



Original Articles

Invasive bivalves increase benthic communities complexity in neotropical reservoirs



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ABSTRACT

Invasive bivalves often act as ecosystem engineers, generally causing physical alterations in the ecosystems in which they establish themselves. However, the effects of these physical alterations over benthic macroinvertebrate communities' structure are less clear. The objective of this study was to characterize the ecological effects of the invasive bivalves *Corbicula fluminea* and *Limnoperna fortunei* on the structure of benthic macroinvertebrate communities in neo-tropical reservoirs. Three hypotheses were tested: (1) invasive bivalves act as facilitator species to other benthic macroinvertebrates, resulting in communities with higher number of species, abundance and diversity; (2) invasive bivalves change the taxonomic composition of benthic macroinvertebrate communities; (3) invasive bivalves increase the complexity of benthic macroinvertebrate communities. For that it was used data from 160 sampling sites from four reservoirs. We sampled sites once in each area, during the dry season from 2009 to 2012. The first hypothesis was rejected, as the presence of invasive bivalves significantly decreased the host benthic communities' number of species and abundance. The second hypothesis was corroborated, as the composition of other benthic macroinvertebrates was shown to be significantly different between sites with and without invasive bivalves. We observed a shift from communities dominated by common soft substrate taxa, such as Chironomidae and Oligochaeta, to communities dominated by the invasive Gastropoda *Melanooides tuberculata*. The biomass data corroborated that, showing significantly higher biomass of *M. tuberculata* in sites with invasive bivalves, but significantly lower biomass of native species. Benthic macroinvertebrate communities presenting invasive bivalves showed significantly higher eco-exergy and specific eco-exergy, which corroborate the third hypothesis. These results suggest that while the presence of invasive bivalves limits the abundance of soft bottom taxa such as Chironomidae and Oligochaeta, it enhances benthic communities' complexity and provide new energetic pathways to benthic communities in reservoirs. This study also suggests a scenario of invasion meltdown, as *M. tuberculata* was facilitated by the invasive bivalves.

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1. Introduction

Invasive species are considered the second highest cause of biodiversity loss at a global scale (Ricciardi, 2007; Thomaz et al., 2015; Vitousek, 1997). Freshwater ecosystems are especially vulnerable, due to widespread human disturbance, such as channelization, pollution and dam and reservoir construction (Havel et al., 2005; Turak et al., 2016).

Invasive bivalves are among the most successful invasive species in freshwater ecosystems (Oliveira et al., 2011; Paschoal et al., 2015; Ricciardi, 2007). As most successful invasive species, invasive bivalves are typically r-selected species, adapted to colonize a wide range of aquatic environments and exhibiting high fecundity, rapid growth and broad physiological tolerance to several abiotic factors (Nakano et al., 2015). Such characteristics allow them to become dominant species, exhibiting high densities and constituting a major fraction of the benthic macroinvertebrates community biomass (Karatayev et al., 2007b).

Most of the impacts on benthic communities caused by invasive bivalves are a direct result on their function as ecosystem engineers, which cause environmental physical modifications (Jones et al., 1994; Sousa et al., 2009 Zaiko and Daunys, 2015). Actually, bivalve shell production, filter feeding and bioturbation, result in

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new interactions or process pathways, markedly affecting ecosystem structure and functioning (Sylvester et al., 2007).

While some studies show negative impacts over benthic macroinvertebrate communities (eg., Nalepa et al., 1998; Lozano et al., 2001), invasive bivalves generally act as facilitators for benthic macroinvertebrates, increasing their abundance, biomass and number of species, as their shells usually form a complex hard substrate that would be otherwise rare in most aquatic ecosystems (Mathers et al., 2016; Norkko et al., 2006; Sardiña et al., 2011). However, different benthic macroinvertebrate taxa do not benefit equally of this facilitation process (Boltovskoy and Correa, 2015). Scrapers, deposit feeders and their predators benefit the most from the physical modifications caused by invasive bivalves, while burrowers and other taxa adapted to soft bottom habitats, may thrive better in bare sediment habitats (Karatayev et al., 2007a). This often results in significant changes in benthic macroinvertebrate communities composition, namely in soft bottom ecosystems, such as reservoirs (Burlakova et al., 2012).

