

## Research Article

# The influence of non-native invertebrate species in the food web structure of two Neotropical reservoirs

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## Abstract

To investigate the influence of non-native aquatic invertebrate species on food web structure, we selected two reservoirs located in the Grande River (upper Paraná River basin, Brazil) with similar fish communities, different age and different taxa introductions history. We quarterly collected fish and benthonic macroinvertebrates samples in the Volta Grande and Funil reservoirs between October 2015 and August 2016. We used conventional methods of diet evaluation to assess the sampled fish and measured the availability of invertebrates (i.e. composition and density) present in the sediment samples from each reservoir. In addition, we performed a structural analysis of trophic interaction networks. Based on the data obtained, it was possible to identify that in Volta Grande most of the energy flow, between benthonic invertebrates (prey) and the fish community (predators), occurred through non-native prey species, especially *Limnoperna fortunei* and *Macrobrachium amazonicum*, while in Funil it was shared between non-native and native prey. Species loss simulations indicated that the networks did not differ substantially between random losses and losses between groups. In general, there was a decrease in the probability of occurrence of highly connected species in both reservoirs and between non-native and native species. Results showed that the new interactions among species influenced the importance of the available energy sources for the fish in the Volta Grande reservoir. The presence of non-native prey, especially *M. amazonicum*, may influence the interaction network structure, promoting community dependence on non-native species to ensure robustness to environmental disturbances. In the absence of pre-invasion data, the comparative study between systems with similar fish communities may provide a better understanding of the impacts caused by the introduction of non-native invertebrate prey.

**Key words:** trophic ecology, fish, *Limnoperna*, predator-prey relationships

## Introduction

Biological invasions can have profound effects on ecosystems (Courchamp et al. 2003; Miehls et al. 2009) which are often difficult to detect, especially regarding the strengths and extent of such effects within an invaded food web (David et al. 2017). Changes in resource availability and use, resulting from the introduction of

non-native species (Dwyer and Morris 2006), can substantially alter the extent of the impact of these organisms on the ecosystem (Tillberg et al. 2007). In aquatic environments in particular, water flow and human activities favor rapid dispersal of organisms, rendering these systems highly vulnerable to impacts of invasive species (Strayer and Dudgeon 2010). Accordingly, disturbances in aquatic food webs caused by non-native invertebrates, such as mollusks and crustaceans, have been extensively documented (Maguire and Grey 2006; Bulté and Blouin-Demers 2008; Rennie et al. 2009; Nilsson et al. 2012; Locke et al. 2014; Wood et al. 2017). However, in some cases, the lack of pre-introduction ecological data has been one of the major challenges faced by studies focused on assessing impacts of non-native species. Thus, an approach that may help address this lack of previous data is comparative studies between systems with similar ecological characteristics, but with a different taxa introduction history (Locke et al. 2014; McEachran et al. 2019). However, it is important to note that in general, the effects of introduced species on native communities have been shown to be dependent on the trophic level, invader taxon, recipient habitat and time after invasion (Bradley et al. 2019), making extrapolation of cases delicate. On the other hand, the similarity found between fish assemblages living in reservoirs of the Paraná River basin (Vitule et al. 2012) and the presence and absence of important non-native prey for fish fauna (e.g. *Limnoperna fortunei*; Rosa et al. 2015, 2021) in these systems may provide an opportunity to study possible dietary change effects, followed by an invasion process.

The mitylid golden mussel *L. fortunei* (Dunker, 1857) and the palaemonid Amazonian prawn *Macrobrachium amazonicum* (Heller, 1862) are non-native aquatic invertebrates widely distributed in southern and southeastern Brazilian reservoirs (Bialetsky et al. 1997; Mansur et al. 2003; Magalhães et al. 2005; Oliveira et al. 2015), wherein they represent the most abundant macroinvertebrate species, particularly in the upper Paraná River basin (Takeda et al. 2003; Silva 2010; Morais et al. 2014; Rosa et al. 2015). *Limnoperna fortunei* is native to southeast Asia that was probably introduced to South America via ballast water between the late 1980s and early 1990s (Pastorino et al. 1993). *Macrobrachium amazonicum* is found in the basins of northern South America, the Amazon river, northeastern Brazil, and the São Francisco and Paraguay rivers (Gomes-Corrêa 1977). In the upper Paraná River basin, *M. amazonicum* was probably introduced by fish stocking programs in regional reservoirs (Torloni et al. 1993). Studies suggest that the establishment of the *M. amazonicum* and *L. fortunei* in the invaded environments (mainly in Paraná River basin) has caused changes in the abundance and distribution of native species, nutrient cycling, productivity, and trophic relationships (Bialetsky et al. 1997; Darrigran et al. 1998; Magalhães et al. 2005; Boltovskoy et al. 2006; Rosa et al. 2021). Regarding trophic relationships, these non-native invertebrates are potential prey for a number of predators, especially fish, which consume them actively (Cantanhêde et al. 2008; Rosa et al. 2015; González-Bergonzoni et al. 2020; Rosa et al. 2021). However, there is no information about the influence that the consumption on these non-native prey may cause on food web structure.

Essentially, trophic relationships are delineated by a schematic description of connectivity (i.e. feeding links), quantifying the flow of energy and matter through the community and finally the interaction networks identifying strong links and dynamically important species (Polis 1994; Post et al. 2000). Although changes in diet regarding consumption of non-native prey can directly affect predators (Bulté and Blouin Demers 2008; Locke et al. 2014; Wood et al. 2017; Rosa et al. 2021), changes in the trophic interaction networks may have effects on local energy dynamics, thus affecting the ecosystem (Hairston and Hairston 1993). Therefore, understanding the range of interactions between fish and non-native

prey is essential for successfully managing disturbed ecosystems. Trophic interaction networks are most commonly studied from diet data (e.g. McCormack et al. 2021), stable isotope data (e.g. Vander Zanden and Vadeboncoeur 2002) or both (e.g. Calizza et al. 2021); diet data reflect direct consumption whereas stable isotopes reflect prey assimilation. In this study, we used diet data to assess trophic interactions, which contribute by providing information on frequency and biomass of native and non-native invertebrates subtracted from the prey population by the fish predators.

In this context, the present study evaluated the influence of non-native invertebrates on food web structure, by comparing fish diet composition, prey availability and network of trophic interactions in two Neotropical reservoirs with different age and distinct introductions history; Funil reservoir built in 2002 where there are no records of the invasive *L. fortunei*, and Volta Grande reservoir built in 1974 where *L. fortunei* is the predominant species of benthonic macroinvertebrate in sediment samples. Two hypotheses were tested: 1) in Volta Grande, the number and density of non-native prey species is higher and they are actively consumed by fish fauna, whereas in Funil the number and density of these prey are lower and they are not actively consumed by fish; and 2) because the invasion of *L. fortunei* and *M. amazonicum* promotes large-scale dietary shifts these non-native species may cause structural changes in the network of trophic interactions and in the control of ecological processes (e.g. nutrient flow through food web), and they are more pronounced in the Volta Grande reservoir.

## Methods

### Study site

The Grande River basin covers 87.000 km<sup>2</sup> within Minas Gerais state, Brazil, is the second largest river basin in this state. The climate in this region is humid temperate, with an annual mean temperature between 22 and 24 °C and an annual mean precipitation between 1.500 and 1.700 mm. This region is marked by two seasonal periods; warm/rainy between October and April and cold/dry between May and September (Braga and Gomiero 1997). To investigate the influence of non-native invertebrate species on the fish community trophic structure, two reservoirs located in the Grande River with similar fish communities were selected. Both areas are part of a series of cascade reservoirs, with the Funil reservoir (built in 2002) located in the upper portion (44°56'45"W, 21°06'18"S) and the Volta Grande reservoir (built in 1974) in the middle portion of this river (42°02'16"W, 20°06'50"S). There is no record of *L. fortunei* in the Funil reservoir to date and the present study did not capture it during the sampling period (between October 2015 and August 2016; neither in the sediment samples nor in the fish stomach contents). However, previous studies on Volta Grande reservoir have shown that *L. fortunei* is the predominant benthic macroinvertebrate in the sediment (Morais et al. 2014) and, together with *M. amazonicum*, represent new components of the local food web, acting as important source of biomass for the fish community (Rosa et al. 2021).

