Rosana (Duke Energy 2008). The last two reservoirs, the Taquaruçu and Rosana, are the focus of this study (Fig. 1).

The Rosana Hydroelectric Power Plant (Rosana Dam) is located between the municipalities of Diamante do Norte (PR) and Primavera (SP). The Reservoir operates as a run-of-river flow, with a length of 110 km, a maximum depth of 26 m and with a flooded area of 220 km^2 (Ferrareze et al. 2014). Its sinuous course closely resembles the original floodplain shape of the Upper Paraná River Basin, facilitating the formation of marginal lagoons along its surroundings (Agostinho et al. 2007). Submerged and floating macrophytes, including *Eichhornia* spp., *Elodea* sp., *Sagittaria* sp. and *Salvinia* sp., are widely distributed throughout the Reservoir (Casatti et al. 2003; Pelicice and Agostinho 2006). Two conservation units border the Reservoir: Morro do Diabo State

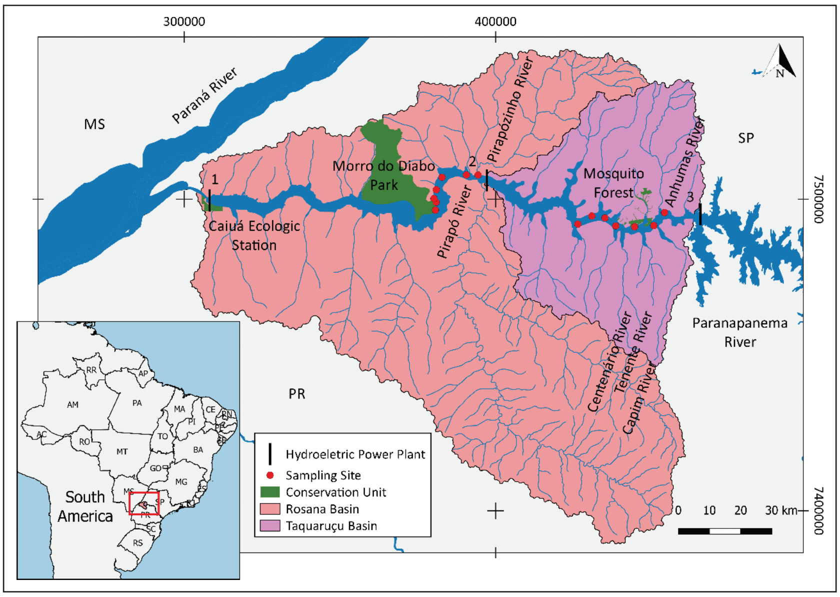

Figure 1. Sampling sites in the Rosana and Taquaruçu Reservoirs, lower Paranapanema River. Hydroelectric power plants: 1 = Rosana; 2 = Taquaruçu; 3 = Capivara. MS = State of Mato Grosso do Sul; PR = State of Paraná; SP = State of São Paulo.

Park (SP) on the right and the Caiuá Ecologic Station (PR) on the left. The Reservoir receives inflows from the Pirapó River (left bank), Pirapozinho River (right bank) and three main streams - Iancã, Cuiabá and Bonito - all on its right bank (Fig. 1).

The Escola Politécnica Hydroelectric Power Plant (Taquaruçu Dam) is located between the municipalities of Itaguajé (PR) and Sandovalina (SP). The Reservoir has a run-of-river system, with a length of 80 km, maximum depth of 18 m and a flooded area of 105.5 km^2 (Britto and Carvalho 2006). Unlike Rosana Reservoir, Taquaruçu follows a relatively straight course with minimal meandering, limiting the formation of marginal lagoons and reducing flooding potential. As a result, submerged macrophytes are sparse (Vidotto-Magnoni et al. 2015). The main tributaries of Taquaruçu Reservoir include the Capim, Centenário and Tenente Rivers on the left bank and the Anhumas River on the right bank, the latter being the only one to undergo a reforestation process (Mosquito Forest) (Leme et al. 2015) (Fig. 1). Despite this, most of the Reservoir's surroundings are dominated by agricultural and pasture land (Rodrigues et al. 2019), while its tributaries face multiple anthropogenic pressures, including riparian deforestation, urbanisation and the discharge of domestic and industrial effluents (Vidotto-Magnoni et al. 2015).

The Paranapanema River experiences two pronounced seasons, a dry season (April to September) and a wet season (October to March), The annual mean temperature is 17 °C (range 13 to 22 °C and 1550 mm as annual precipitation that is focused in the wet season (Alvares et al. 2013; Terassi et al. 2018). Air temperature data from the database of National Institute of Meteorology (INMET) revealed the Rosana Reservoir ranged from 19 °C (August 2019) to 27.2 °C (December 2020). Similar air temperature data were unavailable for the Taquaruçu Reservoir. Precipitation data emphasised the differences between the dry and wet season, where data extracted from the database of the Institute of Waters of Parana State (ANA) revealed the Rosana Reservoir had no precipitation in July 2018 and August 2019, but a monthly maximum of 250 mm in December 2019. The Taquarucu Reservoir had no precipitation in August 2019 and a monthly maximum of 315 mm in December 2019 (Fig. 2).

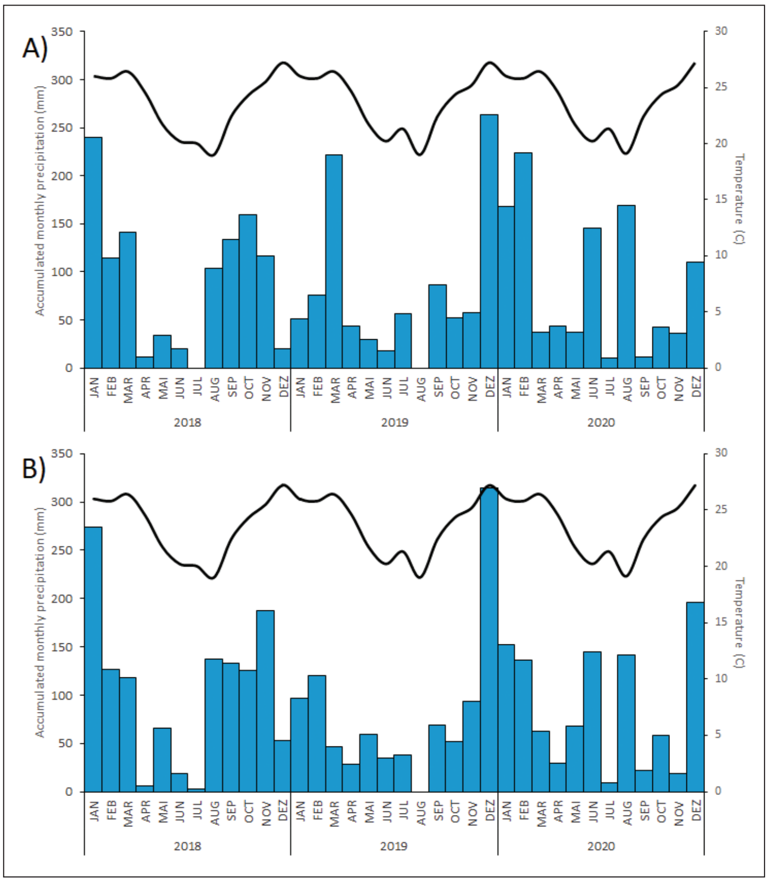

Figure 2. Temperature (Rosana Reservoir) and precipitation from Rosana and Taquarucu Reservoir from the study period. **A.** Paranapoema Meteorological Station (Rosana Reservoir); **B.** Porecatu Meteorological Station (Taquaruçu Reservoir).

