



## Original Articles

# Invasive bivalves increase benthic communities complexity in neotropical reservoirs



Marden Seabra Linares<sup>a,\*</sup>, Marcos Callisto<sup>a,1</sup>, João Carlos Marques<sup>b</sup>

<sup>a</sup> Laboratório de Ecologia de Bentos, Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, CP 486, CEP31270-901 Belo Horizonte, MG, Brazil

<sup>b</sup> MARE-Marine and Environmental Sciences Centre, Department of Life Sciences, Faculty of Sciences and Technology, University of Coimbra, Portugal

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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

\* Corresponding author.

E-mail addresses: [mslx@hotmail.com](mailto:mslx@hotmail.com) (M.S. Linares), [callistom@ufmg.br](mailto:callistom@ufmg.br) (M. Callisto), [jcmimar@ci.uc.pt](mailto:jcmimar@ci.uc.pt) (J.C. Marques).

<sup>1</sup> <http://lebufmg.wixsite.com/bentos>

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 m<sup>3</sup>. 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 km<sup>2</sup>, a total volume of 11 billion m<sup>3</sup> 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 m<sup>3</sup> built for electricity generation. Having started its operation in 1974 (Braga and Gomieiro, 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 km<sup>2</sup>, a total volume of 21 billion m<sup>3</sup> 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 cm<sup>2</sup> area). A

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