Marine Ecology

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RESEARCH ARTICLE

Influence of *Isognomon bicolor*'s Invasion on the Structure of Native Bentonic Communities

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Received: 1 February 2025 | **Revised:** 15 August 2025 | **Accepted:** 7 September 2025

Funding: This work was supported by CAPES.

Keywords: benthic community | biological invasions | experiment | introduced species | invading bivalves | species interaction

ABSTRACT

Many reef ecosystems around the world are threatened by invasive alien species. On the Brazilian coast, the invasive bivalve *Isognomon bicolor* has recently undergone an expansion in distribution and abundance. In this study, we evaluate the impact of invasive *I. bicolor* on the native benthic community through an in situ experiment in which the invasive species was removed and the benthic community monitored over the following year. Post-removal, significant changes were observed in the structure of the native community, but the results were different in the two studied sites. We conclude that the establishment of *I. bicolor* on consolidated substrates can change the structure of the benthic community. Knowledge about the interactions between native and invasive species and how this species alters native communities in different environments is essential for predicting the course of future invasions and mitigating the impacts caused.

1 | Introduction

Reef ecosystems have enormous economic and cultural value, and they are characterized by high levels of ecological complexity (Cesar and van Beukering 2004; Leão et al. 2016). Reefs worldwide are vulnerable to a range of threats including climate change, pollution, inadequate coastal development, and predatory fishing (Scheffer et al. 2001). In addition, many reefs have been impacted by the introduction of invasive alien species, which are species that are present in areas beyond the limits imposed by their biogeographic barriers and can cause significant economic and ecological damage (Simberloff et al. 2013; Williams and Grosholz 2008). Indeed, economic losses attributable to invasive species have been estimated to reach billions of dollars when factoring in damage and cost control (Pimentel et al. 2000). They are also responsible for changes in population biology, community structure, and local extinction of native species (Mack et al. 2005; Sakai et al. 2001).

Along the Brazilian coast, the invasive bivalve *Isognomon bicolor* (C. Adams, 1845) has undergone an expansion in distribution and abundance since its introduction (Ferreira et al. 2009). Originally distributed in the Gulf of Mexico, southern Florida, and the Caribbean (López et al. 2014), this species was first reported in Brazil in 1994, where it was probably accidentally introduced during the creation of new oil platforms (Breves-Ramos et al. 2010; Domaneschi and Martins 2002). Currently, this species' distribution ranges from the northern state of Piauí to the state of Rio Grande do Sul, where it inhabits marine ecosystems from coral reefs to hypersaline estuaries (Dias et al. 2013; Domaneschi and Martins 2002; Loebmann et al. 2010; López et al. 2014; Lopez and Coutinho 2010; Agostini and Ozorio 2016). *Isognomon bicolor* has also been recorded in Uruguay and southern England, where the specimens were found on floating debris rather than on natural substrates (Breves et al. 2014; Holmes et al. 2015). Records of *I. bicolor* have also been found in the Central Mediterranean Sea, Italy (Gatì et al. 2024).

Most studies on *I. bicolor* in Brazil have focused on the species' taxonomy, geographical distribution, range expansion, and population ecology on rocky and artificial reefs (Bezerra 2010; Breves-Ramos et al. 2010; Breves et al. 2014; Domaneschi and Martins 2002; Zamprogno et al. 2010). Isolated studies have compared the genetic variability of *I. bicolor* with that of a native bivalve (Aranha 2010) and described biotic interactions between *I. bicolor* and a native macroalga (Lopez and Coutinho 2010) and native predators (Lopez et al. 2010). Another study described the reproductive cycles of *I. bicolor* and evaluated population parameters (Queiroz et al. 2022). However, little is known about the impact of this invasive bivalve on the native benthic community (Martinez 2012; Queiroz et al. 2023). Although *I. bicolor* has only recently established on the Brazilian coast, it is locally abundant and has a sufficiently broad distribution to significantly change the structure of many communities (Breves-Ramos et al. 2010; Lopes and Villac 2009; Martinez 2012).

In this study, we evaluate the impact of invasive *I. bicolor* on the structure (composition, abundance, richness, and diversity) of the native benthic community. For this purpose, we experimentally removed *I. bicolor* from several sites where it was established and compared the benthic communities in these areas with those of sites that still hosted a population of the bivalve.