Fish sampling

Samples of fish were collected quarterly between September 2018 and September 2020 at seven sites across both Reservoirs (Fig. 1). The samples were collected using trawls, sieves and cast nets from the vegetation in the marginal zone and along aquatic macrophyte beds, when present. At each site, a sampling effort of two hours was used, covering a stretch of 100 m and thoroughly exploring the available microhabitats within the area. All captured individuals were anaesthetised and euthanised by overexposure to 1 g ml^{-1} Eugenol, then fixed in 10% formaldehyde for 48 hours before being stored in 70% alcohol. Sampling was conducted under approval of The Animal Ethics Committee of the Universidade Estadual de Londrina (CEUA N° 21149.2012.53; CEUA N° 24310.2017.78). In the laboratory, fish species were identified using keys in literature (Ota et al. 2018), with voucher specimens (Suppl. material 1: table S1) and were deposited at the Museu de Zoologia da Universidade Estadual de Londrina (MZUEL).

Diet analysis

In laboratory, individuals were dissected and their stomachs removed, with the stomach contents analysed under a stereomicroscope. Prey items were identified to the lowest possible taxonomic level with the help of specific literature (Thomaz et al. 2002; Mugnai et al. 2010; Biolo and Rodrigues 2011). The volume (V) of each of the stomach contents was measured by compression in a millimetre Petri dish, with the volume recorded in mm^3 and later converted to ml (Hellawell and Abel 1971). The prey items were grouped into 10 categories and represented in percentage (%), as follows: Algae (Filamentous Algae); Aquatic Insects (Aquatic Insect Fragment, Coleoptera Larvae, Coleoptera Pupa, Diptera Larvae, Diptera Pupe, Ephemeroptera Nymph, Odonata Nymph and Trichoptera Nymph); Detritus (Inorganic and Organic Detritus); Fish (Fish, Fish Scale); Macrocrustacean (Crab, Shrimp); Microcrustacean (Cladocera, Copepoda, Microcrustacean Fragment, Ostracoda); Mollusc (Bivalvia, Gastropoda); Other (Microplastic); Terrestrial Plant (Fruit, Leaf, Stick, Seed) and Terrestrial Invertebrates (Acari, Aranae, Blattodea (Isoptera), Blattodea Adult, Coleoptera Adult, Diplopoda, Diptera Adult, Ephemeroptera Adult, Hemiptera Adult, Hymenoptera Adult, Lepidoptera Adult, Terrestrial Insect Fragment and Thysanoptera Adult. The prey categories were organised into food resources, based on their origin and were later separated by reservoir and season, with both being represented as percentage (%). The prey categories were classified into two groups: Autochthonous (Aquatic Insect; Microcrustacean; Macrocrustacean; Mollusc; Fish, Algae and Detritus) and allochthonous (Terrestrial invertebrates; Terrestrial Plant; and Others).

Prey categories were represented across reservoirs and later separated by season according to the 'frequency of occurrence' (FO) method, with adaptations from Hamidan et al. (2016). To calculate the frequency of occurrence (defined as the percentage of stomachs in which a particular prey category occurred), the following formula was used: $\%Fi = (ni/n) \times 100$, where: ni = number of stomachs containing prey category and n = total number on stomachs analysed. Next, we calculated the amplitude and dietary niche overlap of the species between the wet and dry seasons. To assess the niche amplitude of species, we used the Shannon-Wiener Index (Shannon 1948): $H' = -\sum pk \times \ln pk$, where H' means the Shannon-Wiener niche width measure, *pk* is the proportion of individuals collected using the *k* resource and ln is the neperian logarithm of the *pk* value. Dietary niche overlap between species was calculated using the Pianka Index: $Ojk = ({}^{n}\sum_{i=j}|P_{ij} - P_{ik}|) / {}^{n}\sum_{i=j} P_{ij}^{2} \cdot {}^{n}\sum_{i=j} P_{ik}^{2}$, where Ojk = measure of Pianka dietary niche overlap between species *j* and species *k*; *pij* = proportion of prey category *i* in the total of prey categories used by species *j*; *pik* = proportion of prey category *i* in the total of prey categories used by species *k*, *n* = total number of prey categories. The results of Ojk were considered as follows: low overlap (< 0.4), intermediate overlap (0.4–0.6) or high overlap (> 0.6) (Grossman 1986). Due to the sample size limitations, it was not possible to include the species *H. marginatus* in the seasonal analyses of Rosana Reservoir.

Data analysis

A permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) was used to test for differences in fish diets within each reservoir, based on a Bray-Curtis similarity matrix of volume data (log transformed, x + 1). The resulting pseudo-F statistic was tested using the Monte Carlo method with 999 randomisations. Species pairs that differed significantly were identified using pairwise post-hoc comparisons, based on the *adonis2()* function (vegan package; Oksanen et al. (2020)). Species pairs that differed significantly were identified using a pairwise adonis test. Next, we visualised the ordination of species according to their diet composition (niche breadth) using a principal coordinate analysis

(PCoA), based on a Bray-Curtis dissimilarity matrix (Bray and Curtis 1957). To test for seasonal differences in species diets, we applied PERMANOVA again, using a Bray-Curtis similarity matrix of log transformed volume data (x + 1) and the pseudo-F statistic was tested by the Monte Carlo method using 999 randomisations. Post-hoc pairwise comparisons were carried out using the *adonis2()* framework to identify significant differences amongst species. A PCoA was also used to visualise the ordering of populations according to diet composition, based on the Bray-Curtis dissimilarity matrix (Bray and Curtis 1957). Due to the sample size limitations, it was not possible to include the species *H. marginatus* in the seasonal analyses of Rosana Reservoir. Instead, only the total abundance for this species in the Reservoir was used. All the analyses were performed using R Programming software version 3.5.3 (R Core Team 2024), with the "vegan" package (Oksanen et al. 2020 and the "ggplot2" package (Wickham 2016). For each species group per reservoir, the following were applied: the completed analyses for stomach contents (total and between seasons), frequency of occurrence of prey, niche breadth and niche overlap. Additionally, differences between species diet in the same reservoir and between seasons were verified using PERMANOVA.

Results

Sample composition by species

A total of 416 individual fish were sampled from seven species within the families Acestrorhamphidae and Characidae (Characiformes) across both Reservoirs, including three non-native and four native species. Of the non-native species, 96 were *Megalamphodus eques* (Steindachner, 1882), 60 were *Aphyocharax dentatus* Eigenmann & Kennedy and 36 were *Roeboides descalvadensis* Fowler, 1937. The native ranges of these non-native species are Paraguay and lower Paraná River Basins for *A. dentatus* and *R. descalvadensis* and Amazon, Guaporé and Paraguay River Basins for *M. eques*. The introductions of *A. dentatus* and *R. descalvadensis* likely followed the flooding of the Salto das Sete Quedas after the construction of the Itaipu Hydroelectric Power Plant, which allowed upstream dispersal of Lower Paraná ichthyofauna, while *M. eques* was probably introduced through aquarium releases (Garcia et al. 2018a). Amongst the native species, 75 were *Astyanax lacustris* (Lütken, 1875), 57 were *Hemigrammus marginatus* Ellis, 1911 and 58 were *Serrapinnus notomelas* (Eigenmann, 1915).