Changes in community taxonomic structure may result in changes in communities' capacity for self-organization, which represents the entropy within a community's boundaries (Jørgensen, 2007). Since entropy is difficult to quantify directly in ecosystems, thermodynamic indicators, such as eco-exergy, may be used to capture ecosystem's self-organization capacity (Marchi et al., 2010). Exergy can be defined as the difference between the system's entropy content and the one from its reference system (Svirezhev, 2000). Eco-exergy constitutes a static structural estimation resulting from dynamic qualities of the communities, which may be seen as biomass with a built in measure of quality, so to say encompassing the biomass in a system and the information embedded in it. Eco-exergy is assumed to express the complexity of the system and providing information about its stability (Li et al., 2016; Marques et al., 2003, 1997; Xu et al., 1999). Specific eco-exergy is defined as the total eco-exergy divided by the total biomass, which is assumed to take into account how well it uses the available resources, independently from the amount of resources, measuring the ability of the ecosystem to use external energy flows and reflecting the degree of complexity and development of the system (Jørgensen, 2007; Jørgensen et al., 1995; Jørgensen and Nielsen, 2007; Silow and Mokry, 2010; Susani et al., 2006). Eco-exergy and specific eco-exergy may be used complementary as ecological indicators to capture the complexity and state of the system, expressing shifts in species composition and trophic structure, as for instance in shallow lakes ecosystems and reservoirs (Marques et al., 2003; Molozzi et al., 2013).

According to Marchi et al. (2010), the establishment of invasive species can result in three outcomes for invaded communities: (1) a gradual decrease of eco-exergy, as the invasive species reduce the community abundance and number of species; (2) no significant changes in eco-exergy in the invaded communities, as the invasive species are integrated into the community without significant effect over other taxa; (3) increase in eco-exergy in the invaded communities, as the invasive species create new interactions and energetic pathways within the community. Previous studies have focused in the outcome from the invasion of north American crayfish species *Procambarus clarkii* in lake Chozas, Spain, showing that it is an example of the first predicted scenario, reducing the communities eco-exergy (Bastianoni et al., 2010; Marchi et al., 2012, 2011).

The objective of this study was to characterize the effects of the presence of invasive bivalves on the structure of benthic macroinvertebrate communities. For that, three hypotheses were tested: (1) invasive bivalves act as facilitator species to other benthic macroinvertebrates, resulting in communities' higher number of species, abundance and diversity in sites where invasive bivalves are present; (2) the presence of invasive bivalves causes changes

in the taxonomic composition of benthic macroinvertebrate communities, reflected in a shift from a community dominated by soft bottom collectors to a new one dominated by scrapers; (3) invasive bivalves cause an increase in benthic macroinvertebrate communities complexity, reflected in significantly higher eco-exergy and specific eco-exergy.

2. Materials and methods

2.1. Study sites

Study sites were four hydropower reservoirs located in neotropical savannah habitats (Brazilian cerrado biome), respectively Nova Ponte, São Simão, Três Marias and Volta Grande, in the states of Goiás, Minas Gerais, and São Paulo, in southeastern region of Brazil (Fig. 1).

The Nova Ponte reservoir is located in the rivers Araguari and Quebra-Anzol, built for hydropower generation. This reservoir is the largest of a series of reservoirs on the river Araguari, with a depth of 120 m near the dam, length of 115 km and volume of 12.8 billion m³. Its floodgates were closed in 1993 and operations began in 1994 (CEMIG, 2014).

The São Simão reservoir is also a large reservoir, with a surface area of 722 km², a total volume of 11 billion m³ and a maximum depth of 126.45 m. It is formed by the regulation of the Parnaíba river and its tributaries: the Alegre, Preto, São Francisco, Rio dos Bois, Meia Ponte, Tijuco and Prata rivers (Pinto-Coelho et al., 2010). It started its operation in 1978 for the production of hydroelectric power (Souza and Souza, 2009).

