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Substrate-driven structuring of an invasive bivalve in a groundwater-influenced rocky mangrove system

Estruturação de um bivalve invasor mediada pelo substrato em um sistema de manguezal rochoso influenciado por águas subterrâneas

Estructuración de un bivalvo invasor mediada por el sustrato en un sistema de manglar rocoso influenciado por aguas subterráneas

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Abstract
Mangrove ecosystems are highly productive coastal environments increasingly threatened by biological invasions, which can alter community structure and ecosystem functioning. The invasive bivalve Isognomon bicolor (C. B. Adams, 1845), native to the Caribbean, has expanded along the Brazilian coast; however, its ecological dynamics in non-conventional mangrove systems remain poorly understood. This study evaluates the population structure of I. bicolor in the Mangue de Pedra, a unique groundwater-influenced rocky mangrove located in Armação dos Búzios (Rio de Janeiro, Brazil). A quantitative sampling design was applied using 30 quadrats (0.09 m² each) distributed across three microhabitats: roots/muddy substrate, rocky talus, and consolidated rocky shore. A total of 1,351 individuals were recorded, with 100% occurrence across all sampled quadrats, indicating widespread distribution at the local scale. However, abundance varied markedly among habitats, with higher densities in consolidated substrates (1120.0 ind m^{-2}), intermediate values in rocky talus (312.2 ind m^{-2}), and lower densities in muddy root-associated environments (68.9 ind m^{-2}). This pattern demonstrates a clear decoupling between occurrence and abundance, indicating that while dispersal facilitates broad colonization, local environmental filtering, particularly substrate stability, plays a key role in regulating population density. The structural heterogeneity and hydrological connectivity of the Mangue de Pedra suggest that this system may function both as a recipient environment and as a potential source of propagules.
Keywords: Marine Bioinvasion; Invasive Bivalve; Mangrove Ecosystem; Habitat Filtering; Coastal Ecology.

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Resumo

Os ecossistemas de manguezais são ambientes costeiros altamente produtivos, crescentemente ameaçados por invasões biológicas, que podem alterar a estrutura das comunidades e o funcionamento dos ecossistemas. O bivalve invasor Isognomon bicolor (C. B. Adams, 1845), nativo do Caribe, expandiu-se ao longo da costa brasileira; entretanto, suas dinâmicas ecológicas em sistemas de manguezais não convencionais permanecem pouco compreendidas. Este estudo avalia a estrutura populacional de I. bicolor no Mangue de Pedra, um manguezal rochoso singular influenciado por água subterrânea, localizado em Armação dos Búzios (Rio de Janeiro, Brasil). Foi aplicado um delineamento amostral quantitativo utilizando 30 quadrats (0,09 m² cada), distribuídos em três micro-habitats: raízes/substrato lodoso, tálus rochoso e costão rochoso consolidado. Um total de 1.351 indivíduos foi registrado, com ocorrência de 100% em todos os quadrats amostrados, indicando ampla distribuição em escala local. No entanto, a abundância variou significativamente entre os habitats, com maiores densidades em substratos consolidados (1120,0 ind m^{-2}), valores intermediários em tálus rochoso (312,2 ind m^{-2}) e menores densidades em ambientes associados a raízes com substrato lodoso (68,9 ind m^{-2}). Esse padrão demonstra um claro desacoplamento entre ocorrência e abundância, indicando que, embora a dispersão favoreça a colonização ampla, o filtro ambiental local, especialmente a estabilidade do substrato, desempenha papel fundamental na regulação da densidade populacional. A heterogeneidade estrutural e a conectividade hidrológica do Mangue de Pedra sugerem que esse sistema pode atuar tanto como ambiente receptor quanto como potencial fonte de propágulos.

Palavras-chave: Bioinvasão Marinha; Bivalve Invasor; Ecossistema de Mangue; Filtragem de Habitat; Ecologia Costeira.