In Rosana Reservoir, *A. dentatus*, *A. lacustris*, *M. eques*, *H. marginatus* and *S. notomelas* were analysed. In Taquaruçu Reservoir, the same five species were recorded, together with *M. intermedia* and *R. descalvadensis*, totalling 12 populations across both Reservoirs; representative images of each species are presented in Fig. 3.

Fish diet by reservoir and season

Amongst all identified prey items, 20 were autochthonous and 18 were allochthonous. In Rosana Reservoir, the stomach contents revealed a predominance of terrestrial invertebrates (allochthonous resources), complemented by other dietary components (Suppl. material 1: table S2). Conversely, in Taquaruçu Reservoir, diets were characterised mainly by aquatic insects, microcrustaceans and fish (Suppl. material 1: table S3).

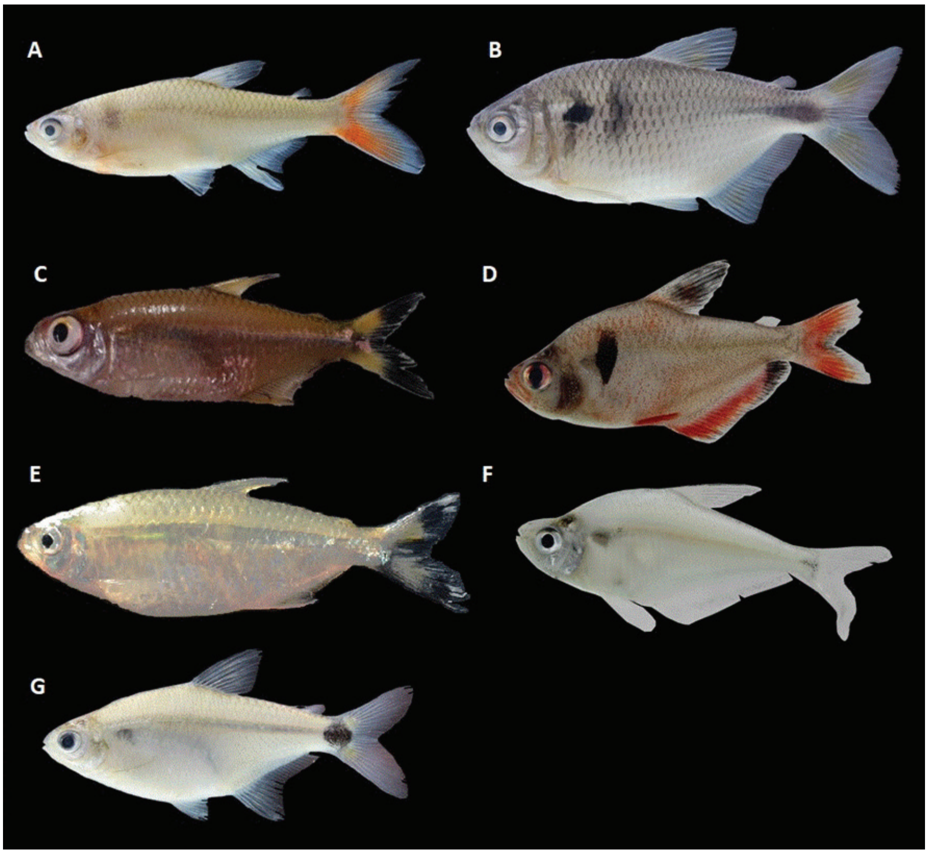

Figure 3. A. *Aphyocharax dentatus* 45 mm (MZUEL20735); B. *Astyanax lacustris* 43 mm (MZUEL20735); C. *Hemigrammus marginatus* 26 mm (MZUEL20773); D. *Megalamphodus eques* 28 mm (MZUEL20732); E. *Moenkhausia intermedia* 55 mm (MZUEL20790); F. *Roeboides descalvadensis* 60 mm (MZUEL20772); G. *Serrapinnus notomelas* 41 mm (MZUEL20736). Extracted from Geller (2021).

Regarding seasonal patterns, species in Rosana Reservoir showed consistent seasonal shifts, feeding more on terrestrial insects during the wet season and increasing consumption of aquatic insects, microcrustaceans and detritus (all autochthonous) in the dry season (Suppl. material 1: table S2). In contrast, species in Taquaruçu Reservoir displayed less consistent seasonal patterns, with diets during the wet season including aquatic insects, algae (autochthonous) and terrestrial plants (allochthonous), while in the dry season, terrestrial insects, microcrustaceans and fish were more frequent prey items.

Dietary patterns of native and non-native species

The non-native *A. dentatus* consumed mainly terrestrial invertebrates and microcrustaceans in both Reservoirs, with additional algae and terrestrial plants during the wet season in Taquaruçu (Suppl. material 1: tables S2, S3). The native *A. lacustris* primarily fed on terrestrial plants in Rosana. Non-native *M. eques* exhibited a diverse diet, dominated by terrestrial insects, aquatic invertebrates and microcrustaceans, incorporating algae and detritus seasonally in Rosana. The native *H. marginatus* mainly consumed terrestrial invertebrates and microcrustaceans in both Reservoirs and added plants during the wet season in Taquaruçu. The native, *M. intermedia*, had a broad diet, feeding on terrestrial invertebrates, aquatic insects and microcrustaceans and expanded its diet to algae and plants in the dry season of Taquaruçu (Suppl. material 1: table S3). The non-native *R. descalvadensis* preferred fish (mainly scales), but also consumed terrestrial invertebrates and aquatic insects across seasons in Taquaruçu (Suppl. material 1: table S3). The native *S. notomelas* primarily fed on detritus in Rosana, showing seasonal variation, with higher intake of terrestrial invertebrates, aquatic insects, microcrustaceans and terrestrial plants in Taquaruçu (Suppl. material 1: tables S2, S3).

Frequency of occurrence, niche breadth and overlap by reservoir and season

Frequency of occurrence (FO) varied between reservoirs and seasons. In Rosana Reservoir, terrestrial invertebrates, terrestrial plants and detritus were the most frequently consumed resources. Terrestrial items dominated during the wet season, while aquatic insects and microcrustaceans were more common in the dry season (Suppl. material 1: table S4). In Taquaruçu Reservoir, patterns were more variable, with high FO values for terrestrial invertebrates, aquatic insects, microcrustaceans and fish, but no consistent seasonal trend (Suppl. material 1: table S5).

Niche breadth (H') also differed amongst species, reservoirs and seasons. In Rosana Reservoir, non-native *A. dentatus* had the narrowest niche in both the wet (H' = 0.66) and dry (H' = 0.67) seasons, indicating dietary specialisation. In contrast, non-native *M. eques* had the broadest niche in the wet season (H' = 1.61), while the native *A. lacustris* showed the largest breadth in the dry season (H' = 1.37). In Taquaruçu Reservoir, *H. marginatus* had the narrowest niche in the wet season (H' = 0.63), whereas *S. notomelas* had the broadest (H' = 1.38). During the dry season, *A. lacustris* exhibited the smallest niche (H' = 0.72), while *M. intermedia* had the largest (H' = 1.68).