### Field and laboratory methods

Fish from two reservoirs located in the Grande River (Funil and Volta Grande reservoirs) were collected quarterly between October 2015 and July 2016 from six sample sites (three per reservoir). Samples were carried out at three equidistant collection sites in each reservoir. These sites were chosen in order to sample the three

compartments of the reservoir: fluvial, intermediate and lacustrine zones (Kimmel and Groeger 1984). We used a set of eleven bottom gillnets per site (10 m length, 1.5 to 2 m height, mesh size 25 to 160 mm; total sampled area = 150 m<sup>2</sup>), totaling twenty-four sampling events (four at each site). Nets were set in series perpendicularly to the shore. We maintained a minimal distance of approximately 20 m between nets, and depths varied from 1.0 to 7.0 meters. We installed all the nets at dusk and collected them at dawn the following day, remaining in the environment for about 14 hours. Were sampled 874 fish from the two reservoir (Funil, n = 476 and Volta Grande, n = 398). Fish were identified, measured on standard length (SL, cm), weighed with a precision scale (0.1 g) and then dissected to remove their stomach and intestine, which were immediately fixed in 10% formalin solution. Subsequently, we analyzed the total gut contents and identified on a stereomicroscope, with the non-native prey identified at species level and other items at the level of large groups (i.e. Order and Family). The food items in each stomach were spread on a Petri dish and identified under a stereoscopic microscope at the level of large groups (i.e. Order and Family). After the removal of excess humidity, using paper towels, the weight ( $\pm$  0.001 g precision) were recorded for each taxon identified in the stomach contents. For the mollusks prey the wet weight of the total individuals (i.e. body and shells fragments) were recorded and used for the subsequent analysis.

We used a Petersen-type bottom dredger (sampler's area = 319 cm<sup>2</sup>) to assess the composition and density of both native and non-native potential invertebrate prey available in sediment from the two reservoirs. The specimens were collected in the littoral zone of the same fish sampling sites. We collected three sediment samples per site in depths that varied from 1.0 to 6.0 m. After collection, all samples were duly identified and fixed in 10% formalin solution. In the laboratory, the sediment samples were washed through sieves with mesh sizes between 2 and 0.25 mm, and the benthic invertebrates were identified, up to higher taxonomic levels, before counting under a stereomicroscope.

### Data analysis

The frequency of occurrence (F) and percentage weight (%W) of food items in the fish stomachs were used to describe the diet of each species (Hyslop 1980). These values were combined to identify the main food items using the Feeding Index (FI) proposed by Kawakami and Vazzoler (1980):  $FI = (F_i \times \%W_i) / F_i \times \%W_i$ , where FI = feeding index of item i;  $F_i$  = frequency of occurrence of item i; and  $\%W_i$  = relative weight of item i.

The densities of invertebrates collected in the sediment samples from both reservoir were calculated according to Welch (1948):  $n = (0/a.s).10\ 000$ , where  $n$  is the number of specimens per m<sup>2</sup>,  $0$  is the number of specimens counted in the sample,  $a$  is the area of the sampler, and  $s$  is the number of samples collected. In addition, we compared densities of native and non-native invertebrates between the two reservoirs using Student's *t*-test. Before performing the test, we checked the normality of the distributions and the homoscedasticity of the data using the Kolmogorov-Smirnov and Levene tests, respectively, as proposed in Sokal and Rohlf (1981).

Species loss simulations were performed, and the network robustness to disturbances was evaluated. Before performing the analyses, we constructed the food web by recording the stomach contents of each predator. Then, an interaction matrix with the data listing prey species in the rows and predator species in the columns. Each matrix cell represents stomach contents measured by the Feeding Index. We that in mind, we constructed one food web for each reservoir. Species

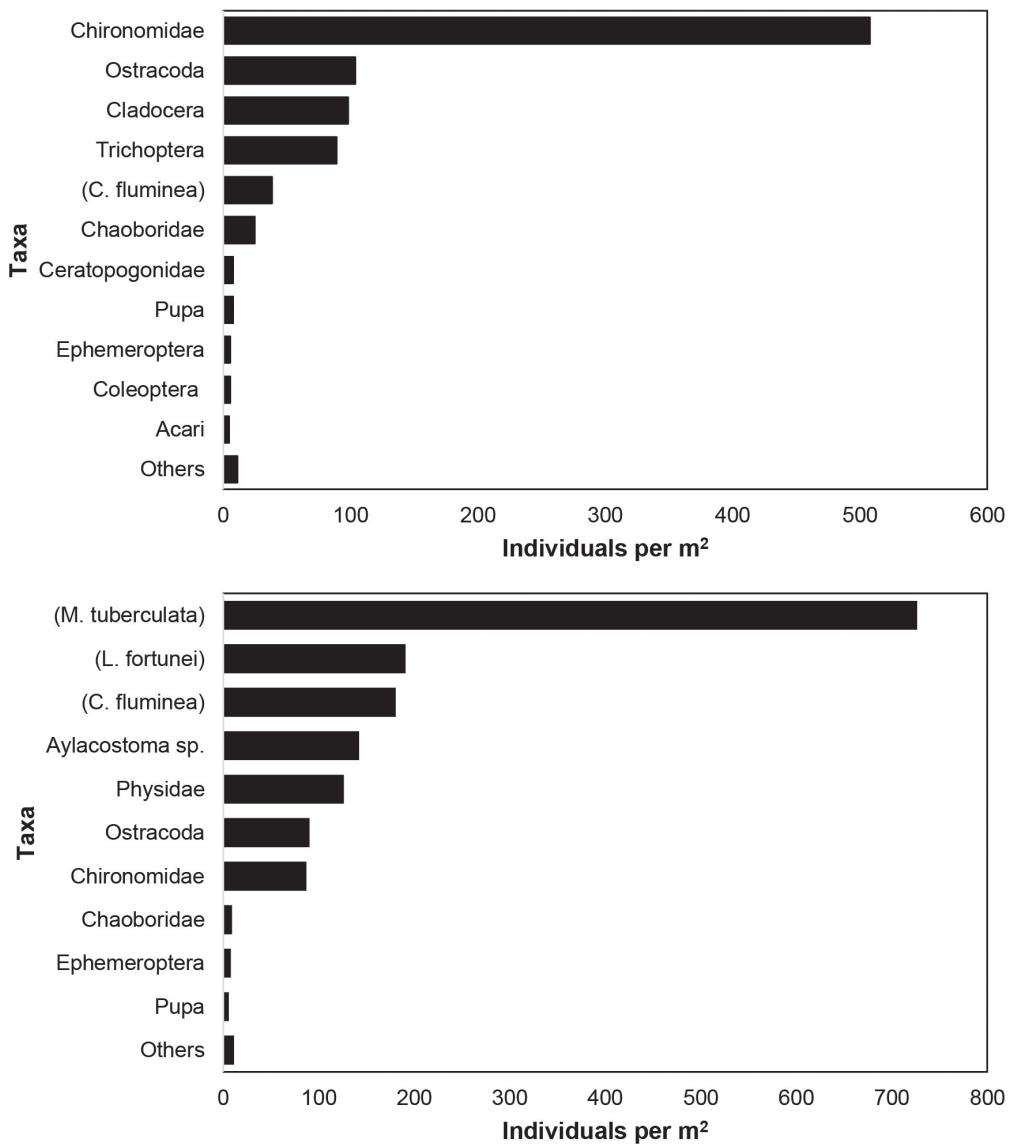
loss simulations were performed, and the network robustness to disturbances was evaluated. For each reservoir food web, species were removed followed by the number of species isolated by it (i.e. secondary extinction). Simulations were run until all species were isolated (i.e. total collapse of the food web). A graphical representation of the species isolated in the network by the proportion of species removed illustrates the community extinction curve, reproducing network structure loss against disturbances. The area under the curve measures the community robustness to the loss of species ( $R$ ), and lower robustness values indicate an intense loss of structure (Bersier et al. 2002). We estimate the robustness to secondary extinction for both food webs, assuming random deletion of species with 1000 replicates for each deleted species. Then, three scenarios under species deletion were assumed: 1) random, where the order of species removal did not obey any specific criterion; 2) per group, where the target species was first randomly drawn among non-native species and later among native species, or vice versa; and 3) given by the number of interactions, where the removal order started with the species with the highest number of interactions and moved gradually to those with the lowest number of interactions. Finally, the cumulative distribution of the number of interactions  $P(x)$  was measured, which infers the probability of obtaining a species with up to  $X$  interactions. This distribution was evaluated between environments and between groups (non-native and native species). All the functions used are presented in the Bipartite package (Dormann et al. 2008). All analyses were carried out in the R 4.0.2 environment (R Core Development Team 2021).

