Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Short Research Note
Acta Limnologica Brasiliensia, 2026, vol. 38, e31
https://doi.org/10.1590/S2179-975X5926
ISSN 2179-975X on-line version

Substrate competition between bivalves: a case study involving the invasive *Limnoperna fortunei* (Dunker, 1857) vs. the native *Rheodreissena lopesi* (Alvarenga & Ricci, 1989)

Competição por substrato entre bivalves: um estudo de caso envolvendo a invasora *Limnoperna fortunei* (Dunker, 1857) e a nativa *Rheodreissena lopesi* (Alvarenga & Ricci, 1989)

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Cite as: Chagas, R.A., Barros, M.R.F. and Santos, W.J.P. Substrate competition between bivalves: a case study involving the invasive *Limnoperna fortunei* (Dunker, 1857) vs. the native *Rheodreissena lopesi* (Alvarenga & Ricci, 1989). *Acta Limnologica Brasiliensia*, 2026, vol. 38, e31. https://doi.org/10.1590/S2179-975X5926

Abstract: This study evaluates the spatial occupancy status and substrate competition between *Rheodreissena lopesi* and *Limnoperna fortunei* in the Tocantins River, discussing the implications of niche overlap for native fauna conservation. Sampling conducted in August 2023 revealed that, although the native *R. lopesi* is still more abundant and constant, the two species rarely coexist on the same substrate, indicating spatial segregation and a pattern of competitive interaction. Data suggest that, at the time of the study, the native species still maintains significant dominance, especially in the river's main channel, while the golden mussel shows a more incipient and peripheral occupation due to its recent colonization of the Amazon. However, we recommend monitoring other locations along the river, given the invasive mollusk's rapid growth and potential for successful colonization of new habitats, which could impact other benthic species.

Keywords: Amazon region; biological invasion; golden mussel.

Resumo: Este estudo avalia o status de ocupação espacial e a competição por substrato entre *Rheodreissena lopesi* e *Limnoperna fortunei* no rio Tocantins, discutindo as implicações da sobreposição de nicho para a conservação da fauna nativa. Uma amostragem realizada em agosto de 2023, revelou que, embora o *R. lopesi* nativo ainda seja mais abundante e constante, as duas espécies raramente coexistem no mesmo substrato, indicando segregação espacial e um padrão de interação competitiva. Os

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dados sugerem que, no momento do estudo, a espécie nativa ainda mantém dominância significativa, especialmente no canal principal do rio, enquanto o mexilhão-dourado apresenta uma ocupação mais incipiente e periférica devido à sua recente colonização da Amazônia. Deste modo, sugerimos um monitoramento em outros pontos do rio, visto que o molusco invasor apresenta crescimento acelerado e potencial sucesso de colonização em novos habitats, o que pode impactar outras espécies bentônicas.

Palavras-chave: região Amazônica; invasão biológica; mexilhão-dourado.

Limnoperna fortunei (Dunker, 1857) is a species of freshwater bivalve mollusk belonging to the family Mytilidae. This species is popularly known as the golden mussel due to the golden and shiny characteristics of its shell (Boltovskoy et al., 2022). The golden mussel is native to Southeast Asia and its introduction to South America was recorded in 1991, in the La Plata Basin, Argentina (Pastorino et al., 1993), through the discharge of ballast water from transoceanic ships (Darrigran & Ezcurra de Drago, 2000). This invasion is considered one of the fastest and most impactful dispersals of an exotic species in continental waters (Boltovskoy et al., 2022). Currently, five South American countries (Brazil, Argentina, Paraguay, Uruguay, and Bolivia) have consolidated records of the presence of the golden mussel (Darrigran et al., 2020; Miyahira et al., 2024).

The first recorded sightings in Brazilian waters occurred in 1998, in Lake Guaíba, Rio Grande do Sul (Mansur et al., 1999). The entry into Brazilian waters initially occurred via the dispersal of larvae by river currents, but was boosted by vessel traffic, fishing activities, and aquaculture (Oliveira et al., 2010; Pestana et al., 2010; Barbosa et al., 2016). Currently, the golden mussel has already been recorded in seven river basins (Miyahira et al., 2024; Chagas et al., 2025a, b) and has recently reached the Amazon region (Barros et al., 2026).

The golden mussel is recognized as an invasive species with high colonization and expansion success, described as an "ecosystem engineer", mainly due to the environmental shift where it establishes itself (Bergonci et al., 2009; Belz et al., 2010, 2012; Lucía et al., 2022). The golden mussel causes multidimensional impacts affecting ecosystem balance, industrial infrastructure, and public health. Notable among the economic impacts is macrofouling in the piping, filters, and cooling systems of hydroelectric power plants and water treatment facilities. This leads to frequent maintenance shutdowns and, consequently, increased operating costs (Perepelizin & Boltovskoy, 2014). There are also reports of impacts on fish farms, where the mussels obstruct water flow—reducing oxygen levels and injuring fish—and necessitate increased investment in maintenance (Costa et al., 2018; Oliveira et al., 2023). Regarding health and societal impacts, mussel aggregations threaten drinking water supplies and increase the potential for the bioaccumulation of heavy metals and parasites within the food web. Environmental impacts include alterations to nutrient cycling and water transparency, as well as competition for food and space with benthic macrofauna (Pereira et al., 2012; Ferraz et al., 2021). In this context, many of the interactions between native species and the golden mussel are still not described in literature, especially between species that inhabit the same environment.