The Pianka Index revealed clear seasonal shifts in dietary overlap. In Rosana, overlap was higher in the wet season, whereas in the Taquaruçu, it was greater in the dry season (Table 1). Non-native species exhibited substantial overlap with natives, particularly in Taquaruçu. For instance, *A. dentatus* overlapped strongly with *H. marginatus* (Ojk = 0.99) and *M. intermedia* (Ojk = 0.68) in the dry season, while *M. eques* overlapped with *M. intermedia* (Ojk = 0.75), suggesting potential interspecific competition.

Dietary variation amongst native and non-native species

PERMANOVA indicated significant dietary differences amongst species in both Reservoirs. In Rosana Reservoir, diet composition varied significantly amongst the five species, while in the Taquaruçu, differences were observed amongst all seven species. Post-hoc pairwise *adonis* test confirmed significant differences between most pairs of species, except for *A. dentatus* and *H. marginatus* (Table 2).

PCoA ordinations separated species according to dietary composition, with Axis 1 and Axis 2 explaining 99.7% of total variance (Fig. 4). In Rosana, non-native *M. eques* and native *S. notomelas* had broader niche sizes (positive side of Axis 2), while *A. lacustris*, *H. marginatus* and *A. dentatus* had narrower niches (negative side of Axis 2) (Fig. 4). In Taquaruçu, *A. dentatus*, *M. intermedia* and *S. notomelas* displayed a broader niche (negative side of Axis 2), *H. marginatus* was centrally distributed and *M. eques* occupied the negative side (Fig. 4).

When assessing seasonal effects, PERMANOVA detected significant dietary differences between wet and dry seasons for all species in Rosana (Table 3). In the

Table 1. Niche breadth (H') and dietary niche overlap by Pianka Index (Ojk) separated by season to species from Rosana and Taquaruçu Reservoirs. Values above 0.60 are considered significant (high overlap) and are marked in bold. * = Non-native species to the Upper Paraná River Basin.

Rosana Reservoir							
Species (Niche Breadth = Wet; Dry)	**Dietary niche overlap = Ojk Wet; Ojk Dry**						
	*A. dentatus**	*A. lacustris*	*M. eques**	*S. notomelas*			
*A. dentatus** (H'= 0.66; 0.67)	-	**0.63**; 0.26	**0.73**; 0.31	**0.90**; 0.08			
A. lacustris (H' = 1.21; 1.37)	-	-	**0.76**; 0.16	**0.61**; 0.16			
*M. eques** (H' = 1.61; 1.09)	-	-	-	**0.81**; 0.26			
S. notomelas (H' = 1.02; 1.24)	-	-	-	-			
Taquaruçu Reservoir							
Species (Niche Breadth = Wet; Dry)	**Dietary niche overlap = Ojk Wet; Ojk Dry**						
	*A. dentatus**	*A. lacustris*	*M. eques**	*H. marginatus*	*M. intermedia*	*R. descalvadensis**	*S. notomelas*
*A. dentatus** (H' = 1.22; 1.12)	-	0.22; **0.92**	0.09; **0.93**	0.61; **0.99**	0.58; 0.68	**0.74**; 0.49	0.44; 0.36
A. lacustris (H' = 0.93; 0.72)	-	-	0.3; **0.85**	0.13; **0.87**	0.41; 0.50	0.32; 0.43	**0.7**; 0.08
*M. eques** (H' = 1.07; 1.63)	-	-	-	0.05; **0.95**	**0.71; 0.75**	0.13; 0.54	**0.78**; 0.32
H. marginatus (H' = 0.63; 1.14)	-	-	-	-	0.27; **0.74**	0.56; 0.53	0.2; 0.38
M. intermedia (H' = 1.26; 1.68)	-	-	-	-	-	**0.69**; 0.41	**0.92**; 0.61
*R. descalvadensis** (H' = 1.41; 1.06)	-	-	-	-	-	-	0.54; 0.07
S. notomelas (H' = 1.38; 1.16)	-	-	-	-	-	-	-

Table 2. Results of the pair-by-pair test of the permutational multivariate analysis of variance (PERMANOVA) species diet from Rosana and Taquaruçu Reservoirs. Values in bold are significant ($p \leq 0.05$). SL = Standard length in millimetres; M = Mean of length; SD = Standard Deviation of length.

Rosana Reservoir								
PERMANOVA (post-hoc pair-by-pair test)								
Species	**SL range - mm (M) ± SD**	*A. dentatus**	*A. lacustris*	*M. eques**	*H. marginatus*	*S. notomelas*		
*A. dentatus**	30.00–40.00 (33.00) ± 0.2	-	$F_{(2.66)}$ = 9.77; ***p* = 0.001**	$F_{(2.45)}$ = 7.88; ***p* = 0.001**	$F_{(0.68)}$ = 2.44; *p* = 0.054	$F_{(3.80)}$ = 15.52; ***p* = 0.001**		
A. lacustris	46.00–81.00 (61.00) ± 1.02	-	-	$F_{(3.74)}$ = 11.9; ***p* = 0.001**	$F_{(1.99)}$ = 6.97; ***p* = 0.001**	$F_{(4.63)}$ = 18.06; ***p* = 0.001**		
*M. eques**	10.4–34.00 (23.00) ± 0.54	-	-	-	$F_{(1.78)}$ = 5.63; ***p* = 0.001**	$F_{(3.30)}$ = 11.20; ***p* = 0.001**		
H. marginatus	11.00–30.00 (21.50) ± 0.60	-	-	-	-	$F_{(3.85)}$ = 14.69; ***p* = 0.001**		
S. notomelas	11.00–30.00 (21.00) ± 0.61	-	-	-	-	-		
Taquaruçu Reservoir								
PERMANOVA (post-hoc pair-by-pair test)								
Species	**SL range - mm (M), SD**	*A. dentatus**	*A. lacustris*	*M. eques**	*H. marginatus*	*M. intermedia*	*R. descalvadensis**	*S. notomelas*
*A. dentatus**	33.00–41.00 (36.00) ± 0.26	-	*F*(1.23) = 3.61; ***p* = 0.001**	*F*(2.74) = 8.43; ***p* = 0.001**	*F*(0.10) = 0.28; *p* = 0.95	*F*(0.95) = 2.76; ***p* = 0.022**	*F*(2.21) = 6.10; ***p* = 0.001**	*F*(1.23) = 3.42; ***p* = 0.005**
A. lacustris	28.00–122.00 (43.00) ± 3.46	-	-	*F*(5.50) = 18.38; ***p* = 0.001**	*F*(0.74) = 2.28; ***p* = 0.020**	*F*(2.58) = 8.18; ***p* = 0.001**	*F*(2.70) = 8.15; ***p* = 0.001**	*F*(3.37) = 10.37; ***p* = 0.001**
*M. eques**	17.00–30.00 (24.00) ± 0.37	-	-	-	*F*(2.44) = 7.94; ***p* = 0.001**	*F*(3.60) = 12.15; ***p* = 0.001**	*F*(4.72) = 15.12; ***p* = 0.001**	*F*(1.47) = 4.87; ***p* = 0.001**
H. marginatus	11.00–33.00 (25.5) ± 0.59	-	-	-	-	*F*(1.03) = 3.12; ***p* = 0.016**	*F*(1.79) = 5.12; ***p* = 0.001**	*F*(1.32) = 3.81; ***p* = 0.004**
M. intermedia	59.00–77.00 (69.50) ± 0.49	-	-	-	-	-	*F*(4.00) = 11.97; ***p* = 0.001**	*F*(1.08) = 3.29; ***p* = 0.001**
*R. descalvadensis**	21.00–78.00 (36.00) ± 1.45	-	-	-	-	-	-	*F*(3.35) = 9.63; ***p* = 0.001**
S. notomelas	11.00–28.00 (24.00) ± 0.41	-	-	-	-	-	-	-

Taquaruçu, *A. lacustris* and *R. descalvadensis* showed no significant seasonal shifts (Table 3). The PCoA plots further illustrated these seasonal differences in niche breadth and resource use across populations (Figs 4–7).