Resumen

Los ecosistemas de manglar son ambientes costeros altamente productivos, cada vez más amenazados por invasiones biológicas, las cuales pueden alterar la estructura de las comunidades y el funcionamiento de los ecosistemas. El bivalvo invasor Isognomon bicolor (C. B. Adams, 1845), nativo del Caribe, se ha expandido a lo largo de la costa brasileña; sin embargo, sus dinámicas ecológicas en sistemas de manglares no convencionales siguen siendo poco comprendidas. Este estudio evalúa la estructura poblacional de I. bicolor en el Mangue de Pedra, un manglar rocoso singular influenciado por aguas subterráneas, ubicado en Armação dos Búzios (Río de Janeiro, Brasil). Se aplicó un diseño de muestreo cuantitativo utilizando 30 cuadrantes (0,09 m² cada uno), distribuidos en tres microhábitats: raíces/sustrato lodoso, talud rocoso y costa rocosa consolidada. Se registró un total de 1.351 individuos, con una ocurrencia del 100% en todos los cuadrantes muestreados, lo que indica una amplia distribución a escala local. No obstante, la abundancia varió notablemente entre hábitats, con mayores densidades en sustratos consolidados (1120,0 ind m^{-2}), valores intermedios en taludes rocosos (312,2 ind m^{-2}) y menores densidades en ambientes asociados a raíces con sustrato lodoso (68,9 ind m^{-2}). Este patrón demuestra un claro desacoplamiento entre ocurrencia y abundancia, indicando que, aunque la dispersión facilita una colonización amplia, el filtrado ambiental local, especialmente la estabilidad del sustrato, desempeña un papel clave en la regulación de la densidad poblacional. La heterogeneidad estructural y la conectividad hidrológica del Mangue de Pedra sugieren que este sistema puede funcionar tanto como un ambiente receptor como una posible fuente de propágulos.

Palabras clave: Bioinvasión Marina; Bivalvo Invasor; Ecosistema de Manglar; Filtrado de Hábitat; Ecología Costera.

1. Introduction

Mangrove ecosystems are among the most productive and ecologically important coastal environments worldwide, providing essential ecosystem services such as shoreline protection, carbon sequestration, nutrient cycling, and nursery habitats for a wide range of marine organisms (Lacerda et al., 2022; Schaeffer-Novelli, 2008). Despite their ecological and socio-economic relevance, mangroves are increasingly threatened by anthropogenic pressures and global environmental changes, leading to habitat degradation, fragmentation, and biodiversity loss (Ferreira & Lacerda, 2016; Romañach et al., 2018; Valiela et al., 2001).

Among the multiple stressors affecting coastal ecosystems, biological invasions have emerged as a major driver of ecological change, particularly in marine environments where dispersal pathways are highly connected and difficult to control. Invasive species are capable of altering community structure, ecosystem functioning, and species interactions, often resulting in long-term ecological shifts. These impacts are especially pronounced in structurally complex systems, where environmental heterogeneity can facilitate both the establishment and expansion of non-native species (Carlton, 2001; Ferreira et al., 2008; Lima & Passos, 2021).

In this context, the bivalve I. bicolor (Adams, 1845), native to the Caribbean, has become one of the most successful

marine invaders along the Brazilian coast. Since its introduction, likely associated with shipping activities and offshore structures (Domaneschi & Martins, 2002), the species has expanded its distribution across a variety of coastal habitats. Previous studies have demonstrated its high colonization capacity and competitive ability, particularly in rocky intertidal environments, where it can reach high densities and alter benthic community composition (Breves & Junqueira, 2017; Breves-Ramos et al., 2010; López et al., 2014).

Despite the growing body of knowledge on the species, most studies have focused on conventional rocky shore systems, while its occurrence and ecological dynamics in non-traditional environments remain poorly understood. This gap is particularly relevant in transitional coastal ecosystems, where the interaction between environmental gradients and structural complexity may influence invasion processes in distinct ways.