## Results

A total of 340 fish from 21 species caught in Volta Grande reservoir were subjected to stomach content analysis. Of these fish, 201 stomachs from 16 species contained food items, which were grouped into seven categories: *L. fortunei*, *Melanoides tuberculata* (Müller, 1774), *M. amazonicum*, fish (scales, muscle fragments, fins, whole fish, and highly digested fish), other invertebrates (mollusks, aquatic and terrestrial insects, crustaceans, annelids, and nematodes), plants (macrophytes, grasses, filamentous algae, cyanobacteria, fruits, and seeds), and detritus/sediment. Only the species that ingested non-native prey and/or reached a minimum of 5 stomachs containing a food item were considered by the diet analysis, totaling 13 species in this reservoir. The FI showed that non-native invertebrates were ingested by 11 fish species (Suppl. material 1); four of which consistently consumed the non-native *M. amazonicum* (i.e. *Plagioscion squamosissimus* (Heckel, 1840), *Cichla kelberi* Kullander & Ferreira, 2006, *C. piquiti* and *H. intermedius*), and likewise, three species consumed the non-native *L. fortunei* (i.e. *L. friderici*, *Australoheros facetus* (Jenyns, 1842) and *Crenicichla britskii* Kullander, 1982).

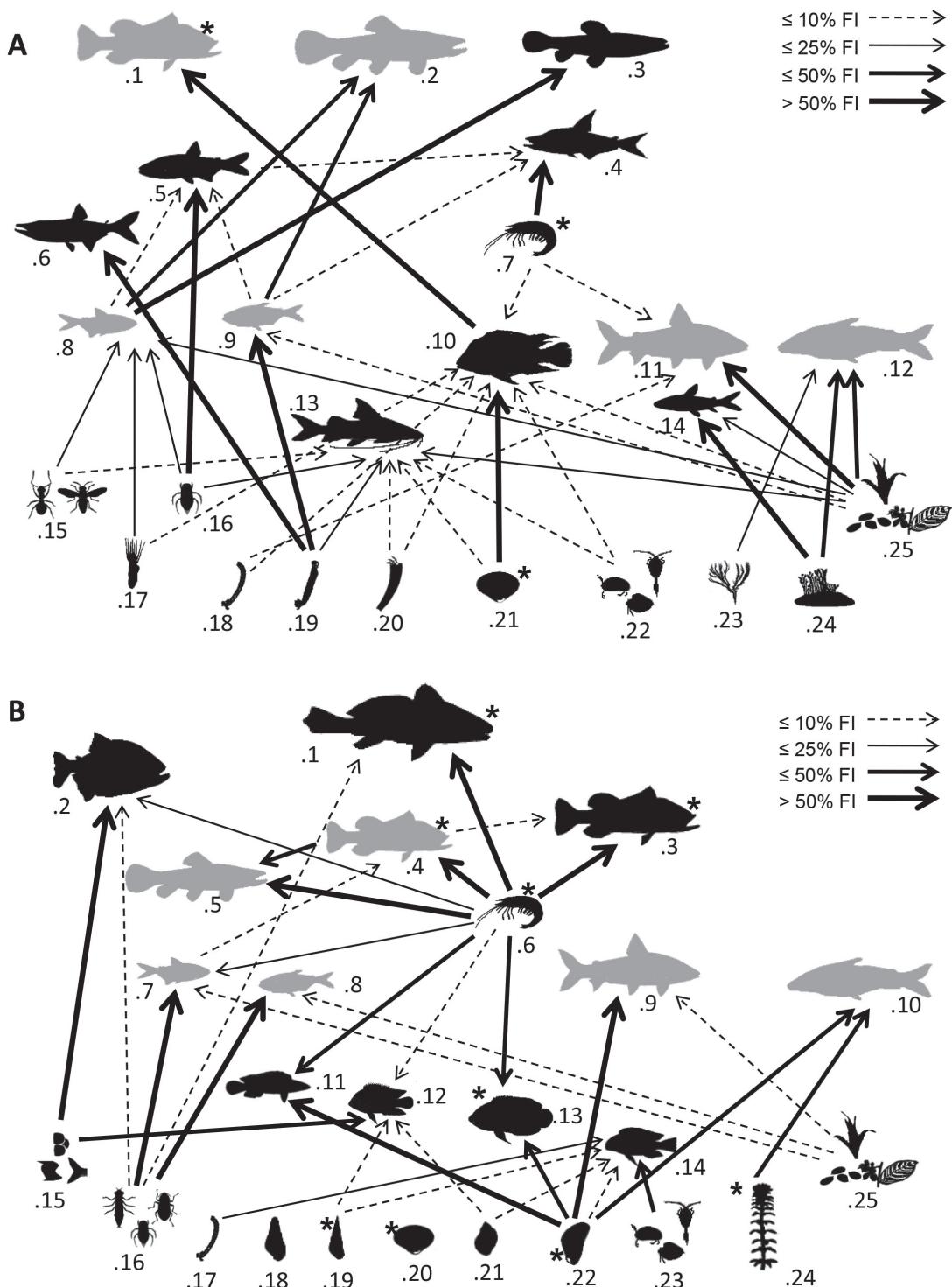
In the Funil reservoir, 347 fish stomachs were analyzed from 20 fish species. A total of 227 stomachs belonging to 16 species contained food items, which were grouped into eight categories: *Corbicula fluminea* (Müller, 1774), *M. amazonicum*, fish (scales, muscle fragments, fins, whole fish, and highly digested fish), insects (larval forms, pupae, and terrestrial and aquatic adults), other invertebrates (mollusks, crustaceans, arachnids, and nematodes), periphyton, plants (macrophytes, grasses, filamentous algae, fruits, and seeds) and detritus/sediment. Using the same species exclusion criterion adopted for the Volta Grande reservoir, only 12 species were used in the diet analysis. According to the FI, non-native prey were consumed extensively by two species; *C. fluminea* was the main prey ingested by *Geophagus brasiliensis* (Quoy & Gaimard, 1824) and *M. amazonicum* was the main item in the diet of *Galeocharax knerii* (Steindachner, 1879) (Suppl. material 2).

In the sediment samples, 2,222 benthic invertebrates were captured, with 1,418 in Volta Grande and 804 in Funil. A total of 14 and 20 taxonomic groups were identified in the Volta Grande and Funil reservoirs, respectively. The reservoir presented the same density of native invertebrates ( $F = 0.11$ ;  $df = 21$ ;  $p = 0.75$ ), but the density of non-native ones was higher in Volta Grande ( $F = 29.6$ ;  $df = 21$ ;  $p < 0.001$ ). The non-native species *M. tuberculata* ( $n = 644$ ), *C. fluminea* ( $n = 175$ ), and *L. fortunei* ( $n = 169$ ) were the most abundant taxa in Volta Grande, while Chironomidae larvae ( $n = 450$ ), Ostracoda ( $n = 92$ ), and Cladocera ( $n = 87$ ) were the most abundant in Funil (Fig. 1).



**Figure 1.** Densities of the macroinvertebrate taxa found in the sediment samples from the Funil (above) and Volta Grande (below) reservoirs, Grande River, Brazil. Non-native taxa are between parentheses.