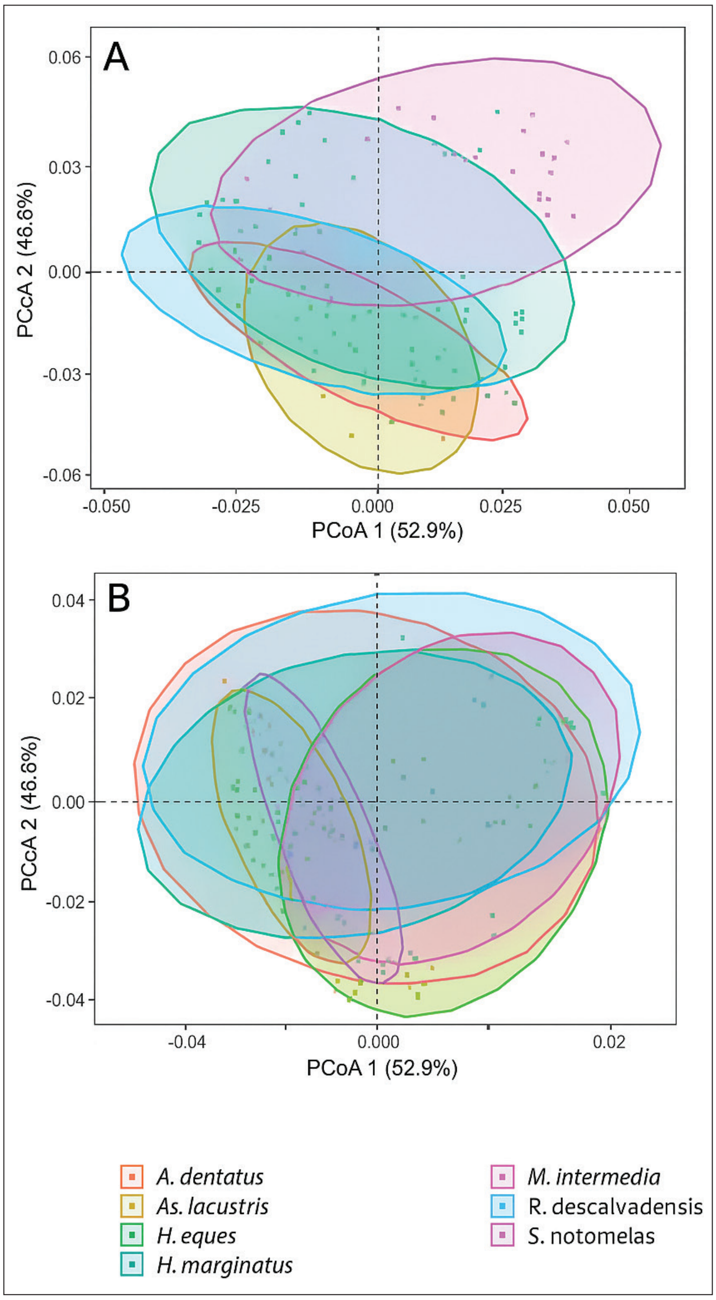

Figure 4. Ordering of the first two PCoA axes for the fish diet from Rosana and Taquaruçu Reservoirs. **A.** Rosana Reservoir; **B.** Taquaruçu Reservoir.

Discussion

Here, we examined the diet, feeding strategies and relationships of 12 populations of seven co-existing native and non-native small-bodied fish species inhabiting the marginal zones of the Lower Paranapanema River. Our results revealed clear differences between fish populations across two reservoirs in terms of resource use, niche breadth and dietary overlap, feeding strategies and seasonal responses – patterns that appear to reflect differences in environmental heterogeneity. In the Rosana Reservoir, both native and non-native species made greater use of terrestrial invertebrates (allochthonous resources), likely due to enhanced connectivity with the surrounding terrestrial environment.

Table 3. Results of permutational multivariate analysis of variance (PERMANOVA) of species diet from Rosana and Taquaruçu Reservoirs separated by season. Values in bold denote significant variance ($p \leq 0.05$). * = Non-native species to the Upper Paraná River Basin.

Rosana Reservoir (Wet x Dry)		Taquaruçu Reservoir (Wet x Dry)	
Species	**PERMANOVA**	**Species**	**PERMANOVA**
*A. dentatus**	$F_{(0.51)} = 16.73$; $\mathbf{p = 0.001}$	*A. dentatus**	$F_{(1.40)} = 4.07$; $\mathbf{p = 0.02}$
A. lacustris	$F_{(0.09)} = 2.71$; $\mathbf{p = 0.014}$	*A. lacustris*	$F_{(0.68)} = 2.22$; $p = 0.072$
*M. eques**	$F_{(0.05)} = 2.87$; $\mathbf{p = 0.001}$	*M. eques**	$F_{(1.36)} = 5.36$; $\mathbf{p = 0.001}$
S. notomelas	$F_{(2.86)} = 19.49$; $\mathbf{p = 0.001}$	*H. marginatus*	$F_{(1.47)} = 4.83$; $\mathbf{p = 0.002}$
		M. intermedia	$F_{(1.03)} = 3.49$; $\mathbf{p = 0.021}$
		*R. descalvadensis**	$F_{(0.72)} = 2.14$; $p = 0.052$
		S. notomelas	$F_{(2.63)} = 10.78$; $\mathbf{p = 0.001}$