The Mangue de Pedra, located in Armação dos Búzios (Rio de Janeiro State), represents a unique and understudied coastal system. Unlike typical mangroves, which develop over unconsolidated muddy substrates, this environment is characterized by a consolidated rocky matrix and strong groundwater influence, resulting in a hybrid system that combines mangrove vegetation with rocky shore features. Such conditions create a highly heterogeneous habitat mosaic that may facilitate both the establishment and structuring of invasive populations (Soffiati, 2011).

Given the ecological singularity of the Mangue de Pedra and the lack of studies addressing invasion processes in non-conventional mangrove systems, this study goes beyond a simple occurrence record and investigates the population structure of *I. bicolor* across contrasting microhabitats. This study aims to evaluate the population structure of *I. bicolor* in the Mangue de Pedra, a unique groundwater-influenced rocky mangrove located in Armação dos Búzios (Rio de Janeiro, Brazil). Specifically, we aim to (i) quantify its abundance and spatial distribution, and (ii) evaluate the role of substrate type as a driver of population structuring. By integrating quantitative data with ecological interpretation, this study provides mechanistic insights into how environmental heterogeneity regulates invasion success.

2. Methodology

2.1 Study area

An experimental field study was conducted (Risemberg et al., 2026), combining a qualitative approach for visual identification of specimens with a quantitative approach for the measurement of ecological variables (Pereira et al., 2018). Descriptive statistical analyses were applied, including mean and standard deviation, to characterize population patterns (Shitsuka et al., 2014).

The study was conducted in the Mangue de Pedra, located at Praia Gorda, municipality of Armação dos Búzios, Rio de Janeiro State, southeastern Brazil (Figure 1). This ecosystem is unique along the Brazilian coast due to its development over a consolidated substrate composed of rocky blocks, gravel, and coarse sand, in contrast to the muddy and unconsolidated substrates typically found in mangrove systems (Figure 2) (Albuquerque et al., 2022; Soffiati, 2011).

Figure 1 - Geographic location of the study area, showing the municipality of Armação dos Búzios (Rio de Janeiro State,

southeastern Brazil) and the position of the Mangue de Pedra within the Praia Gorda embayment.

Source: Research data (2026).

Hydrologically, the system is influenced by groundwater discharge from a local aquifer, which reduces salinity and maintains semi-estuarine conditions even during dry periods. This results in a structurally heterogeneous environment characterized by a mosaic of microhabitats that support diverse biological assemblages. The vegetation is dominated by Laguncularia racemosa, Avicennia schaueriana, and Rhizophora mangle, forming complex structural arrangements that generate shaded areas, root systems, and consolidated surfaces, thereby increasing habitat availability for benthic organisms (Figure 3).

Figure 2 - Structural characteristics of the Mangue de Pedra substrate, highlighting the consolidated matrix composed of rocky

blocks, gravel, and coarse sand, in contrast to typical muddy mangrove environments.

Source: Research data (2026).

Figure 3 - Vegetation structure of the Mangue de Pedra, illustrating the spatial arrangement of Laguncularia racemosa,

Avicennia schaueriana, and Rhizophora mangle, forming a heterogeneous mosaic of microhabitats.

Source: Research data (2026).

2.2 Sampling Design

Field sampling was conducted on June 17, 2025, during a spring low tide (syzygy), under mean air temperature of 26 °C and salinity of 33‰. Three microhabitats were defined based on substrate type and structural complexity: (1) roots associated with muddy substrate, (2) rocky talus, and (3) consolidated rocky shore (Figure 4).

Figure 4 - Representative microhabitats sampled in the study: (1) roots associated with muddy substrate, (2) rocky talus, and (3) consolidated rocky shore, differing in substrate stability and structural complexity.

Source: Research data (2026).

A quantitative sampling design was implemented using fixed-area quadrats to ensure standardized comparisons among habitats. In each microhabitat, ten quadrats (30 × 30 cm; 0.09 m²) were randomly distributed along the intertidal zone, totaling 30 sampling units and a total sampled area of 2.7 m².