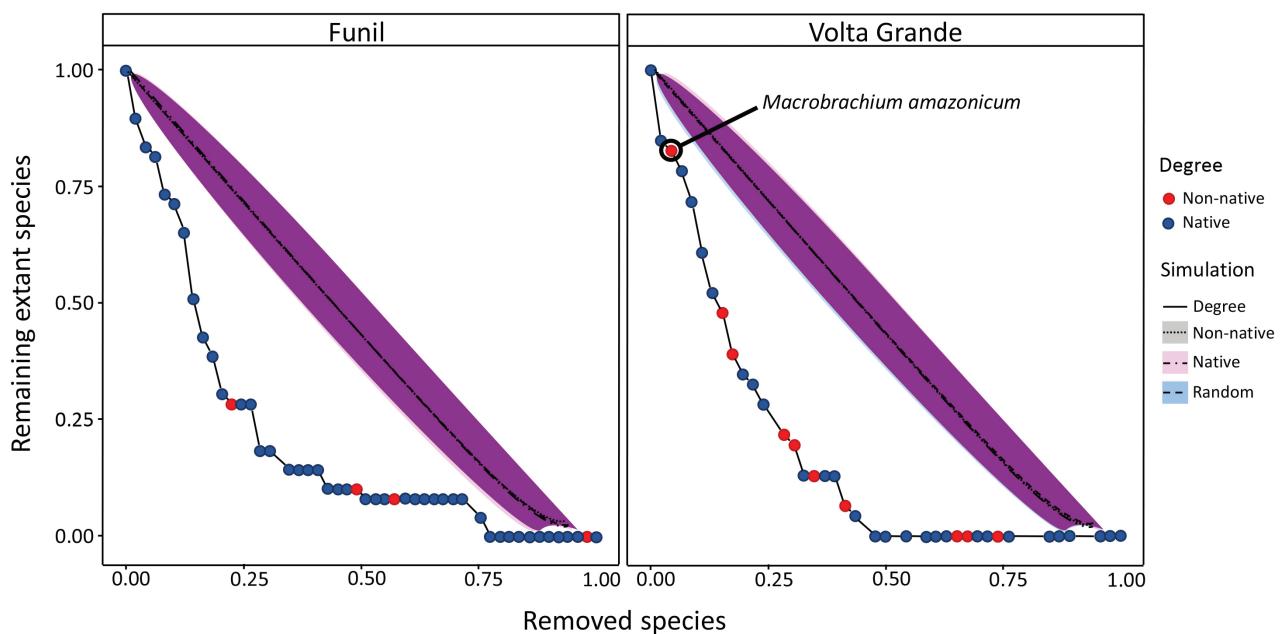
Based on the data obtained from the stomach contents analyses it was possible to estimate the diet of the fish assemblages of the two reservoirs. The fish assemblages shared many trophic relationships. However, in Volta Grande a greater number of fish species (6 species = 46%) were found actively consuming non-native invertebrates (i.e. FI > 50%), whereas in Funil only two fish species (15%) actively consumed non-native prey (Fig. 2). This suggests that whereas in Volta



**Figure 2.** Food web diagram based on the catches of fish and benthic macroinvertebrates, as well as on the diet analysis of selected fish, showing the main trophic interactions in the two reservoirs analyzed. FI = Feeding Index (the main trophic interactions were derived from FI results). **Funil reservoir (A):** *C. piquiti* (1), *H. intermedius* (2), *H. malabaricus* (3), *G. kneri* (4), *O. pintoi* (5), *A. lacustris* (6), *M. amazonicum* (7), *A. altiparanae* (8), *P. fasciatus* (9), *G. brasiliensis* (10), *L. friderici* (11), *S. nasutus* (12), *P. maculatus* (13), *S. insculpta* (14), terrestrial insects (15), Corixidae (16), pupae (17), Chironomidae larvae (18), Chaoboridae larvae (19), Trichoptera larvae (20), *C. fluminea* (21), Cladocera, Ostracoda, and Copepoda (22), filamentous algae (23), periphyton (24), and plants (25). **Volta Grande reservoir (B):** *P. squamosissimus* (1), *S. maculatus* (2), *C. kelberi* (3), *C. piquiti* (4), *H. intermedius* (5), *M. amazonicum* (6), *A. altiparanae* (7), *P. fasciatus* (8), *L. friderici* (9), *S. nasutus* (10), *C. britskii* (11), *A. facetus* (12), *A. crassipinnis* (13), *S. pappaterra* (14), fish scales, fins, and muscle (15), adult insects (16), Chironomidae larvae (17), *A. tenuilabris* (18), *M. tuberculata* (19), *C. fluminea* (20), *Physa* sp. (21), *L. fortunei* (22), Cladocera, Ostracoda, and Copepoda (23), submerged macrophyte (24), and plants (25). The fish species common to the two reservoirs are represented in gray, and the non-native taxa are indicated with asterisks.

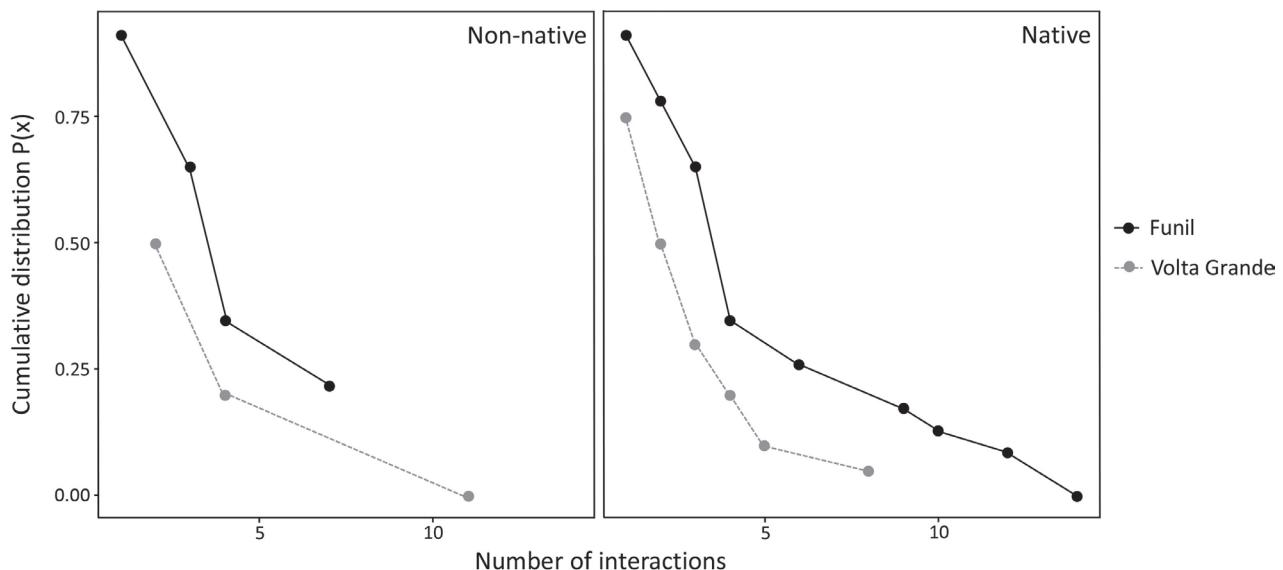
Grande much of the energy flow between benthic organisms (prey) and the fish assemblage (predators) occurs through non-native species, especially *M. amazonicum* and *L. fortunei*, in Funil the opposite is true.

Species loss simulations indicated that the networks did not differ significantly between random losses and losses between groups. The random simulations indicated a mean robustness of  $R = 0.42 \pm 0.03$  for Volta Grande and  $R = 0.43 \pm 0.03$  for Funil. The robustness observed for the loss of non-native species followed by the loss of native taxa was  $R = 0.40 \pm 0.03$  for Volta Grande and  $R = 0.44 \pm 0.02$  for Funil. The probability of occurrence of these values in the random simulations was 0.29 and 0.54, respectively. Similarly, the robustness observed for the loss of native taxa followed by the loss of non-native species was  $R = 0.44$  for Volta Grande and  $R = 0.42$  for Funil, with a probability of occurrence of 0.70 and 0.33 in the random simulations, respectively (Fig. 3).



**Figure 3.** Species removal simulation. At each simulation step, all interactions of a target species are removed, and the number of other species isolated by that loss is evaluated. The simulation is run until all species are isolated. The area below the extinction curve measures the community robustness to the loss of species. Random: species are randomly removed. Non-native: the target species are randomly drawn first among non-native species and later among native species. Native: target species are randomly drawn first among native species and later among non-native species. Degree: the species with the highest number of interactions is first removed, gradually removing those with the lowest number of interactions.