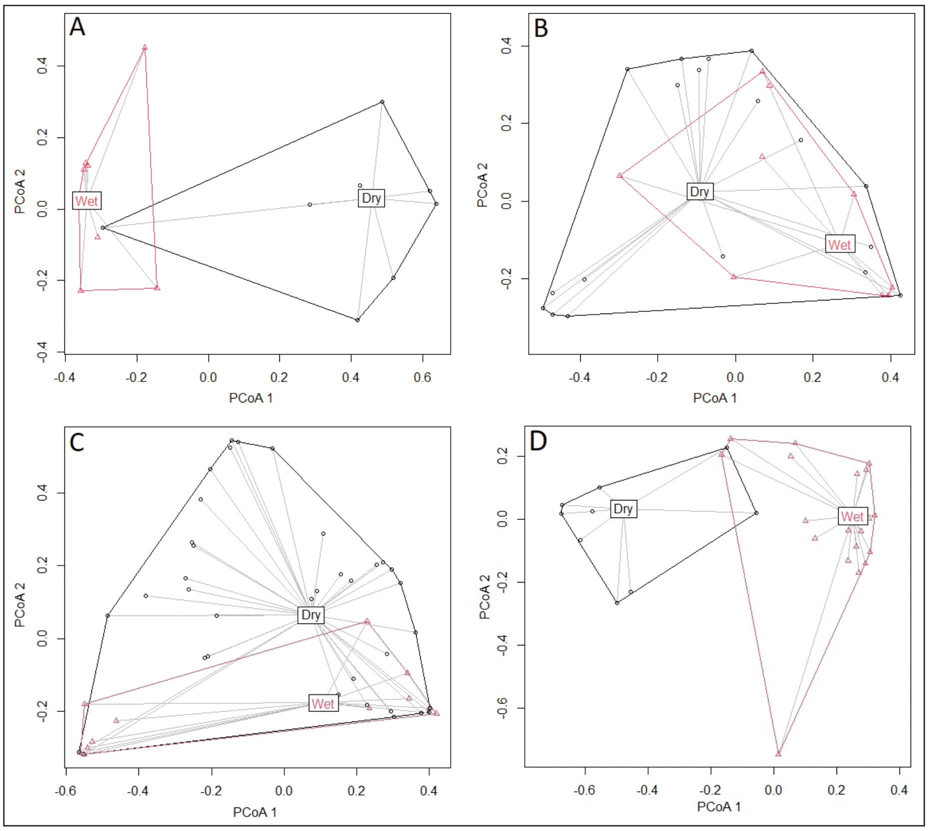

Figure 5. Ordination of population's niche breadth of Rosana Reservoir by season using the first two axes of PCoA: **A.** *A. dentatus* (PCoA explanation = 42%); **B.** *A. lacustris* (PCoA explanation = 50.4%); **C.** *M. eques* (PCoA explanation = 78%); **D.** *S. notomelas* (PCoA explanation = 48%).

This is supported by the presence of numerous large tributaries that increase terrestrial input (Nogueira et al. 2012; Quirino et al. 2017; Smith et al. 2018), a winding channel bordered by forested margins within a conservation unit (Vidotto-Magnoni and Carvalho 2009; Bennemann et al. 2011) and the occurrence of marginal lagoons (Ferrareze et al. 2015). Previous studies in Rosana reported diets dominated by aquatic insects and microcrustaceans (autochthonous resources) amongst small-bodied fishes (Casatti et al. 2003; Pelicice and Agostinho 2006). This difference may reflect our broader spatial sampling, which included both lagoonal areas rich in macrophytes – known to support autochthonous resource production (Agostinho et al. 2007) - and the main

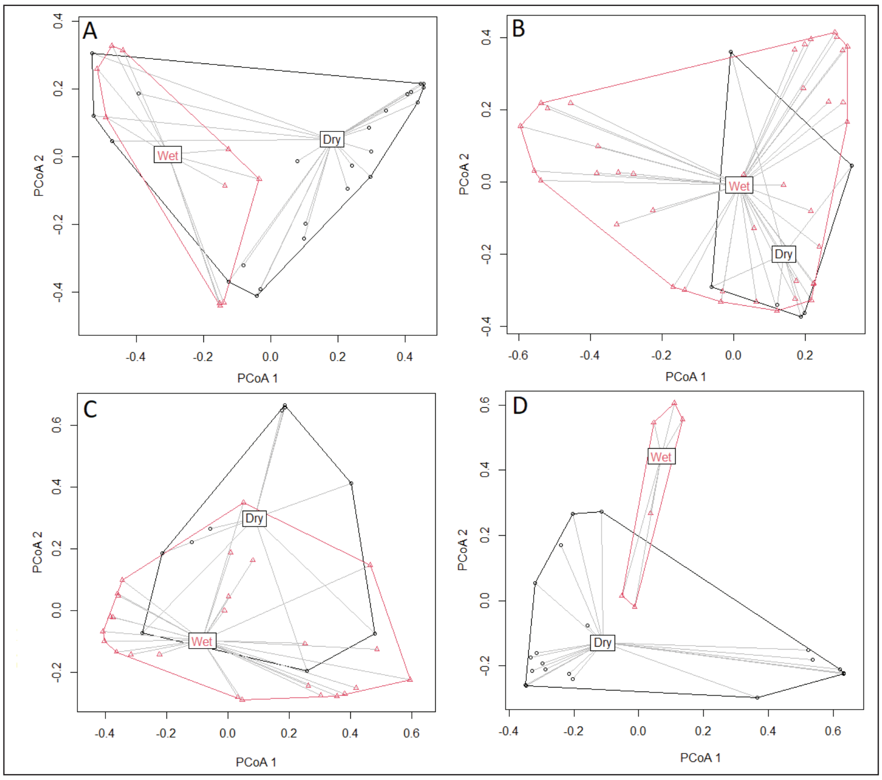

Figure 6. Ordination of population's niche breadth of Taquaruçu Reservoir by season using the first two axes of PCoA: **A.** *A. dentatus* (PCoA explanation = 42%); **B.** *A. lacustris* (PCoA explanation = 50.4%); **C.** *M. eques* (PCoA explanation = 78%); **D.** *H. marginatus* (PCoA explanation = 44.3%).

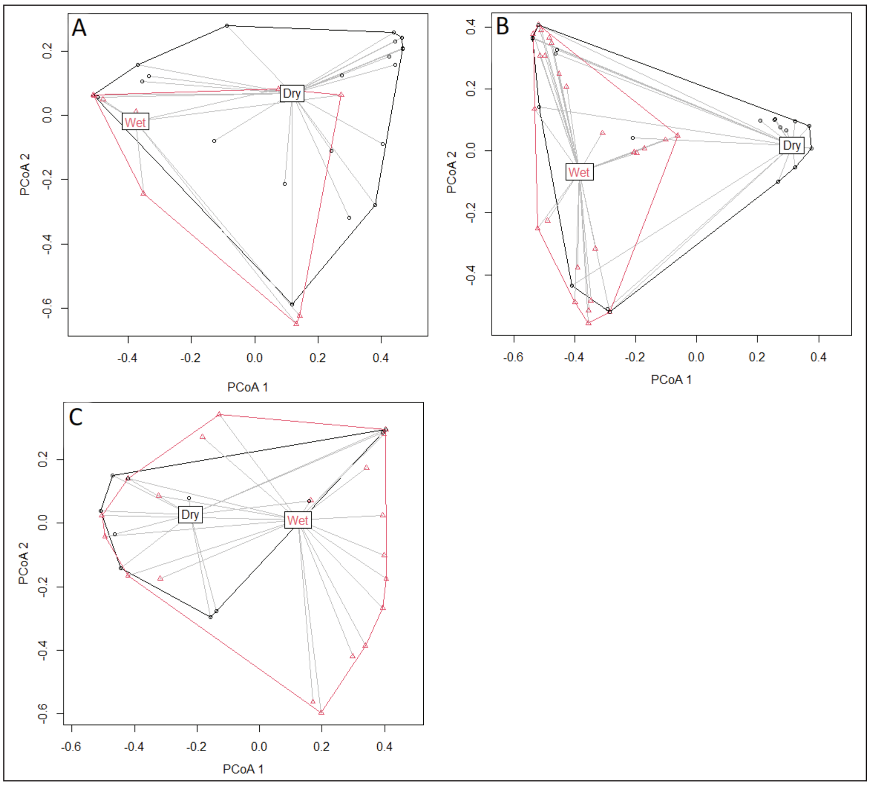

Figure 7. Ordination of population's niche breadth of Taquaruçu Reservoir by season using the first two axes of PCoA: **A.** *M. intermedia* (PCoA explanation = 49.8%); **B.** *R. descalvadensis* (PCoA explanation = 72%); **C.** *S. notomelas* (PCoA explanation = 48%).

channel of the reservoir. This approach contributes new insights into the feeding ecology of small-bodied fish in this impounded system.