The Volta Grande reservoir is located in the lower Rio Grande basin, between the states of Minas Gerais and São Paulo. It covers the municipalities of Conceição das Alagoas, Água Comprida and Uberaba (MG), Miguelópolis, Aramina and Igarapava (SP). It is a medium-sized reservoir, with a flooded area of approximately 222 km, perimeter of 80 km (Rolla et al., 1990) and a volume of 2.3 billion m³ built for electricity generation. Having started its operation in 1974 (Braga and Gomeiro, 1997; Campos 2003).

The Três Marias Reservoir is located on the upper reaches of the São Francisco river basin. It is one of the largest reservoirs in Brazil, with a surface area of 1040 km², a total volume of 21 billion m³ and a maximum depth of 58.5 m (CEMIG, 2014). Its waters come primarily from the São Francisco river and tributaries, such as the rivers São Vicente, Paraopeba, Sucuriú, Indaiá, Ribeirão do Boi, Ribeirão da Extrema and Borrachudo (Esteves et al., 1985). It began operating in 1962 to control flooding, improve navigation, encourage development and irrigation, and generate hydroelectric power (Freitas and Filho, 2004).

Sampling sites were defined according to the concept of spatially balanced sampling (Stevens and Olsen, 2004) adapted to large reservoirs (Macedo et al., 2014). From a point randomly selected, each reservoir's perimeter was divided into 40 sections with the same size. Sampling stations were located at the beginning of each section and at equidistant distances from each other.

Samples were collected at 160 sampling sites during the dry season, respectively in 2009 (Nova Ponte), 2010 (São Simão), 2011 (Três Marias), and 2012 (Volta Grande). Water quality was estimated in each sampling site using the Trophic State Index (CETESB, 2000). All the sampling sites were classified as Ultra Oligotrophic, therefore showing similar water quality. In consequence of that we treated the 160 sampling sites as a single data set.

2.2. Benthic sampling

Benthic macroinvertebrates were collected at the littoral zone of each sampling site using an Eckman–Birge grab (0.0225 cm² area). A