Lastly, Fig. 4 shows the probability (i.e. by chances) of species occurrence in the food web regarding the number of interactions. Most food web species are more likely to depict a low number of interactions regardless of native or non-native species and reservoirs. Evaluating the cumulative probability of the number of interactions for non-native and native taxa between reservoirs explains this pattern. In general, there was a decrease in the probability of occurrence of highly connected taxa in both reservoirs and between non-native and native taxa. In addition, there was generally a higher probability of occurrence of highly connected taxa among native ones. In this regard, Funil was more likely to exhibit highly connected native taxa than Volta Grande. However, Volta Grande showed higher chances of exhibiting highly connected taxa among the non-native ones (Fig. 4). This difference can be explained mainly by the strong effect that *M. amazonicum* exerts on the Volta Grande community, as the species with the second greatest number of interactions.



**Figure 4.** Cumulative distribution of the probability of occurrence of a species with a certain number of interactions or less.

## Discussion

Based on results from Volta Grande reservoir, this study suggest that when non-native invertebrate prey become an important energy source for fish fauna, they can also influence the food web by acting on ecological processes such as nutrient flow, ensuring robustness to environmental disturbances in such an invaded system. On the other hand, the results from Funil showed lower contribution of non-native invertebrates in the fish diet and according to the species loss simulations they do not seem to have a major influence on food web structure. Reservoirs are more prone to biological invasion processes due to the abiotic conditions such as morphological habitat and water quality degradation that create conditions more suitable for invasive species and those tolerant of degraded ecosystems (Havel et al. 2005; Früh et al. 2012a, b; Bates et al. 2013; Thomaz et al. 2014). The Volta Grande Reservoir was filled in the 1970s and has historically been subject to introductions of non-native vertebrate and invertebrate species (Braga 2001; Morais et al. 2014), which currently have a strong influence on both predator and prey composition (Rosa et al. 2021). The above information may help to explain in part the greater influence of non-native taxa on food web structure of the older reservoir (i.e. Volta Grande). The increasing anthropogenic activities around reservoirs can deteriorate their habitat quality over time through processes such as sedimentation, eutrophication, chemical and thermal pollution (Schmutz and Moog 2018; Sunardi et al. 2020). In this context, older reservoirs tend to have lower abiotic conditions than newer ones, thus the former would be more susceptible to the establishment of non-native benthonic invertebrates (Früh et al. 2012b). Accordingly it could be expected that the influence of these species would be stronger on the food web of Volta Grande than Funil, a reservoir that is 28 years younger. Therefore, in light of the aforementioned, the following question arises: Can older reservoirs become highly dependent on non-native species for maintenance and functioning of ecological processes such as energy flow? Although our results do not support this hypothesis they may encourage future research to evaluate long-term data to test it, since non-native species are widespread and biotic homogenization processes have been ruling in reservoirs of the Paraná River basin (see Vitule et al. 2012; Miyahira et al. 2020), possibly making scenarios like the ones presented here increasingly common in this basin.

The sediment sampling in Volta Grande revealed a community of benthic invertebrates predominantly composed of non-native mollusks, among which *L. fortunei* was identified as an important trophic resource for benthic fish, according to the fish diet analysis. In a previous study, *L. fortunei* was the dominant benthic invertebrate in the sediment collected in several regions of this reservoir (Morais et al. 2014). Similar results were observed in the Ilha Solteira reservoir (upper Paraná River), where this non-native bivalve was the most abundant organism in the sediment samples and the non-native prey most consumed by some fish species (Rosa et al. 2015). Although sediment is not the preferred substrate of *L. fortunei*, the mobility of smaller individuals allows their movement over sediment, where they may be exposed to predation by benthic fish (Uryu et al. 1996; Vieira and Lopes 2013). Studies from reservoirs of the Paraná River basin suggest that in systems invaded by *L. fortunei*, where they reach high densities, some fish species may actively consume them (Oliveira et al. 2010; Rosa et al. 2015). On the other hand, in systems where this species may not be the main component of the benthic community, such as floodplains, its consumption by fish does not appear significant (Isaac et al. 2014). A similar pattern may have occurred with *M. amazonicum*, which although its relative abundance in the environment was not considered by the present study, its importance as a food item for the analyzed fish suggests high availability in the Volta Grande reservoir during the sampling period. Some reproductive characteristics of both *M. amazonicum* and *L. fortunei*, such as continuous reproduction, high fecundity, and planktonic larvae, enable them to occupy environments that have undergone changes in the hydrological regime, such as reservoirs, in which both species can reach high abundance (Bialetzky et al. 1997; Takeda et al. 2003; Magalhães et al. 2005; Silva 2010; Morais et al. 2014). In addition, the increased light penetration in the water column promoted by settling out of suspended sediment from the water column as the environment transitions from riverine to lacustrine in the reservoir stimulates macrophyte production (Thomaz 2002), which favour the development of species such as *M. amazonicum* (Odinetz-Collart and Moreira 1993) and *L. fortunei* (Michelan et al. 2014), as well as several fish species (Pelicice et al. 2005). Therefore, the new environmental conditions created by reservoir formation seemingly contributed to the establishment of these non-native species that, because they are consumed as prey, promoted new interactions among species.

Although Funil reservoir presents a fish assemblage similar to Volta Grande, the difference found in invertebrate composition suggests that these environments produce different food supplies for their fish community. In addition to introduced species that may influence the benthic fauna composition (Darrigan et al. 1998), characteristics such as morphology, presence of tributaries, human activities, and type of power plant operation may be responsible for the differences in benthic invertebrate composition among reservoirs (Santos et al. 2016). Due to limited dispersal, these organisms are directly dependent on local environmental characteristics (Callisto et al. 2005; Behrend et al. 2012), with neighboring communities showing differences in taxa composition (Poff 1997). Accordingly, the food resources available for exploitation by benthic fish also vary among these environments (Smith 2004) and may contribute to differences in the fish diet as found by this study. Although the analyses in the present study revealed the presence of the non-native *M. amazonicum* in the fish diet also in Funil reservoir, it was less representative in terms of consumption when compared to Volta Grande. In general, predatory fish exploit smaller prey, such as *M. amazonicum*, when these prey are more abundant and available (Neves et al. 2015). However, to compensate for the energy cost, the number of prey should be substantially higher (Bozza and Hahn 2010), as explained by the optimal forage theory (Pyke 1984). In this context, the hight abundance of

small fish caught in Funil, such as *A. altiparanae* and *P. fasciatus* may be supplying the diet of piscivorous species, and possibly *M. amazonicum*, a smaller prey, was less exploited by these fish. A similar pattern may have occurred with *C. fluminea* that, although it is a component of the benthic fauna in the Funil reservoir, was not among the most abundant taxa and was consumed by only a single fish species.

Regarding the diet composition of common species between the two reservoirs, it was possible to observe a substantial spatial difference in the diet of *L. friderici*, a relatively abundant species in both reservoirs. In Volta Grande, a predominantly carnivorous diet composed almost exclusively of *L. fortunei* was detected (Suppl. material 1) while in Funil an exclusively herbivorous diet was observed (Suppl. material 2). *Leporinus friderici* is a species considered omnivorous and euphagic, with opportunistic behaviour, consuming mainly allochthonous food items of plant origin (Albrecht and Caramaschi 2003). A study developed in the Tocantins River, identified the opportunistic behaviour of this species during the filling phase of a reservoir, during which *L. friderici* rapidly changed its diet when a vast amount of easy prey was offered (Albrecht and Caramaschi 2003). In this context, the results obtained by the present study corroborate the opportunistic feeding behaviour of this species, since the supply of an easy and abundant prey (i.e. non-native *L. fortunei*; semi-sesile organism) possibly influenced the carnivorous diet recorded for *L. friderici* in Volta Grande. Furthermore, the active consumption of *L. fortunei* by *L. friderici* in Volta Grande may have some consequences on the food web energy flow as described by Rosa et al. (2021). Using isotopic analysis tools, the authors identified that individuals of *L. friderici* derived a large part of their biomass from *L. fortunei*, that is, from autochthonous energy sources and not from allochthonous sources as observed in reservoirs devoid of *L. fortunei*. This suggests that after the establishment of *L. fortunei* in Volta Grande, *L. friderici* possibly changed its diet composed of allochthonous food items (as observed by Albrecht and Caramaschi 2003 and by the present study in Funil) to a predominantly autochthonous diet, thus influencing the energy distribution dynamics of the food web. However, future studies considering fish diet data from pre-invasion of *L. fortunei* in reservoirs are necessary to confirm such hypothesis.