In the Taquaruçu Reservoir, both native and non-native small-bodied fish populations primarily consumed aquatic insects, microcrustaceans and fish (i.e. autochthonous resources), showing a notable divergence from the patterns observed in the neighbouring Rosana Reservoir. This finding highlights the feeding plasticity of small-bodied species in reservoirs (Vidotto-Magnoni and Carvalho 2009; Bennemann et al. 2011), which we suggest is associated with local prey availability (Neves et al. 2018; Fonseca et al. 2022; Santiago et al. 2022), although prey abundance was not measured here. The Taquaruçu Reservoir is characterised by a relatively small watershed, a straight and simplified river channel, few and short tributaries (Nogueira et al. 2012; Smith et al. 2018), a lack of surrounding forest (Vidotto-Magnoni and Carvalho 2009; Bennemann et al. 2011) and the absence of marginal lagoons (Cassatti et al. 2003; Ferrareze et al. 2015). These features likely limit the input of allochthonous material (Nogueira et al. 2012), which is reflected in the low proportion of terrestrial items in the stomach contents of the species examined. This oligotrophic condition is typical of reservoirs with limited habitat heterogeneity (Ferrareze et al. 2014), where reliance on autochthonous resources is also documented in other impoundments along the Paranapanema River, as well as in the Tietê (Vidotto-Magnoni and Carvalho 2009; Smith et al. 2018) and Iguaçu Rivers (Delariva et al. 2013).

Fish populations in the Rosana Reservoir responded uniformly to seasonal changes, with shifts apparent amongst prey frequency, volume and resource types. This seasonal dietary shift is commonly observed in small-bodied species inhabiting free flowing river stretches (Fonseca et al. 2022; Santiago et al. 2022). As suggested by Agostinho et al. (2007), rainfall events promote flooding of the terrestrial zone, increasing the availability of invertebrates and plant material. Consequently, environments with habitats that enhance terrestrial-aquatic connectivity often support greater consumption of allochthonous resources by fishes (Novakowski et al. 2008; Quirino et al. 2015; Quirino et al. 2017), particularly during seasonal pulses, such as insect emergence (Galinha and Hahn 2004) or fruits and seeds crops (Correa et al. 2015) in the wet season. In contrast, fish populations of Taquaruçu Reservoir exhibited no significant seasonal differences in their use of autochthonous versus allochthonous resources – an uncommon pattern for Neotropical fishes typically influenced by seasonal resource dynamics (Neves et al. 2021; Fonseca et al. 2022; Santiago et al. 2022). This consistency likely reflects a year-round limitation in resource availability, possibly linked to the lack of habitat heterogeneity. Additionally, the observed seasonal shifts in diet composition (prey frequency and volume) amongst Taquaruçu populations were uncoordinated across species, suggesting potential trophic segregation as a mechanism to reduce interspecific competitive and avoid competitive exclusion (Schoener 1974; Quirino et al. 2015; Barros et al. 2017).

Contrary to our predictions, we observed high dietary overlap amongst species in the wet season in Rosana Reservoir, despite the typically greater food availability during this period – a finding that contrasts with previous studies (Casatti et al. 2003; Pelicice and Agostinho 2006; Quirino et al. 2015). Such overlap may reflect opportunistic feeding behaviour exhibited by small-bodied fishes in response to seasonal resource abundance, as documented for *Astyanax* spp. (Fonseca et al. 2022), *H. marginatus* (Barreto et al. 2018) and *S. notomelas* (Santiago et al.

2022). However, even when dietary overlap occurs between native and non-native species, it does not necessarily indicate interspecific competition, as spatial segregation, use of different microhabitats or feeding at different times can mitigate direct interactions (Pelicice and Agostinho 2006; Ferrareze et al. 2015). In Taquaruçu Reservoir, by contrast, increased dietary overlap during the dry season was expected, given the reduction in flooded areas and the consequent decline in allochthonous inputs. Under these conditions, fish become increasingly dependent on limited autochthonous resources (Agostinho et al. 2007). This trend was particularly evident in interactions involving the non-native *A. dentatus* and *M. eques*, which exhibited high overlap with native species, such as *A. lacustris* and *H. marginatus*. This pattern resembles those observed in other Brazilian reservoirs (Vidotto-Magnoni and Carvalho 2009; Delariva et al. 2013; Smith et al. 2018), where food scarcity during certain periods forces species to share resources (Sánchez-Hernández et al. 2017). The presence of non-native species with highly competitive feeding strategies (Jarduli et al. 2021; Ferraz et al. 2024) is particularly concerning in this context, as it may intensify interspecific competition and eventually lead to the displacement or local extinction of native species.

The non-native *A. dentatus* primarily functioned as an invertivore, consuming aquatic insects and microcrustaceans, but also exhibited notable feeding flexibility by shifting from a narrow dietary niche in Rosana Reservoir to a broader one in Taquaruçu. In Rosana, where small-bodied species tend to exhibit trophic segregation (Casatti et al. 2003; Pelicice and Agostinho 2006), *A. dentatus* behaved as a specialist – consistent with patterns observed in its native range in the Brazilian Pantanal, where its niche is constrained by the presence of the congener *A. anisitsi* (Corrêa et al. 2009). Nonetheless, seasonal opportunism was evident, with increased consumption of terrestrial invertebrates during the wet season and microcrustaceans during the dry season, similar to feeding patterns reported for *Aphyocharax* species in the Upper Paraná River (Quirino et al. 2015). In contrast, under the more resource-limited conditions of Taquaruçu Reservoir, *A. dentatus* expanded its dietary niche to include algae and terrestrial plant material – a generalist strategy commonly associated with non-native species (Bennemann et al. 2011). This shift is particularly concerning given the increased dietary overlap with native species, such as *A. lacustris* and *H. marginatus*, suggesting a potential for intensified interspecific competition in simplified, oligotrophic environments.

The native *A. lacustris* demonstrated a predominantly insectivorous diet with a consistently narrow niche in both Reservoirs, showing only minor seasonal variation. This finding is particularly noteworthy given that the species is often reported as a generalist in other reservoir systems (Delariva et al. 2013; Smith et al. 2018). The observed pattern suggests that *A. lacustris* may engage in niche partitioning to minimise interspecific competition (Neves et al. 2018), as previously documented in Rosana Reservoir (Casatti et al. 2003; Pelicice and Agostinho 2006). Some degree of dietary flexibility was observed, with occasional consumption of plant material - likely an opportunistic response to the seasonal availability of fruits and seeds (Correa et al. 2015), a pattern consistent with previous findings in the Lower Paranapanema River (Casatti et al. 2003; Fonseca et al. 2022). However, overlap with the non-native *M. eques* — particularly in Taquaruçu Reservoir — raises concerns. *Megalamphodus eques* is a widespread and abundant invader in the Upper Paraná River Basin (see Ota et al. (2018) and references therein), known for its preference for aquatic resources, especially microcrustaceans (Casatti et al.

2003), as well as larval aquatic insects and algae (Pelicice and Agostinho 2006). Its diet composition tends to fluctuate seasonally in response to resource availability (Quirino et al. 2015). In our study, *M. eques* maintained this broad dietary niche and frequently overlapped with other species, including the more specialised *A. lacustris*. Such overlap could intensify competition and potentially threaten the persistence of native species with more restricted diets.