Within each quadrat, all individuals of I. bicolor were counted in situ and subsequently collected, ensuring complete representation of local abundance. This approach enabled robust estimation of abundance, density, and dispersion patterns, allowing the assessment of substrate-related variation in population structure.

2.3 Sample Processing and Identification

Specimens were carefully removed using spatulas and soft brushes to minimize damage to both shells and substrate. All collected individuals were stored in labeled containers and fixed in 70% ethanol.

Taxonomic identification was performed based on morphological characteristics following Rios (2009), including shell morphology, coloration, and nacre presence. Identification was validated through comparison with reference material from the malacological collection of the Museu Nacional (UFRJ). Taxonomic nomenclature was updated according to MolluscaBase (2025), ensuring consistency with current classification standards.

2.4 Data Analysis

For each microhabitat, descriptive quantitative metrics were calculated, including total abundance, mean abundance per quadrat, standard deviation, variance, density (ind m^{-2}), and frequency of occurrence (%). Density values were calculated by dividing the total number of individuals by the total sampled area per microhabitat (0.9 m²).

Data distribution and variability were explored using descriptive statistics and visualized through boxplots, allowing the assessment of central tendency, dispersion patterns, and differences in abundance among microhabitats. This approach enabled the identification of spatial patterns and variability without the application of inferential statistical tests.

Ecological Interpretation Framework

The interpretation of the results was guided by conceptual frameworks from invasion ecology and benthic community

dynamics, with emphasis on habitat filtering, substrate-driven population structuring, spatial aggregation, and the decoupling between occurrence and abundance.

This framework allowed the integration of quantitative patterns with ecological processes, providing a mechanistic understanding of the distribution and population dynamics of I. bicolor within the Mangue de Pedra system.

3. Results

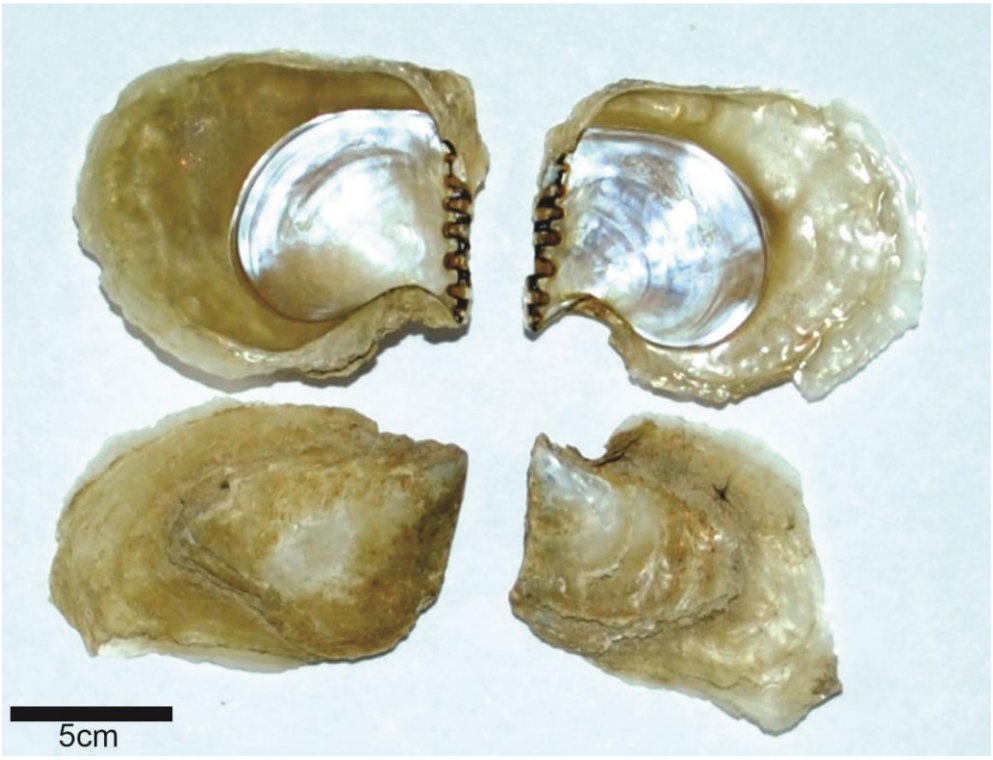
A total of 1,351 individuals of I. bicolor were recorded across 30 quadrats distributed among three microhabitats, with 100% occurrence across all sampled quadrats, indicating consistent presence at the local scale. This pattern suggests that dispersal limitation is not a primary constraint within the study area, allowing the species to occupy a wide range of substrate conditions. Individuals were predominantly associated with consolidated and semi-consolidated substrates, where they occupied crevices and irregular surfaces, indicating that substrate characteristics structure local distribution patterns (Figure 5).