One example is the mollusk *Rheodreissena lopesi* (Alvarenga & Ricci, 1989), a freshwater bivalve belonging to the Dreissenidae family, which is native to the Amazon and Tocantins/Araguaia river basins. This species reaches a maximum length of 13 mm, inhabits clusters attached to rocks and river outcrops via its byssus, and is found in shallow areas with little current (Pereira et al., 2014; Mansur et al., 2019). Although *R. lopesi* is not on the list of threatened species, it is a bivalve that has been impacted in several ways, including siltation, marginal erosion, pollution, damming, and due to special competition from exotic species (Pereira et al., 2012).

This study is important because simulations indicated that the invasion of the golden mussel in the Amazon region was predicted only after the 2030s, with consolidation expected in the 2050s (Barbosa et al., 2018). However, as the first record occurred well before predicted (October 2023) (Chagas et al., 2025a), several studies are being carried out so that the impacts of its invasion are well clarified. In this context, the present study aims to evaluate the occupancy status of *Rheodreissena lopesi* (Alvarenga & Ricci, 1989) regarding the expansion of the invasive species *Limnoperna fortunei* in the Tocantins River, discussing the possible implications of niche overlap for the conservation of native fauna.

The study area is located in the lower Tocantins River, in a stretch that crosses the Municipality of Marabá (5°22'52.08" S, 49°7'59.18" W). The portion of the Tocantins River that flows through the municipality of Marabá is predominantly rocky,

with the Pedral do Lourenço (located downstream from Marabá) being a notable feature. Its depth varies considerably, reaching up to 12 meters during the Amazonian winter (December to May). Sampling was carried out in the morning between the 8th and 12th of August 2023, during the Amazonian summer, when the river water level drops, facilitated sampling in the river channel and, consequently, the colonization of the species. The sampling site for the present study is the same as where the species was first recorded in the Amazon region (Chagas et al., 2025a). Sampling points were selected to cover the entire cross-section of the river, with riverbank and the main channel section represented. In total, 18 sampling points were selected, 12 on the riverbank and six on the main channel (Figure 1).

Samples of bivalve mollusks were collected using two types of instruments: (1) D-frame dip net and (2) Van Veen dredge. The D-frame dip net sampler (250 µm mesh) was used for active sampling on the riverbanks, within an area of 1 m^2, and in environments with a depth of up to 50 cm where hard substrates were observed (e.g., stone or gravel, leaf litter, twigs, etc.). The Van Veen dredge (area 0.068 m^2) was used for sampling in the main river channel. After each sampling, the material collected from both environments was properly coded and fixed in 70% ethanol. The methodology employed in the sampling of this study, as well as the type of instrument used, is indicated in the scientific literature (Ferraz et al., 2021; Chagas et al., 2025a).

In the laboratory, the samples were washed in running water using sieves with a 0.5 mm mesh size. After washing, the taxonomy of the bivalve mollusks (*R. lopesi* and *L. fortunei*) was confirmed based on specific literature (Pereira et al., 2012; Mansur et al., 2019), quantified, and the abundance at each point expressed as the number of individuals per square meter (m^2). Subsequently, the specimens were preserved in 70% alcohol and deposited in the Malacological Collection of the Zoology Museum of the Federal Rural University of the Amazon (MZUFRA).

To evaluate the spatial distribution, stability, and frequency of occurrence of both native and invasive bivalves across sampling units, the constancy index (*C*) (Dajoz, 1983) was calculated using the Equation 1:

$$C = (Ni/N)*100 \quad (1)$$

where: *Ni* is the number of samples containing the target species and *N* is the total number of samples analyzed.

Species were classified as constant ($C > 50\%$), accessory ($25\% \leq C < 50\%$), or accidental ($C < 25\%$). This analysis allows us to determine whether the invasive *L. fortunei* has established persistent populations throughout the study area compared to the native *R. lopesi*.

In total, the presence of *L. fortunei* was recorded at five points along the riverbanks (average density of 38 ind.m^{-2}; min: 1 ind.m^{-2} and max: 168 ind.m^{-2}) and at only two points in the main channel (average density of 2 ind.m^{-2}; min: 1 ind.m^{-2} and max: 3 ind.m^{-2}). The mussels had an average anteroposterior length of 8.20±2.27 mm, with 4.40 mm as minimum and 14.20 mm as maximum, indicating that the individuals found were adults, given that scientific literature indicates the golden mussel begins reproducing at a size of 5-6 mm (Darrigran et al., 1999; Xu et al., 2015). In turn, *R. lopesi* was found