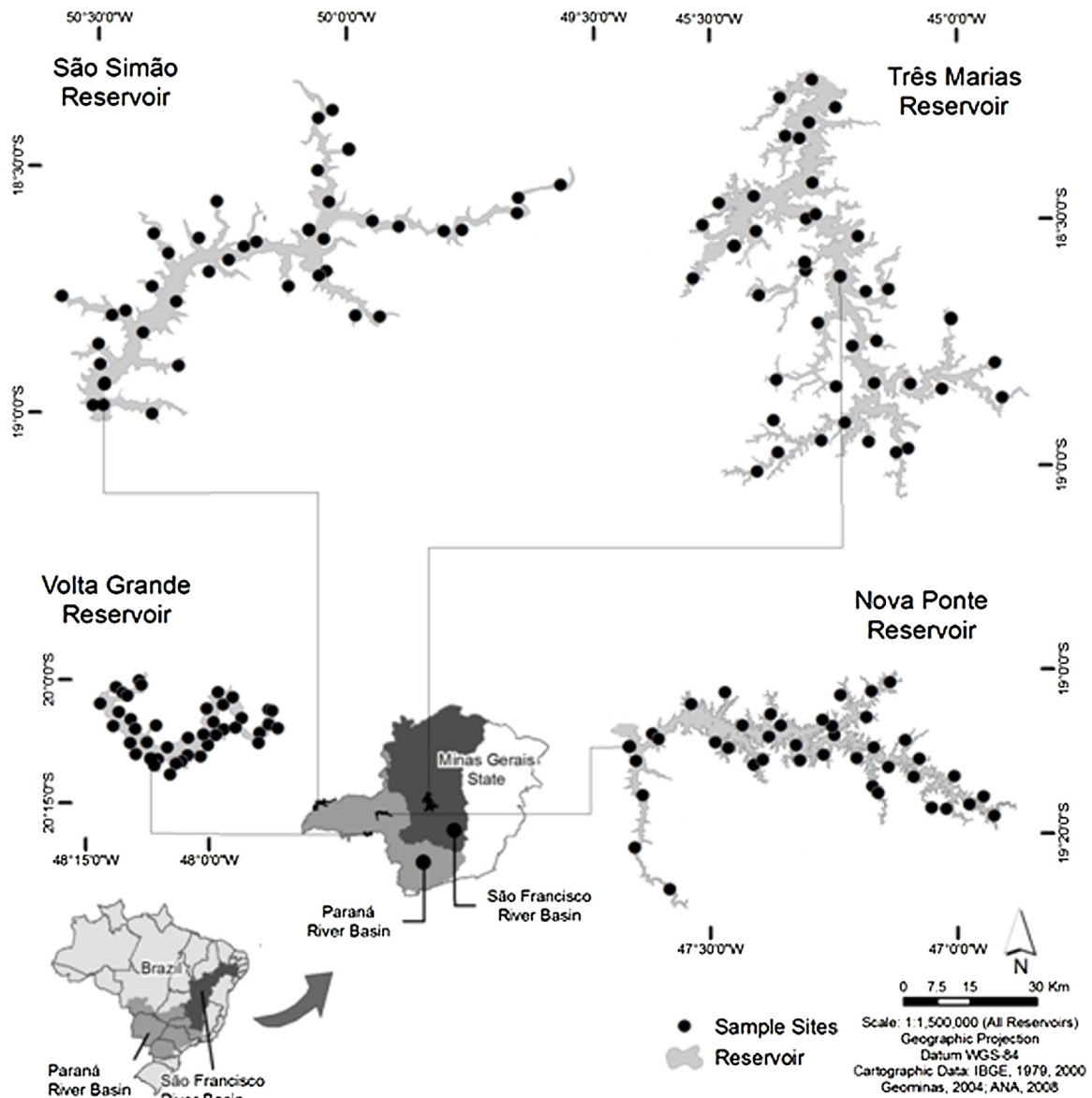


Fig. 1. Location of Nova Ponte, São Simão, Volta Grande, and Três Marias reservoirs and distribution of sampling sites.

single sample was collected at each site and stored in plastic bags, fixed in 10% formalin, and subsequently washed through a sieve (0.5 mm mesh) in the laboratory.

Macroinvertebrates were identified under a stereo-microscope using specialized literature (Merritt and Cummins, 1996; Mungnai et al., 2010; Trivinho-Strixino, 2011): Specimens from the invasive bivalve species *Limnoperna fortunei* (Mytilidae) and *Corbicula fluminea* (Corbiculidae) were identified to species level, while the specimens from the Chironomidae family (Diptera) were identified to genus level. Other taxa were identified to family (Insecta) or subclass (Anellida) levels. All specimens collected were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

Due to their capacity to cause physical alteration in the sediment, their sessile nature and aggregate distribution (Sousa et al., 2009), the absence or presence of individuals of invasive bivalve species was used to classify the sampling sites in two groups: **Absent** and **Present**. Of the 160 sites, 118 were categorized as

Absent and 38 as Present. 4 sites did not show any individuals, and were excluded from the analysis.

To test if invasive bivalves act as facilitators to other benthic macroinvertebrates originating communities with higher abundances and diversity, the Simpson (dominance) and Margalef (taxa richness) indices, as well as total abundance (excluding the invasive bivalves), were calculated for each sampling site.

2.3. Biomass calculation

Biomass (dry weight) was estimated using length-mass equations (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). The specimens were photographed in a stereomicroscope (model Leica M80) equipped with a digital camera (model Leica IC 80 HD). Each specimen's length was measured using the software Motic Image Plus 2.0. Using the length-mass equations the dry biomass (g/m^2) of each sampled taxon was estimated.

For each site we estimated total biomass, biomass of native species and the biomass of *Melanoides tuberculata*.

Table 1
Exergy conversion factors for benthic communities, based on Jørgensen et al. (2005). The values in bold were used in this study.