2 | Materials and Methods

2.1 | Study Site

This study was performed in the intertidal zone of sandstone reefs on the northeastern coast of Brazil, in the cities of Maceió and Marechal Deodoro, Alagoas (Figure 1). We examined two sites: Saco da Pedra Sandstone Reef (9°44′45,2″ S, 35°49′13,6″ W) and Sereia Sandstone Reef (9°34′03,2″ S, 35°38′48,3″ W). These sites are geomorphologically characterized by being relatively steep sandstone reefs, with Sereia Reef having a greater number of cracks and water pools and Saco da Pedra Reef having a more extensive rocky strip and its close to estuary areas. The tidal regime is semidiurnal, from −0.1 to +2.3 m (DHN/Brazilian Navy).

2.2 | Removal Experiment

To evaluate the impact of *I. bicolor* on the benthic community, an in situ removal experiment was carried out on the two sandstone reefs. On each reef, 20 PVC quadrats (50 × 50 cm) were arbitrarily distributed over approximately 80 m of reef. Each quadrat was established within a minimum distance of 2 m from each other, and were alternately assigned to be control or treatment. On Day 1 of the experiment, the quadrats were photographed to allow characterization of the biota before removal of the invasive species. After photographing, *I. bicolor* individuals were carefully experimentally removed (treatment) with a spatula from 10 of the 20 quadrats with minimum impact on other benthic species, whereas the other 10 squares were not manipulated (control). The bivalves were removed only at this point in the experiment. Before the PVC quadrats were removed, the upper left corners of their locations were marked with marine tubolit cement as a physical reference for subsequent monitoring. The percent coverage of benthic species in the quadrats was monitored on a monthly basis from October 2016 to September 2017 through geo-referenced photos (Figures S1–S4).

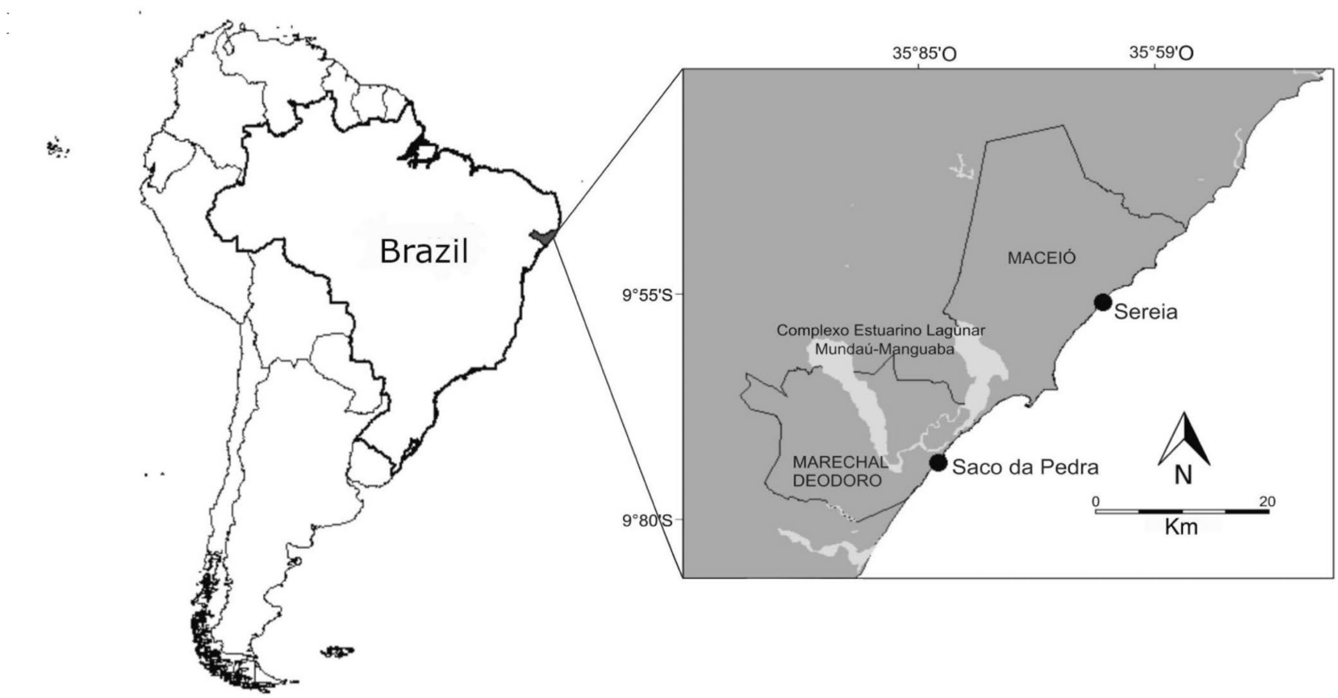

FIGURE 1 | Area of study, located on the coast of the state of Alagoas (AL) represented in the larger map on the right. The black spots indicate the studied sites (sandstone reefs of Sereia and Saco da Pedra).