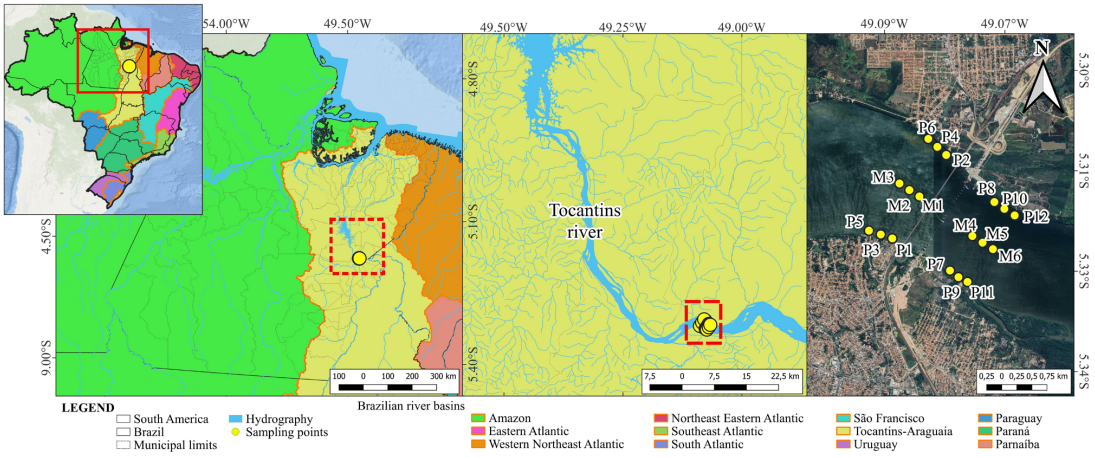


Figure 1. Study area map showing the Brazilian hydrographic divisions, with emphasis on the Tocantins-Araguaia river basin and the respective sampling points on the riverbank and in the main channel of the Tocantins River.

at only four points along the riverbanks (average density of 136 ind.m^{-2}; min: 1 ind.m^{-2} and max: 442 ind.m^{-2}), however, it was present at all points in the main channel (average density of 3,806 ind.m^{-2}; min: 1 ind.m^{-2} and max: 20,982 ind.m^{-2}). No measurement was performed in the native bivalve.

Observing the occupancy pattern of the two species, we noted that in only one point on the riverbank (P8) and two points on the main channel (M3 and M4) did the two species share the sampling location. At points P8 and M4, *L. fortunei* with 168 and three individuals (respectively) was substantially more abundant than *R. lopesi* (with only one individual at each point). At point M3, we found the opposite, with 1539 individuals of *R. lopesi* and only one individual of *L. fortunei*. Another interesting observation is that in the other sample points, when one of the species was present, the other did not coexist.

This distribution pattern may reflect the early stages of establishment of *L. fortunei* in the study area, with the species already widely distributed across the sampling units but still showing differences in occurrence between the P and M zones. The higher frequency of *L. fortunei* in the P zone may indicate that the species is progressively expanding its distribution, while its absence from the M zone may reflect the more recent stage of colonization of this area. This widespread initial occurrence represents a severe warning sign, as further population expansion will inevitably increase microhabitat overlap and heighten ecological pressures on native epifaunal species such as *R. lopesi*.

The constancy results indicate that *R. lopesi* is classified as a constant species (*C*=55.6%) and *L. fortunei* as an accessory species (*C*=38.9%). This pattern demonstrates that *R. lopesi* was overall more frequent across the study area and remained predominant in most sampling sites, although *L. fortunei* already exhibited higher local densities at specific locations. The golden mussel is recognized as an invasive species that drastically alters the ecosystem where it is colonized, potentially altering the native biota (Ferraz et al., 2021; Boltovskoy et al., 2022), especially those that inhabit the same niche, as in the case of *R. lopesi* in this study. As the sampling period coincided with a recent colonization of the golden mussel in the region (Barros et al., 2026), the impacts caused by this invasive species were in an initial stage.

In the Amazon region, studies on the golden mussel are recently and constantly being conducted, and the results mainly address dispersal and population structure data (Chagas et al., 2025a, b; Barros et al., 2026). Further studies focusing on socioeconomic and environmental impacts must be conducted.

In the present study, we conclude that *L. fortunei* is in an active phase of spatial expansion in the lower Tocantins River, increasing the potential for microhabitat overlaps with the native bivalve *R. lopesi*. Given the high reproductive capacity, rapid growth, and dense biofouling of the golden mussel, its continued expansion may progressively increase its occupation of benthic substrates, with potential consequences for native benthic communities. *R. lopesi* is an important native component of Neotropical riverine benthic communities, and changes in their abundance and distribution may affect local community structure and ecological interactions. The potential displacement of *R. lopesi* by *L. fortunei* and the subsequent increase in dominance of the invasive mussel may alter benthic community composition and ecosystem functioning, particularly in hard-bottom habitats such as rocky outcrops. Therefore, we recommend that further studies be carried out in the same location, now with more than two years of colonization by the species along the Tocantins River.

Acknowledgements

The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) granted a doctoral scholarship (Financial Code 001).

Data availability

The authors declare that the research data supporting the findings of this study have been published in the article itself.

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Received: 18 May 2026
Accepted: 30 September 2026

Associate Editor: Andre Andrian Padial.