Organisms	Energy Conversion Factor (β)
Virus	1.01
Bacteria	8.5
Algae	20
Yeast	17.4
Cnidaria	91
Platyhelminthes	120
Gastropoda	312
Bivalvia	297
Crustacea	232
Coleoptera	156
Diptera	184
Hymenoptera	267
Lepidoptera	221
Other Insecta	167
Fish	499

2.4. Exergy based indicators computation

Eco-exergy and specific eco-exergy indices were calculated for each sampling site.

Eco-exergy was computed as follows (Jørgensen et al., 2010):

$$EX = \sum_i^{i=0} \beta_i c_i$$

Where β_i is a weighting factor (Table 1) based on the information contained in the components (i) of the ecosystem, defined by Jørgensen et al. (2005) and c_i is the concentration (biomass) of component i of the ecosystem.

Specific eco-exergy is given by:

$$SpEX = \frac{EX}{BM}$$

Where EX is the total eco-exergy and BM is the total biomass.

2.5. Data analysis

To assess if invasive bivalves act as facilitators originating more diverse associated benthic communities, a Generalized Linear Model (GLM) with a Quasipoisson error structure for the number of species, abundance and a Gaussian error structure for the Simpson and Margalef indices based on the benthic macroinvertebrate taxa found at each site, were used to test for possible differences between sites categorized as Absent and Present. The model's significance was tested by an Analysis of Deviance (F test). The calculations were performed on R software, version 3.2.3, (R Core Team, 2013).

To verify if the presence of invasive bivalves changes the taxonomic composition of associated benthic communities, data on abundance (excluding the invasive bivalves) underwent a square root transformation, then we used the Bray-Curtis distance to build the similarity matrix. PERMANOVA (1000 permutations) was used to test if the benthic macroinvertebrate communities in Absent and Present sites were significantly different from each other. We also used a Generalized Linear Model (GLM) with a Gaussian error structure was used to test the values of biomass for native species and for *Melanoides tuberculata* calculated at each site, testing for possible differences between sites categorized as Absent and Present. The calculations were performed on R software, version 3.2.3, (R Core Team, 2013) and the vegan package (Oksanen et al., 2016).

To check if invasive bivalves increase benthic macroinvertebrate communities complexity, a Generalized Linear Model (GLM) with a Gaussian error structure was used to test the values of eco-exergy and specific eco-exergy calculated for the benthic

Table 2
Mean (\pm SE) and GLM results of richness, abundance, simpson diversity index and Margalef diversity index for sites with invasive bivalves absent and present.

	Mean (\pm SE)		GLM	
	Absent	Present	F	P
Abundance	43.44 (\pm 6.16)	23.84 (\pm 3.34)	5.3726	0.021
Richness	7.00 (\pm 0.37)	5.36 (\pm 0.43)	5.4721	0.020
Margalef	1.81 (\pm 0.08)	1.50 (\pm 0.11)	3.7484	0.054
Simpson	0.63 (\pm 0.01)	0.58 (\pm 0.03)	1.6643	0.199

macroinvertebrate communities at each site, testing possible differences between sites categorized as Absent and Present. The model's significance was tested by an Analysis of Deviance (F test). The calculations were performed on R software, version 3.2.3, (R Core Team, 2013).

3. Results

The number of species, abundance, and the Simpson and Margalef indices were consistently lower in Present sites. Nevertheless, we only observed statistically significant differences for the number of species and abundance (Table 2). Results of PERMANOVA analysis showed that taxonomic composition was significantly different between Absent and Present sites ($F_{1,155} = 14.685$, $p = 0.000999$). Regarding abundances (Fig. 2) benthic communities at Absent sites were dominated by Chironomids and Oligochaeta, while at Present sites were dominated by the invasive Gastropoda *Melanoides tuberculata* (Thairidae).

Total biomass was significantly higher in Present sites (Table 3), as was *Melanoides tuberculata* biomass. However, native species biomass was not significantly different between Absent and Present sites.

Eco-exergy and specific eco-exergy showed statistically significant higher average values in Present sites (Table 4, Supplementary Material).