Figure 5 - In situ occurrence of I. bicolor in the Mangue de Pedra system, showing individuals firmly attached to consolidated and semi-consolidated substrates within intertidal environments.

Source: Research data (2026).

Collected specimens exhibited diagnostic morphological features consistent with I. bicolor, including a nacreous inner layer and a characteristic hinge structure (Figure 7).

Figure 6 - Morphological characteristics of I. bicolor, including external shell shape and nacreous inner surface. Diagnostic hinge features used for species identification are visible. Scale bar = 5 cm.



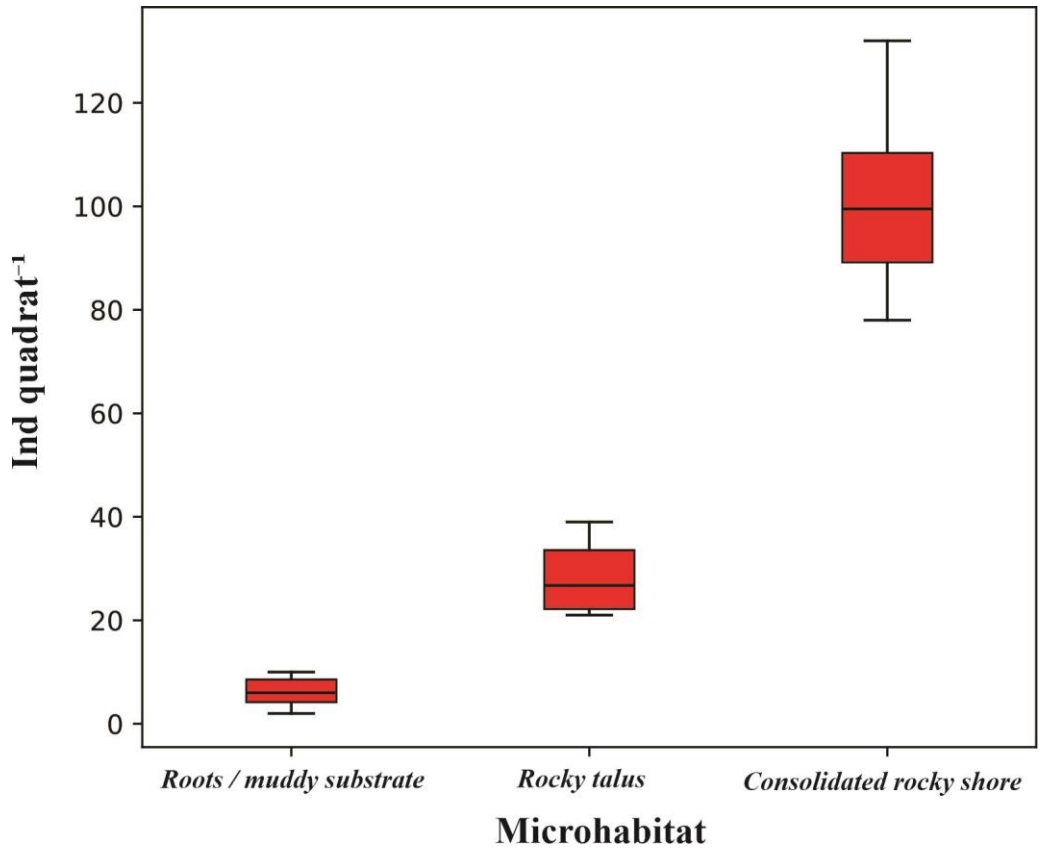
Source: Research data (2026).