2.3 | Identification and Analysis of Native Biota

The identification of the biota to the lowest possible taxonomic level in monthly photos of the quadrats was performed based on relevant literature (Dias et al. 2013; Domaneschi and Martins 2002; Rios 1985, 2009) and by consultation with taxonomic specialists. The percentage coverage of each taxon was calculated using the program Coral Point Count with Excel Extension 4.1 (Kohler and Gill 2006). To use this program, a database was created with the names of the macrobenthic species found in the analyzed quadrats. For each of the 480 images obtained during the 12 monthly sampling events, 100 points were created (totaling 48,000 points), which were identified and marked with the species present at the points of intersection. Points with no macrobenthic species present were attributed to a Pavement, Rubble, or Sand category and were later removed from the analysis to calculate indices of richness, diversity, and community structure.

2.4 | Statistical Analysis

Species richness and the Simpson diversity index were calculated for each sample unit and used as response variables in a repeated measures analysis of variance (ANOVA), considering the treatment as a factor, the month of collection as a covariate, and the interaction between both. Thus, four replicate measures ANOVAs were carried out, one for richness and one for diversity on each reef. The presence of the invasive species *I. bicolor* was not counted in the measures of richness and diversity. In order to assess a potential undesirable effect of *I. bicolor* removal on the studied quadrats, we performed Student's *t*-tests to compare the average initial species richness and diversity before removal with the first month measures.

A Bray–Curtis similarity matrix was calculated for each reef considering the sum of the data collected in 1 month and each quadrat as the sample unit. The statistical differences between the community structure with and without the mollusk were tested with a permutational multivariate ANOVA (PERMANOVA) adapted for distance matrices ("adonis" function of the "vegan" package in the R software). In order to visualize and interpret these possible differences, the matrices were used in a bidimensional non-metric Multidimensional Scaling (NMDS) plot to show the differences between the sample treatment and control units.

A principal component analysis (PCA) of the densities of native species was performed for each reef studied after a Hellinger transformation (again, using months as sample units). The Hellinger transformation, as indicated by Borcard et al. (2018), allows the application of a PCA generating a result equivalent to the use of Hellinger distance. This is considered as a robust metric for species abundance data in grouping or ordination. The first two main components of each analysis were then used for biplot graphic visualization (removing the native species poorly correlated with the components) to observe the possible effects of the experimental treatment on the densities of the species.

To evaluate the variation in the density of native species and invasive species throughout the year, graphs were created comparing the abundance of the native species in quadrats where the invasive species was not removed (control quadrats) with quadrats where it was removed (treatment quadrats).

All statistical analyses were performed in R (R Core Team, 2018).

3 | Results

Among the 20 taxa detected in the two sandstone reefs, 17 were recorded from Sereia Reef and 14 from Saco da Pedra Reef before the removal experiment started (Table 1). The most abundant taxa in quadrats on Sereia Reef prior to the removal experiment were the gastropod *Vermitidae incertae sedis irregulares* (d'Orbigny, 1841), crustacean *Chthamalus bisinuatus* (Pilsbry, 1916), algae of the genus Chaetomorpha spp., and cyanobacteria of the order Oscillatoriales. The most abundant taxa in quadrats on Saco da Pedra Reef before the removal of *I. bicolor* were the gastropods *V. irregulares* (d'Orbigny, 1841), *Echinolittorina ziczac* (Gemelin, 1791), and the bivalve *Mytilaster solisianus* (d'Orbigny, 1842).