4. Discussion

The results show that the presence of invasive bivalves causes a significant decrease in the benthic macroinvertebrate communities' number of species and abundance. Although this was not captured by diversity measures like the Simpson and Margalef indices, in general we could not confirm the first hypothesis. However, the communities' composition with regard to the other benthic macroinvertebrates, taxa was significantly different between Absent and Present sites, corroborating the second

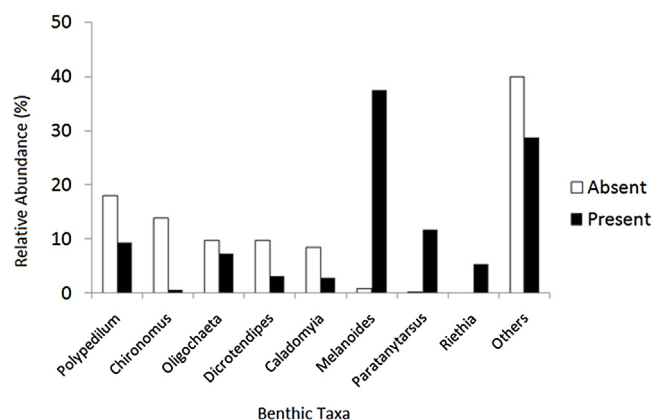


Fig. 2. Relative abundance of associated benthic macroinvertebrate communities for sites with invasive bivalves Absent and Present.

Table 3

Mean (\pm SE) and GLM results of total dry-weight biomass (g/m^2), *Melanoides tuberculata* dry-weight biomass (g/m^2) and native species dry-weight (g/m^2) biomass for sites with invasive bivalves absent and present.

	Mean (\pm SE)		GLM	
	Absent	Present	F	P
Total Biomass	0.33(\pm 0.05)	1.09(\pm 0.37)	11.031	0.00119
<i>M. tuberculata</i> Biomass	0.002 (\pm 0.001)	0.04(\pm 0.008)	63.148	<0.001
Native Biomass	0.32(\pm 0.05)	0.18(\pm 0.06)	2.4686	0.1182

Table 4

Mean (\pm SE) and GLM results of eco-exergy and specific eco-exergy for sites with invasive bivalves absent and present.

	Mean (\pm SE)		GLM	
	Absent	Present	F	P
Eco-exergy	56.44 (\pm 8.44)	301.26 (\pm 110.95)	14.504	0.0002
Specific Eco-exergy	173.93 (\pm 1.96)	298.28 (\pm 6.51)	279.18	<0.001

hypothesis. Finally, assuming that eco-exergy and specific eco-exergy are able to express the communities' complexity, given that the values of these two indicators were significantly higher in sites with invasive bivalves, our results appear to corroborate the third hypothesis.

4.1. First hypothesis

Present sites show benthic communities with a significantly lower number of species and abundance in comparison with those found in Absent sites, and therefore invasive bivalves did not act as facilitators to new benthic macroinvertebrate taxa. Physical changes caused by invasive bivalves as ecosystem engineers may eventually explain results observed, in the sense that their aggregations formed a kind of biological modified hard substrate that otherwise would be rare in reservoirs, which are typically characterized by soft sediment (Johnson et al., 2008; Sousa et al., 2009; White, 2014). As a consequence, soft bottom taxa, such as the Chironomids *Polypedium* and *Chironomus* (Corbi and Trivinho-Strixino, 2017) and Oligochaeta, normally dominant in benthic macroinvertebrate communities in reservoirs (Havel et al., 2005; Horsák et al., 2009; Martins et al., 2015), have most probably been negatively influenced by this biological modified substrate, exhibiting relatively lower abundances in Present sites. However, as both Margalef and Simpson indices failed to show significant difference between Absent and Present sites, suggesting that the benthic communities show similar structure of dominance (Simpson index) and taxa diversity (Margalef index) (Gamito, 2010; Peet, 1974).