Table 1 - Habitat-dependent variation in abundance, density (ind m^{-2}), and dispersion metrics of the invasive bivalve I. bicolor in the Mangue de Pedra system (RJ, Brazil).

Microhabitat	N	Total (ind)	Mean (± SD) (ind $quadrat^{-1}$)	Variance	Density (ind m^{-2})
Roots / muddy substrate	10	62	6.2 ± 2.7	7.4	68.9
Rocky talus	10	281	28.1 ± 6.2	38.4	312.2
Consolidated rocky shore	10	1008	100.8 ± 16.3	265.6	1120.0

Source: Research data (2026).

Figure 7 - Boxplot showing habitat-dependent variation in the abundance of I. bicolor across three microhabitats in the Mangue de Pedra system (RJ, Brazil): roots/muddy substrate, rocky talus, and consolidated rocky shore. The figure highlights a pronounced increase in median abundance and variability toward consolidated substrates, indicating strong substrate-driven population structuring.

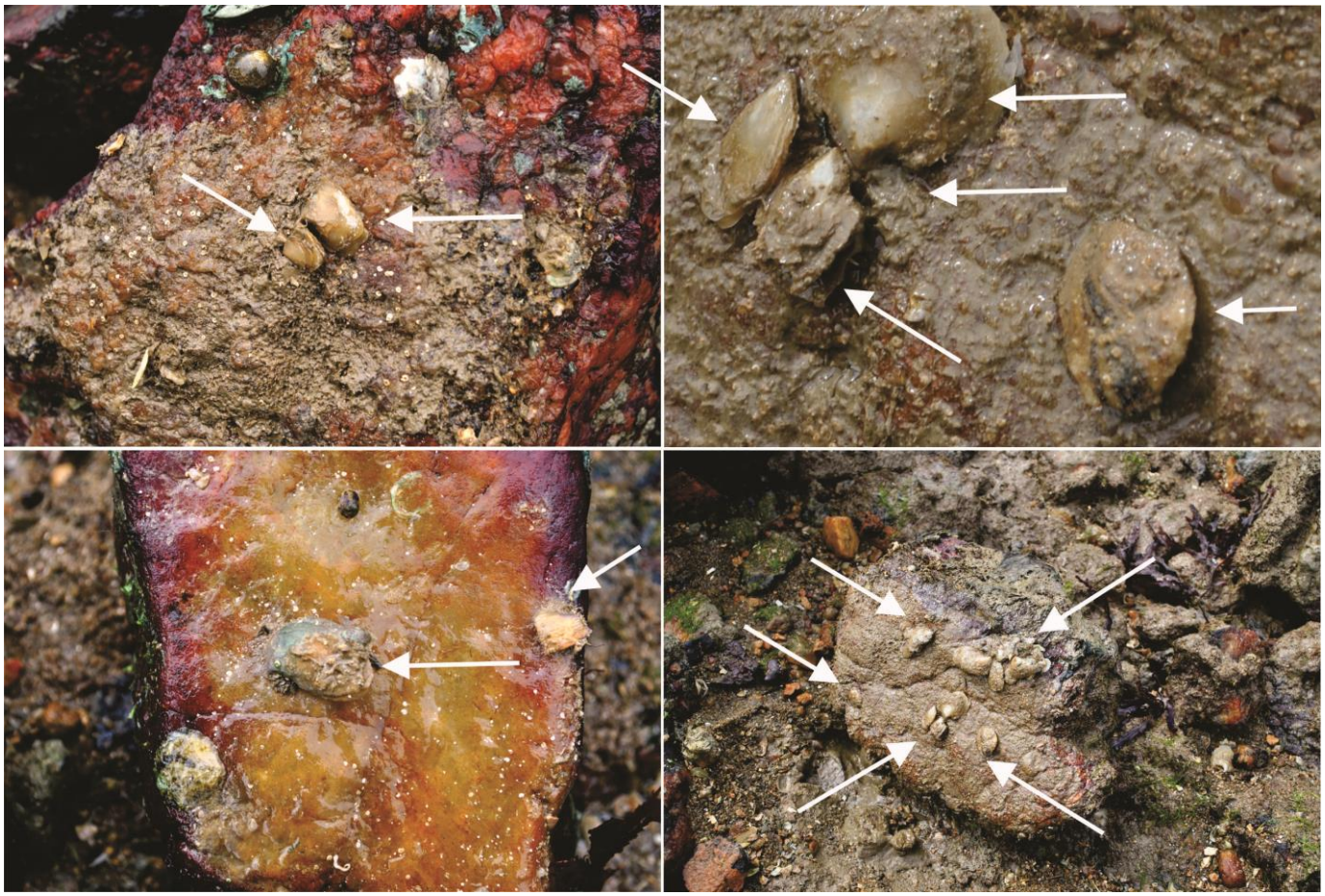


Source: Research data (2026).

Despite this widespread occurrence, abundance varied markedly among microhabitats, revealing a clear gradient from muddy substrates to consolidated rocky environments (Table 1; Figure 7). The highest densities were recorded in the consolidated rocky shore (1120.0 ind m^{-2}), followed by the rocky talus (312.2 ind m^{-2}), while the lowest values were observed in root-associated muddy substrates (68.9 ind m^{-2}).

Variability increased with substrate consolidation, as indicated by higher variance values in rocky environments. The boxplot (Figure 7) shows a pronounced shift in median abundance and reduced overlap among microhabitats, particularly between consolidated and muddy substrates, indicating strong habitat-dependent differences in population structure.

Figure 8 - Occurrence of I. bicolor in contrasting microhabitats within the Mangue de Pedra system. Individuals are predominantly associated with rocky and consolidated substrates, with occasional presence in muddy environments, indicating substrate-dependent habitat use and attachment behavior.



Source: Research data (2026).