Regarding the trophic network structure, highly connected taxa control the dispersion of community energy flow and provide multiple energy pathways to compensate for the loss of one taxon (MacArthur 1955; Dunne et al. 2002), despite its low occurrence probability (see Pimm 2002 for more information about it). Ecological effects on a community after disturbance should not be inferred solely from the number of taxa affected but also from the taxa role in the community, which can promote significantly faster side effects in the community structure than random taxa loss (Dunne et al. 2002; Srinivasan et al. 2007). The results show that the presence of non-native prey, especially *M. amazonicum*, influences the trophic network structure, promoting community dependence on non-native species to ensure robustness to environmental disturbances, thus confirming the second hypothesis. Species that have a larger than expected effect on the ecological rates and processes of a community based on their abundance are classified as keystone species in the system (Power et al. 1996). In this sense, non-native species with a large number of interactions in disturbed communities, such as Volta Grande reservoir, can play as keystone species in a community structure, and species removal must be evaluated for potential impacts exerted on such a community. As for the fish community, studies suggest that the presence of fish with a highly diverse diet promotes plasticity in prey consumption after an initial loss, reducing the secondary impacts of environmental disturbances (Staniczenko et al. 2010; Monteiro et al. 2018). However, notably, this evaluation only infers local and direct effects of species loss (Jordán 2009). Species also have indirect effects on other species, and the secondary effect of species loss may be even more pronounced

under conditions of low functional redundancy (Borrrell et al. 2000; Jordán 2009). Thus, future studies should evaluate not only the presence or absence of interactions but also the role of energy flows through simulations on quantitative networks.

In a previous work, Rosa et al. (2021) showed strong evidence that non-native invertebrates represent an important food source for fish assemblage in Volta Grande where they have influence on the importance of energy pathways. According to the study, non-native invertebrates were responsible for supporting more than half of the biomass of native and non-native fish. Therefore, the present work further highlights the important role played by these non-native prey that besides supporting fish assemblages, in some cases they can act as keystone species in reservoirs. In addition, we showed not only the feasibility of using reservoirs with different ages and distinct species introduction history to study the influence of non-native invertebrates, but also the caution required in interpreting ecological findings from extremely altered reservoirs (e.g Volta Grande) that have non-native organisms acting as keystone species.

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### Authors' contributions

D.R. and P.P. conceived the ideas, designed methodology and collected the data; D.R. did laboratory work, analyzed the data and led the writing of the manuscript. A.M. and L.F. analyzed the data, and provided suggestions for data analysis and feedback on the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### Ethics and permits

The authors have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects. This research was permitted by Sistema de Autorização e Informação em Biodiversidade (SISBIO/ICMBio) by means of the Permanent License N° 10327. We are willing to share the original data and materials if so requested.

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## References

- Albrecht MP, Caramaschi EP (2003) Feeding ecology of *Leporinus friderici* (Teleoste; Anostomidae) in the upper Tocantins River, Central Brazil, before and after installation of a hydroelectric plant. *Studies on Neotropical Fauna and Environment* 38: 33–40. <https://doi.org/10.1076/snfe.38.1.33.14033>
- Bates AE, McKelvie CM, Sorte CJB, Morley SA, Jones NAR, Mondon JA, Bird TJ, Quinn G (2013) Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131958. <https://doi.org/10.1098/rspb.2013.1958>
- Behrend RDL, Takeda AM, Gomes LC, Fernandes SEP (2012) Using oligochaeta assemblages as an indicator of environmental changes. *Brazilian Journal of Biology* 72: 873–884. <https://doi.org/10.1590/S1519-69842012000500014>
- Bersier L, Banašek-Richter C, Cattin M (2002) Quantitative descriptors of food-web matrices. *Ecology* 83: 2394–2407. [https://doi.org/10.1890/0012-9658\(2002\)083\[2394:QDOFWM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2)
- Bialetzki A, Nakatani K, Baumgartner G, Bond Buckup G (1997) Occurrence of *Macrobrachium amazonicum* (Heller 1862) (Decapoda, Palaemonidae) in Leopoldo's inlet (Ressaco do Leopoldo), upper Paraná river, Porto Rico, Paraná, Brazil. *Revista Brasileira de Zoologia* 14: 379–390. <https://doi.org/10.1590/S0101-81751997000200011>
- Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Leinoir J, Vilà M, Sorte CJB (2019) Disentangling the abundance–impact relationship for invasive species. *Proceedings of the National Academy of Sciences* 116(20): 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Boltovskoy D, Correa N, Cataldo D, Sylvester F (2006) Dispersion and ecological impacts of the invasive freshwater bivalve *Limnoperna fortunei* in Río de la Plata watershed and beyond. *Biological Invasions* 8: 947–963. <https://doi.org/10.1007/s10530-005-5107-z>
- Borrrell C, Ebenman B, Jonsson TJT (2000) Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3: 131–136. <https://doi.org/10.1046/j.1461-0248.2000.00130.x>
- Bozza AN, Hahn NS (2010) Uso dos recursos alimentares por peixes imaturos e adultos de espécies piscívoras em uma planície de inundação neotropical. *Biota Neotropica* 10: 217–226. <https://doi.org/10.1590/S1676-06032010000300025>
- Braga FMS (2001) Reprodução de peixes (OSTEICHTHYES) em afluentes do reservatório de Volta Grande, rio Grande, sudeste do Brasil. *Iheringia Série Zoologia* 91: 67–74. <https://doi.org/10.1590/S0073-47212001000200009>
- Braga FMS, Gomiero LM (1997) Análise da pesca experimental realizada no reservatório de Volta Grande, rio Grande (MG-SP). *Boletim do Instituto de Pesca* 24: 131–138.
- Bulté G, Blouin-Demers G (2008) Northern map turtles (*Graptemys geographica*) derive energy from the pelagic pathway through predation on zebra mussels (*Dreissena polymorpha*). *Freshwater Biology* 53: 497–508. <https://doi.org/10.1111/j.1365-2427.2007.01915.x>
- Calizza E, Rossi L, Careddu G, Caputi SS, Costantini ML (2021) A novel approach to quantifying trophic interaction strengths and impact of invasive species in food webs. *Biological Invasions* 23: 2093–2107. <https://doi.org/10.1007/s10530-021-02490-y>
- Callisto M, Goulart M, Barbosa FAR, Rocha O (2005) Biodiversity assessment of benthic macroinvertebrates along a reservoir cascade in the lower São Francisco river (northeastern Brazil). *Brazilian Journal of Biology* 2: 229–240. <https://doi.org/10.1590/S1519-69842005000200006>
- Cantanhêde G, Hahn NS, Gubiani EA, Fugi R (2008) Invasive mollusks in the diet of *Pterodoras granulosus* (Valenciennes, 1821) (Pisces, Doradidae) in the upper Paraná River floodplain, Brazil. *Ecology of Freshwater Fish* 17: 47–53. <https://doi.org/10.1111/j.1600-0633.2007.00258.x>
- Cataldo D (2015) Trophic relationships of *Limnoperna fortunei* with adult fishes. In: Boltovskoy D (Ed.) *Limnoperna fortunei*. The ecology, distribution and control of a swiftly spreading invasive fouling mussel. Springer, London, 231–248. [https://doi.org/10.1007/978-3-319-13494-9\\_13](https://doi.org/10.1007/978-3-319-13494-9_13)
- Courchamp F, Chapuis J-L, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78: 347–383. <https://doi.org/10.1017/S1464793102006061>