Studies in Brazil highlight the wide distribution and the dominant status of the invasive bivalves in reservoirs, but do not present a clear pattern of their effects over benthic macroinvertebrate communities (e.g., Martins et al., 2015; Morais et al., 2016; Suriani et al., 2007). Most studies in reservoirs in South America (e.g., Boltovskoy et al., 2009; Burlakova et al., 2012; Karatayev et al., 2003) showed contrary results, highlighting the capability of invasive bivalves to act as facilitators to other benthic macroinvertebrates.

4.2. Second hypothesis

Lower number of species and abundances, as well as the shift in communities' taxonomic composition observed in Present sites may be explained by the dominance of *Melanoides tuberculata*. This invasive Asian Gastropoda species occurs presently in most Brazilian river ecosystems (Fernandez et al., 2003), namely in reservoirs where it usually exhibits high densities. This usually results in a decrease in the number of native taxa, as well as a decrease in

their populations' densities (Lima et al., 2013; Santos and Eskinazi-Sant'Anna, 2010; Souto et al., 2011).

Since *Melanoides tuberculata* only were dominant and showed higher biomass than the native species in sites with invasive bivalves, our results also suggest an invasion meltdown scenario, where positive interspecific relationships between two or more invasive species occur, leading to an acceleration of the impacts of these species on the ecosystem and an increased rate of establishment of introduced species (Simberloff, 2006; Simberloff and Von Holle, 1999). Johnson et al. (2008) found a similar pattern in reservoirs located in northern USA, where the establishment of invasive species increased the chances of subsequent invasions and determined cumulative impacts and associated effects on the native benthic macroinvertebrate communities. However, the invasion meltdown scenario should be considered carefully, as with our results it is not possible to discern if the negative impacts over the native benthic macroinvertebrates number of taxa, abundance and biomass were directly resultant from the increased *Melanoides tuberculata* abundance or the physical habitat alterations caused by the invasive bivalves.

4.3. Third hypothesis

Higher eco-exergy values found in the presence of invasive bivalve species, however, suggest that invaders became integrated with their host benthic macroinvertebrate communities, contributing afterwards to increase the overall communities' complexity. Actually, introduced ecosystem engineers, such as invasive bivalves, generally tend to increase their host communities complexity (Burlakova et al., 2012; Crooks, 2002). Such increased complexity should result in new energetic pathways and interactions in the invaded communities (Bastianoni et al., 2010). Our results show that this stem from the dominance of the invasive species, as reservoirs are highly altered ecosystems in which such generalist species probably have competitive advantage (Havel et al., 2005; Johnson et al., 2008; Thomaz et al., 2015). In this context higher eco-exergy is reflecting communities dominated by species with higher fitness to their environment (Jørgensen, 2007).

Increased specific eco-exergy values also suggest a more efficient use of ecosystems' resources. For instance, South American freshwaters lacked powerful benthic suspension feeders able to provide a direct link between benthic and water column components of the ecosystem (Karatayev et al., 2007b), role eventually undertaken by invasive bivalve species. Resources produced in the water column captured by invasive bivalves may then become available to the benthic communities as feces and pseudo-feces, constituting an important food source for benthic collectors (Sardiña et al., 2008). Therefore, invasive bivalves may open new energetic pathways for benthic macroinvertebrate communities, making accessible resources that otherwise would not be so available (Boltovskoy and Correa, 2015).

5. Conclusions

The present study in neo-tropical reservoirs illustrates that the presence of invasive bivalves does not forcibly act as facilitator to benthic macroinvertebrate communities, and may instead have a negative impact over the most common taxa, which contradicts most previous studies.

However, we also observed that the presence of bivalve invasive species caused a significant taxonomic shift, from communities dominated by soft sediment reservoir taxa to those dominated by *M. tuberculatus*, and results in their increased overall complexity.

Eco-exergy and specific eco-exergy, used complementary, were able to capture the effects of invasive bivalve species on the benthic macroinvertebrate communities.

Finally, our results appear to illustrate an invasion meltdown scenario between *Corbicula fluminea* and *Limnoperna fortunei*, invasive bivalves and the invasive gastropod *Melanoides tuberculata*.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.12.046>.

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