The native *H. marginatus* was another species that showed variations in niche breadth between reservoirs, while maintaining a consistent preference for terrestrial insects and microcrustaceans in both systems. Species often become more specialised when their preferred food resources are readily available (Sánchez-Hernández et al. 2017). For instance, in the Mogi-Guaçu River (south-eastern Brazil), *H. marginatus* has been described as primarily insectivorous (Fragoso-Moura et al. 2017), although it may shift towards omnivory in more degraded habitats (Barreto et al. 2018). These findings align with our results: in Rosana Reservoir, *H. marginatus* showed a narrow niche centred on terrestrial invertebrates and microcrustaceans, while in Taquaruçu Reservoir, it broadened its diet to include aquatic insects and terrestrial plants, likely as a response to seasonal resource fluctuations. The overlap in dietary composition with non-natives, such as *A. dentatus* and *M. eques*, as well as the native *A. lacustris*, suggest potential for trophic interactions that could lead to competitive pressure – especially in Taquaruçu Reservoir, where food resource limitations are more pronounced. Despite this, a previous study reported good body condition amongst these populations in both Reservoirs (Ferraz et al. 2021b), indicating that, at least for now, food resources may be sufficient to support co-occurrence. However, sustained overlap with competitively dominant non-native species could pose longer-term risks to native populations.

The native *M. intermedia* and the non-native *R. descalvadensis* were only sufficiently abundant for analysis in the Taquaruçu Reservoir, which limits further interpretation. *Moenkhausia intermedia* demonstrated a broad dietary niche composed of multiple prey types, with a preference for terrestrial invertebrates and aquatic insects – similar to Tietê River (Vidotto-Magnoni and Carvalho 2009; Smith et al. 2018). However, the species also consumed notable amounts of microcrustaceans, algae and terrestrial plants across seasons, a generalist and opportunistic feeding strategy previously documented in reservoir environments (Bennemann et al. 2011), positioning *M. intermedia* as a strong competitor - particularly with co-occurring non-natives like *A. dentatus* and *R. descalvadensis*, as well as with the broadly overlapping *M. eques*. In contrast, *R. descalvadensis* displayed a narrow, specialist niche focused on fish scales, a behaviour typical of lepidophagous species. While member of this genus are usually scale-eaters targeting larger fish, they may also opportunistically consume other available resources (Albrecht et al. 2013). Our results are similar to those of Casatti et al. (2003), who reported consumption of terrestrial invertebrates and aquatic insects, but diverge from Pelicice and Agostinho (2006), who described a microcrustacean-based diet. These discrepancies could be attributed to spatial variation, differential use of microhabitats (e.g. macrophyte beds within marginal lagoons) and particularly the nocturnal feeding habits of *R. descalvadensis* (Pelicice and Agostinho 2006), making diet overlap with other species of lesser concern, given the temporal division of feeding activity. The native *S. notomelas* exhibited an unusual dietary pattern, characterised by a broad niche and a diet dominated by detritus in the Rosana Reservoir, which contrasts with previous studies in the area (which reported a specialised algivorous diet) (Casatti et al. 2003; Pelicice and Agostinho 2006). In Taquaruçu Reservoir, *S. notomelas* showed feeding patterns more aligned with previous studies, including the consumption of terrestrial invertebrates, aquatic insects, microcrustaceans, algae and plants across the seasons (Casatti et al. 2003; Pelicice and Agostinho 2006; Santiago et al. 2022). It is important to note that soft materials, such as algae and animal tissue, degrade rapidly during digestion (Garcia et al. 2018b), potentially leading to an over-representation of more resilient items such as detritus. Additionally, the species' benthic feeding behaviour may contribute to the incidental ingestion of sediments (Santiago et al. 2022). The species exhibited significant dietary overlap with the non-native *A. dentatus* and *M. eques*, as well as with the native *M. intermedia*. This overlap highlights the potential for interspecific competition, particularly with non-native species that display high trophic plasticity and competitive advantage.

Our results have implications for the ongoing global freshwater biodiversity crisis, which is driven by habitat alteration, invasive species, hydrological regulation and climate change (Harrison et al. 2018; Albert et al. 2020). Small-bodied fishes, such as characoids in this study, are often ignored in conservation priorities; however, they play critical roles in vulnerable tropical freshwater ecosystems. They have specific features, such as high functional diversity and short generation times and their sensitivity to environmental change makes them early indicators of ecosystem degradation and biotic homogenisation (Darwall et al. 2018; Dudgeon and Strayer 2025).

Our findings documenting trophic interactions and resources partitioning between native and non-native characoids clearly indicate how even subtle shifts at the lower trophic levels can propagate through food webs and alter ecosystem stability. In an attempt to "bend the curve" of freshwater biodiversity loss, these findings support international calls to improve integrative, process-based assessments of invasion impacts (Tickner et al. 2020; Ottoni et al. 2023, 2025). Effective conservation and management must take into account both the presence of non-native species and the ways in which local environmental filters shape their ecological effects. This is demonstrated by context-dependent outcomes, such as those found between Rosana and Taquaruçu Reservoirs.

In conclusion, we report novel insights into the understudied interactions between native and non-native small-bodied fishes co-existing in the marginal zones of Neotropical reservoirs. By analysing the diets of seven native and non-native from the Lower Paranapanema River, we provide an important update on fish trophic ecology in the region. Notable dietary differences were observed between species across reservoirs and seasons, likely driven by environmental variability and feeding plasticity. In the Rosana Reservoir, fish relied more heavily on allochthonous resources and responded consistently to seasonal changes – patterns likely facilitated by the presence of riparian habitats that promote terrestrial-aquatic exchange. In contrast, fish in the Taquaruçu Reservoir were restricted to autochthonous resources and exhibited uncoordinated seasonal responses, likely due to the lack of habitat heterogeneity. The narrower niche breadths and lower dietary overlap in Rosana suggest greater trophic specialisation and segregation, whereas the broader niches and higher overlap observed in Taquaruçu –especially amongst non-native species during the dry season – may reflect food limitation, leading to resource sharing and generalist strategies. These findings are particularly concerning, as they highlight the potential for negative interactions in source-poor environments, potentially resulting in population declines or local extinctions of native species. Given the ecological importance of small-bodied fishes in mediating energy flow and nutrient cycling, we emphasise the need for ongoing monitoring of these species within reservoir marginal zones.

Acknowledgements

We would like to thank China Three Gorges Corporation (CTG Brasil) for granting financial assistance for this work. Additionally, we would like to thank Aparecido de Souza, Edson Santana da Silva and Lucas Ribeiro Jarduli for helping with the fieldwork and Thiago Deruza Garcia for helping with analysis and Iago Vinicios Geller for helping with species photographs. Finally, we acknowledge the constructive and insightful comments from the Academic Editor Josie South and reviewer Felipe Ottoni, which substantially improved the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This study was funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil – finance code 001.

Author contributions

JDF: conceptualisation, data collection, data analysis, writing; ACRC: data collection, review; DAZG: data collection, review; APVM: data analysis, review; ALBM: conceptualisation, review; AST: conceptualisation, data analysis, review; JRB: conceptualisation, data analysis, review; MLO: conceptualisation, data analysis, review.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

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Data type: docx

Link: https://doi.org/10.3897/neobiota.104.167161.suppl1