- Darrigran G, Martin SM, Gullo B, Armendariz L (1998) Macroinvertebrate associated to *Limnoperna fortunei* (Dunker, 1857) (Bivalvia, Mytilidae) in Río de la Plata, Argentina. *Hydrobiologia* 367: 223–230. <https://doi.org/10.1023/A:1003244603854>
- David P, Thébaud E, Anneville O, Loeuille N (2017) Impacts of invasive species on food webs: a review of empirical data. *Advances in Ecological Research* 56: 1–60. <https://doi.org/10.1016/bs.aecr.2016.10.001>
- Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing ecological networks. *R News* 8: 8–11.
- Dwyer G, Morris WF (2006) Resource-dependent dispersal and the speed of biological invasions. *American Naturalist* 167: 165–176. <https://doi.org/10.1086/498944>
- Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5: 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>
- Früh D, Stoll S, Haase P (2012a) Physicochemical and morphological degradation of stream and river habitats increases invasion risk. *Biological Invasions* 14: 2243–2253. <https://doi.org/10.1007/s10530-012-0226-9>
- Früh D, Stoll S, Haase P (2012b) Physico-chemical variables determining the invasion risk of freshwater habitats by alien mollusks and crustaceans. *Ecology and Evolution* 2: 2843–2853. <https://doi.org/10.1002/ece3.382>
- Gomes-Correa MM (1977) Paleomonídeos do Brasil (Crustacea, Decapoda, Natantia). MsC Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil, 135 pp.
- González-Bergonzi I, Silva I, Mello FT, D'Anatro A, Boccardi L, Stebniki S, Brugnoli E, Tesitore G, Vidal N, Naya DE (2020) Evaluating the role of predatory fish controlling the invasion of the Asian golden mussel *Limnoperna fortunei* in a subtropical river. *Journal of Applied Ecology* 57: 717–728. <https://doi.org/10.1111/1365-2664.13573>
- Hairston Jr NG, Hairston Sr NG (1993) Cause effect relationships in energy flow trophic structure and interspecific interactions. *American Naturalist* 142: 379–411. <https://doi.org/10.1086/285546>
- Havel JE, Lee CE, Vander Zanden MJ (2005) Do reservoirs facilitate invasions into landscapes? *BioScience* 55: 518–525. [https://doi.org/10.1641/0006-3568\(2005\)055\[0518:DRFIIL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2.0.CO;2)
- Hyslop EJ (1980) Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* 17: 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>
- Isaac A, Fernandes A, Ganassin MJM, Hahn NS (2014) Three invasive species occurring in the diets of fishes in a Neotropical floodplain. *Brazilian Journal of Biology* 74: 16–22. <https://doi.org/10.1590/1519-6984.18312>
- Jordán F (2009) Keystone species and food webs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364: 1733–1741. <https://doi.org/10.1098/rstb.2008.0335>
- Kawakami E, Vazzoler G (1980) Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico* 29: 205–207. <https://doi.org/10.1590/S0373-55241980000200043>
- Kimmel BL, Groeger AW (1984) Factors controlling primary production in lakes and reservoirs: a perspective. *Lake and Reservoir Management* 1: 277–281. <https://doi.org/10.1080/07438148409354524>
- Locke SA, Bulté G, Marcogliese DJ, Forbes MR (2014) Altered trophic pathway and parasitism in a native predator (*Lepomis gibbosus*) feeding on introduced prey (*Dreissena polymorpha*). *Oecologia* 175: 315–324. <https://doi.org/10.1007/s00442-014-2898-6>
- MacArthur R (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533–536. <https://doi.org/10.2307/1929601>
- Magalhães C, Bueno SLS, Bond-Buckup G, Valenti WC, Silva HLM, Kiayohara F, Mossolin EC, Rocha SS (2005) Exotic species of freshwater decapod crustaceans in the state of São Paulo, Brazil: records and possible causes of their introduction. *Biodiversity and Conservation* 14: 1929–1945. <https://doi.org/10.1007/s10531-004-2123-8>

- Maguire C, Grey J (2006) Determination of zooplankton dietary shift following a zebra mussel invasion, as indicated by stable isotope analysis. *Freshwater Biology* 51: 1310–1319. <https://doi.org/10.1111/j.1365-2427.2006.01568.x>
- Mansur MCD, Santos CP, Darrigran G, Heydricht I, Callil CT, Cardoso FR (2003) Primeiros dados quail-quantitativos do mexilhão dourado, *Limnoperna fortunei* (Dunker), no Delta do Jacuí, no lago Guaíba e na Laguna dos Patos, Rio Grande do Sul, Brasil e alguns aspectos de sua invasão no novo ambiente. *Revista Brasileira de Zoologia* 20: 75–84. <https://doi.org/10.1590/S0101-81752003000100009>
- McCormack SA, Melbourne-Thomas J, Trebilco R, Blanchard JL, Raymond B, Constable A (2021) Decades of dietary data demonstrate regional food web structures in the Southern Ocean. *Ecology and Evolution* 11(1): 227–241. <https://doi.org/10.1002/ece3.7017>
- McEachran MC, Trapp RS, Zimmer KD, Herwig BR, Hegedus CE, Herzog CE, Staples DF (2019) Stable isotopes indicate that zebra mussels (*Dreissena polymorpha*) increase dependence of lake food webs on littoral energy sources. *Freshwater Biology* 63: 183–196. <https://doi.org/10.1111/fwb.13206>
- Michelan TS, Petsch DK, Pinha GD, Silveira MJ, Thomaz SM (2014) The invasive aquatic macrophyte *Hydrilla verticillata* facilitates the establishment of the invasive mussel *Limnoperna fortunei* in Neotropical reservoirs. *Journal of Limnology* 73: 598–602. <https://doi.org/10.4081/jlimnol.2014.909>
- Miehls AJ, Mason DM, Frank KA, Krause AE, Peacor SD, Taylor WW (2009) Invasive species impacts on ecosystem structure and function: a comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. *Ecological Modelling* 220: 3194–3209. <https://doi.org/10.1016/j.ecolmodel.2009.07.013>
- Monteiro AB, Contente RF, Faria LDB (2018) Resource depletion and mechanisms for food web robustness in a Neotropical estuary. *Marine and Freshwater Research* 69: 1755–1761. <https://doi.org/10.1071/MF17141>
- Morais L, Farias RL, Martins I, Barbosa JEL, Molozzi J, Anacléto MJ, Callisto M (2014) Bioindicadores bentônicos de qualidade ambiental em reservatórios da Cemig. In: Callisto M, Alves CBM, Lopes JM, Castro MA (Eds) Condições ecológicas em bacias hidrográficas de empreendimentos hidrelétricos. Companhia Energética de Minas Gerais, Série Peixe Vivo, Belo Horizonte, 161–184.
- Miyahira IC, Pereira LS, dos Santos LN (2020) Non-native freshwater molluscs in the Neotropics: what can be learned from Brazilian reservoirs? *Aquatic Invasions* 15(3): 455–472. <https://doi.org/10.3391/ai.2020.15.3.06>
- Neves MP, Delariva RL, Guimarães ATB, Sanches PV (2015) Carnivory during ontogeny of the *Plagioscion squamosissimus*: a successful non-native fish in a lentic environment of the Upper Paraná River Basin. *PLoS ONE* 10: e0141651. <https://doi.org/10.1371/journal.pone.0141651>
- Nilsson E, Solomon CT, Wilson KA, Willis TV, Larget B, Vander Zanden MJ (2012) Effects of an invasive crayfish on trophic relationships in north-temperate lake food webs. *Freshwater Biology* 57: 10–23. <https://doi.org/10.1111/j.1365-2427.2011.02688.x>
- Odinetz-Collart O, Moreira LC (1993) Potencial pesqueiro do camarão *Macrobrachium amazonicum* na Amazônia Central (Ilha do Careiro): variação da abundância e do comprimento. *Amazoniana* 12: 399–413.
- Oliveira CRC, Fugi R, Brancalhão KP, Agostinho AA (2010) Fish as potential controllers of invasive mollusks in a neotropical Reservoir. *Natureza & Conservação* 8(2): 140–144. <https://doi.org/10.4322/natcon.00802006>
- Oliveira MD, Campos MCS, Paolucci EM, Mansur MCD, Hamilton SK (2015) Colonization and spread of *Limnoperna fortunei* in South America. In: Boltovskoy D (Ed.) *Limnoperna fortunei. The ecology, distribution and control of a swiftly spreading invasive fouling mussel*. Springer, London, 333–355. [https://doi.org/10.1007/978-3-319-13494-9\\_19](https://doi.org/10.1007/978-3-319-13494-9_19)
- Pastorino G, Darrigran GA, Martín SM, Lunaschi L (1993) *Limnoperna fortunei* (Dunker, 1857) (Mytilidae), nuevo bivalvo invasor en aguas del Río de la Plata. *Neotropica* 39: 101–102.
- Pelicice FM, Agostinho AA, Thomaz SM (2005) Fish assemblages associated with *Egeria* in a tropical reservoir: investigating the effects of plant biomass and diel period. *Acta Oecologica* 27: 9–16. <https://doi.org/10.1016/j.actao.2004.08.004>