The spatial distribution of individuals varied among habitats, with dense aggregations observed in consolidated substrates and more dispersed occurrences in muddy environments (Figure 8). This pattern suggests that, although I. bicolor is widely distributed across the study area, its population density and spatial organization are strongly associated with substrate characteristics.

4. Discussion

The results clearly demonstrate that I. bicolor is widely distributed within the Mangue de Pedra system, with occurrence in all sampled quadrats, but exhibits strong habitat-dependent variation in abundance. This pattern reflects an advanced stage of invasion in which dispersal limitation is no longer a primary constraint, and local environmental conditions become the dominant drivers of population structure.

The marked gradient in abundance among microhabitats provides clear evidence of a decoupling between occurrence and ecological dominance. While I. bicolor is capable of occupying the full range of available substrates, its population density is strongly regulated by habitat-specific factors, particularly substrate characteristics. This pattern is consistent with invasion ecology frameworks in which early colonization is driven by dispersal processes, followed by a phase in which environmental filtering determines local population performance (Dechoum et al., 2024; Ferreira et al., 2008).

The substantially higher densities observed in consolidated rocky substrates highlight the importance of physical stability as a key determinant of population success. Hard substrates provide suitable conditions for byssal attachment, reduce hydrodynamic disturbance, and enhance both survival and recruitment. These factors contribute to increased population persistence and local expansion. Similar patterns have been reported along the southeastern Brazilian coast, where I. bicolor reaches high densities in structurally stable environments and can alter benthic community composition. In contrast, muddy and structurally unstable substrates impose mechanical and hydrodynamic constraints that limit population growth, despite allowing initial colonization (Breves & Junqueira, 2017; Breves-Ramos et al., 2010; López et al., 2014; Rapagna et al., 2025).