- Poff NL (1997) Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16: 391–409. <https://doi.org/10.2307/1468026>
- Polis GA (1994) Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19: 121–136. <https://doi.org/10.1111/j.1442-9993.1994.tb00475.x>
- Post DM, Conners ME, Goldberg DS (2000) Prey preference by a top predator and the stability of linked food chains. *Ecology* 81(1): 8–14. <https://doi.org/10.2307/177129>
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the Quest for Keystones. *BioScience* 46: 609–620. <https://doi.org/10.2307/1312990>
- Pimm S [Ed.] (2002) Food webs, Volume 2. University of Chicago Press, Chicago, 258 pp. <https://doi.org/10.1007/978-94-009-5925-5>
- Pyke GH (1984) Optimal foraging theory a critical review. *Annual Review of Ecology and Systematics* 15: 523–575. <https://doi.org/10.1146/annurev.es.15.110184.002515>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rennie MD, Sprules WG, Johnson TB (2009) Resource switching in fish following a major food web disruption. *Oecologia* 159: 789–802. <https://doi.org/10.1007/s00442-008-1271-z>
- Rosa DM, Santos GB, Gomes PLA, Campos MCS, Dias JHP (2015) Occurrence of *Limnoperna fortunei* (Dunker, 1857) in the fish diet from a south-eastern Brazilian reservoir. *Journal of Applied Ichthyology* 31: 188–191. <https://doi.org/10.1111/jai.12623>
- Rosa DM, Sene AM, Moreira MZ, Pompeu PS (2021) Non-native prey species supporting fish assemblage biomass in a Neotropical reservoir. *Biological Invasions* 23: 2355–2370. <https://doi.org/10.1007/s10530-021-02510-x>
- Santos NCL, Santana HS, Dias RM, Borges HLF, Melo VF, Severi W, Gomes LC, Agostinho AA (2016) Distribution of benthic macroinvertebrates in a tropical reservoir cascade. *Hydrobiologia* 765: 265–275. <https://doi.org/10.1007/s10750-015-2419-6>
- Schmutz S, Moog O (2018) Dams: Ecological Impacts and Management. In: Schmutz S, Sendzimir J (Eds) *Riverine Ecosystem Management - Science for Governing Towards a Sustainable Future*. Springer, Germany, 111–127. [https://doi.org/10.1007/978-3-319-73250-3\\_6](https://doi.org/10.1007/978-3-319-73250-3_6)
- Silva CJ (2010) Biologia e ecologia dos camarões de água doce *Macrobrachium amazonicum* (Heller 1862) e *Macrobrachium jelskii* (Miers 1778) (Crustacea: Caridea: Palaemonoidea) no Rio Grande, região de Planura, MG. PhD Thesis, Universidade Estadual Paulista, São Paulo, Brasil, 85 pp.
- Smith WS (2004) A importância dos tributários, a influência da fragmentação artificial de rios e da introdução de espécies exóticas na comunidade de peixes dos reservatórios do Médio e Baixo Tietê. PhD Thesis, Universidade de São Paulo, São Paulo, Brasil, 295 pp.
- Sokal R, Rohlf F [Eds] (1981) *Biometry: the principles and practice of statistics in biological research*. 2<sup>nd</sup> ed. W.H. Freeman and Company, New York, 859 pp.
- Srinivasan UT, Dunne JA, Harte J, Martinez ND (2007) Response of complex food webs to realistic extinction sequences. *Ecology* 88: 671–682. <https://doi.org/10.1890/06-0971>
- Staniczenko PPA, Lewis OT, Jones NS, Reed-Tsochas F (2010) Structural dynamics and robustness of food webs. *Ecology Letters* 13: 891–899. <https://doi.org/10.1111/j.1461-0248.2010.01485.x>
- Strayer DL, Dudgeon D (2010) Freshwater biodiversity conservation: recent progress and future challenges. *Journal of North American Benthological Society* 29: 344–358. <https://doi.org/10.1899/08-171.1>
- Sunardi S, Ariyani M, Agustian M, Withaningsih S, Parikesit P, Juahir H, Ismail A, Abdoellah OS (2020) Water corrosivity of polluted reservoir and hydropower sustainability. *Science Reports* 10: 1–8. <https://doi.org/10.1038/s41598-020-68026-x>
- Takeda AM, Mansur MCD, Fujita DS, Bibian JPR (2003) Ocorrência da espécie invasora de mexilhão dourado, *Limnoperna fortunei* (Dunker, 1857), em dois pequenos reservatórios próximos a Curitiba, PR. *Acta Biologica Leopondensia* 25: 251–254.

- Tillberg CV, Holway DA, Lebrun EG, Suarez AV (2007) Trophic ecology of invasive Argentine ants in their native and introduced ranges. *Proceedings of the National Academy of Sciences* 104: 20856–20861. <https://doi.org/10.1073/pnas.0706903105>
- Thomaz SM (2002) Fatores ecológicos associados à colonização e ao desenvolvimento de macrófitas aquáticas e desafios de manejo. *Planta Daninha* 20: 21–34. <https://doi.org/10.1590/S0100-8358200200040003>
- Thomaz SM, Mormul RP, Michelan TS (2014) Propagule pressure, invasibility of freshwater ecosystems by macrophytes and their ecological impacts: a review of tropical freshwater ecosystems. *Hydrobiologia* 295: 135–140. <https://doi.org/10.1007/s10750-014-2044-9>
- Torloni CEC, Santos JJ, Carvalho Junior AA, Corrêa ARA (1993) A pescada-do-piauí *Plagioscion squamosissimus* (Heckel, 1840) (Osteichthyes, Perciformes) nos reservatórios da Companhia Energética de São Paulo-Cesp. CESP Série Pesquisa e Desenvolvimento No 84, 24 pp.
- Welch P [Ed.] (1948) Limnological Methods. McGraw-Hill Book Co., New York, 381 pp.
- Wood KA, Hayes RB, England J, Grey J (2017) Invasive crayfish impacts on native fish diet and growth vary with fish life stage. *Aquatic Sciences* 79: 113–125. <https://doi.org/10.1007/s00027-016-0483-2>
- Uryu Y, Iwasaki K, Hinque M (1996) Laboratory experiments on behaviour and movement of a freshwater mussel, *Limnoperna fortunei* (Dunker). *Journal of Molluscan Studies* 62: 327–341. <https://doi.org/10.1093/mollus/62.3.327>
- Vander Zanden MJ, Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83(8): 2152–2161. [https://doi.org/10.1890/0012-9658\(2002\)083\[2152:FAIOBA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2)
- Vieira JP, Lopes MN (2013) Size-selective predation of the catfish *Pimelodus pictado* (Siluriformes: Pimelodidae) on the golden mussel *Limnoperna fortunei* (Bivalvia: Mytilidae). *Zoologia* 30: 43–48. <https://doi.org/10.1590/S1984-46702013000100005>
- Vitule JRS, Skóra F, Abilio V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. *Diversity and Distributions* 18(2): 111–120. <https://doi.org/10.1111/j.1472-4642.2011.00821.x>

## Supplementary material 1

Food items found in gut contents of the fish from Volta Grande reservoir

Authors: Daniel Melo Rosa, Angelo Barbosa Monteiro, Lucas Del Bianco Faria, Paulo Santos Pompeu  
 Data type: table (docx. file)

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## Supplementary material 2

Food items found in gut contents of the fish from Funil reservoir

Authors: Daniel Melo Rosa, Angelo Barbosa Monteiro, Lucas Del Bianco Faria, Paulo Santos Pompeu  
 Data type: table (.docx file)

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