The higher variability observed in consolidated substrates suggests a spatially aggregated distribution, indicative of patch dynamics. Such aggregation patterns may arise from localized recruitment, microhabitat heterogeneity, and intraspecific facilitation. Dense clusters can enhance larval retention and create favorable microenvironmental conditions, reinforcing local population persistence through positive feedback mechanisms. This type of spatial organization has been widely documented in invasive bivalves and reflects the interaction between biological processes and habitat structure (Breves & Junqueira, 2017; Dias et al., 2021; Zamprogno et al., 2010).

From a seascape ecology perspective, the Mangue de Pedra presents environmental conditions that likely promote invasion success. The combination of substrate heterogeneity, availability of consolidated surfaces, and hydrological connectivity creates a mosaic of habitats that facilitate both settlement and persistence. Highly connected coastal systems are recognized as invasion corridors, where propagule supply and habitat suitability interact to increase the likelihood of establishment and spread. In this context, the Mangue de Pedra may function not only as a recipient environment but also as a potential source of propagules for adjacent coastal areas (Carr et al., 2017; Podda & Porporato, 2023).

Additionally, the proximity to the Cabo Frio upwelling system may further enhance propagule supply and contribute to population persistence. Regional oceanographic processes, such as upwelling and coastal circulation, can influence larval transport and settlement, interacting with local habitat characteristics to shape invasion dynamics in complex coastal systems (Albuquerque et al., 2012; Bauer et al., 2024; Belem et al., 2013; Valentin, 2001; Valentin, 1984).

From a functional perspective, the high densities of I. bicolor in consolidated substrates raise important ecological concerns. As a filter-feeding organism, the species may alter organic matter fluxes, influence nutrient cycling, and modify resource availability within benthic communities. Furthermore, its extensive occupation of substrate space can lead to competitive exclusion of native species, such as Crassostrea rhizophorae and Brachidontes solisianus, potentially resulting in shifts in community composition and ecosystem functioning. These characteristics are consistent with invasive species that act as ecosystem engineers, capable of producing long-term structural and functional changes (Queiroz et al., 2023; López et al., 2014; Souza et al., 2025).

Overall, the invasion of I. bicolor in the Mangue de Pedra system appears to be governed by environmental filtering rather than dispersal limitation. Substrate type emerges as the primary factor structuring population density and spatial organization, demonstrating that environmental heterogeneity emerges as a key driver of invasion success in this system.

5. Conclusion

This study shows that I. bicolor is widely distributed within the Mangue de Pedra system, exhibiting consistent occurrence across sampled quadrats but pronounced habitat-dependent variation in population structure. The observed decoupling between occurrence and abundance indicates that, although dispersal enables broad colonization, local environmental conditions, particularly substrate stability, play a central role in regulating population density and ecological dominance.

These findings underscore the importance of environmental heterogeneity in shaping invasion dynamics, especially in hybrid coastal systems that integrate characteristics of distinct ecological environments. The Mangue de Pedra, characterized by consolidated substrates and strong hydrological connectivity, provides favorable conditions for both establishment and persistence, and may also act as a potential source of propagules for adjacent coastal areas.

From a broader ecological perspective, this study highlights the need to move beyond occurrence-based assessments and adopt quantitative, habitat-specific approaches when evaluating marine invasions. Understanding how environmental filters influence population structure is essential for predicting invasion trajectories and identifying habitats more susceptible to high-density establishment.

Given the elevated densities observed in consolidated substrates and the potential for interactions with native benthic species, continued monitoring of I. bicolor populations is recommended. Future research should focus on quantifying ecological impacts on community composition and ecosystem functioning, as well as examining the role of regional oceanographic processes in facilitating dispersal.

Overall, this study provides robust evidence that invasion success in complex coastal systems is primarily governed by habitat-specific processes, highlighting environmental filtering as the central mechanism structuring invasive populations.

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