We observed an increase in species richness in the quadrats on Sereia Reef with the invasive species *I. bicolor* (control) compared to the experimental squares without *I. bicolor* (treatment) ($F=0.07$ and $p=0.008$) (Figure 2). Species richness on Sereia Reef varied throughout the year ($F=25.5$ and $p<0.001$), with control quadrats' richness decreasing slightly below removal quadrats during December and January. In the other months, species richness was higher in the control quadrats than in the treatment quadrats. On Saco da Pedra Reef, no statistically significant difference was found in the richness between control and treatment quadrats ($F=2.5$ and $p=0.11$). Species richness also varied throughout the year ($F=6.9$ and $p=0.009$), with the highest decreases on control quadrats compared to treatment quadrats happening in February, March, and September (Figure 2). No statistical differences were detected when the species richness and diversity were compared on control treatments before the removal and the first month assessment, both on Sereia Reef ($t=-0.47$, df = 18, $p=0.643$ for richness and $t=-0.25$, df = 18, $p=0.806$ for diversity) and on Saco da Pedra Reef ($t=1.01$, df = 18, $p=0.322$ for richness and $t=-0.31$, df = 18, $p=0.764$ for diversity).

Species diversity on Sereia Reef increased in control quadrats in relation to the treatment ($F=7.3$ and $p=0.007$), according to the repeated measures ANOVA. Similarly, species diversity also varied during the year ($F=12.7$ and $p<0.001$), but it was always higher in quadrats where the invasive species was not removed (control quadrats) than in the treatment quadrats (Figure 3). Similar results for species richness were found for Saco da Pedra Reef, though no statistical differences between treatment and control quadrats were noted ($F=0.87$ and $p=0.35$). Species diversity in this reef also varied throughout the year ($F=8.1$ and $p=0.004$), with decreases from Months 1 to 6 in the control quadrats followed by smaller decreases in Months 9 and 10 (Figure 3).

We detected statistically significant differences in community structure between treatment and control groups (Sereia Reef: $F=18.5$, $p=0.001$, $R^2=0.46$; Saco da Pedra Reef: $F=4.81$,

TABLE 1 | Taxonomic list with the mean densities (±SD) of the species recorded in the sandstone reefs of Sereia and Saco da Pedra prior to the experiment.

Taxa	Sereia	Saco da Pedra
Porifera		
Cliona celata Grant, 1826	0	0.50 ± 0.60
Cnidaria		
Bunodosoma cangicum Belém and Preslercravo, 1973	0	0.05 ± 0.22
Zoanthus sociatus (Ellis, 1768)	0	0.10 ± 0.44
Mollusca		
Echinolittorina ziczac (Gemelin,1791)	0.75 ± 2.26	2.60 ± 5.71
Fissurella clenchi Pérez Farfante, 1943	0.20 ± 0.41	0
Isognomon bicolor (C. B. Adams, 1845)	8.8 ± 6.67	17.9 ± 12.42
Lottia subrugosa (d'Orbigny, 1846)	0	0.05 ± 0.22
Mytilaster solisianus (d'Orbigny, 1842)	0.05 ± 0.22	25.25 ± 22.50
Vermitidae incertae sedis irregulares (d'Orbigny, 1841)	15.20 ± 10.35	23.45 ± 10.95
Arthropoda		
Chthamalus bisinuatus (Pilsbry, 1916)	5.55 ± 7.44	0
Tetraclita stalactifera (Lamarck, 1818)	0.65 ± 2.00	0
Echinodermata		
Echinometra lucunter (Linnaeus, 1758)	0.10 ± 0.30	0.05 ± 0.22
Cyanophyta		
Oscillatoriales	10.90 ± 17.69	0
Chlorophyta		
Chaetomorpha spp.	5.35 ± 5.50	0
Ulva lactuca Linnaeus, 1753	0	
Ulvales	0	0
Ulvaceae	0.65 ± 1.66	0
Rhodophyta		
Bostrychia montagnei Harvey, 1853	0	0
Centroceras clavulatum (C. Agardh) Montagne, 1846	0	0
Ceramium corniculatum Montagne, 1861	0	0

(Continues)

TABLE 1 | (Continued)

$p = 0.016$, $R^2 = 0.18$). These differences can be visualized in the NMDS plot, which shows a very clear separation between community composition in treatment quadrats compared to the control ones (Figure 4). Bray–Curtis' analysis showed that these differences were greater in Sereia Reef than in Saco da Pedra Reef.

The PCA of the densities of the native species of the Sereia reef over time showed that *M. solisianus*, *E. ziczac*, and *Chaetomorpha* spp. were most abundant in quadrats where the invasive mollusk was not removed. Other species (*C. clavulatum*, *C. bisinuatus*, and *F. clenchi*) were also abundant in the presence of *I. bicolor*, but to a lesser extent. In the treatment quadrats, *C. aerea*, *Oscillatoriales*, *T. stalactifera*, and *V. irregulares* had the greatest abundance (Figure 5). The PCA, used to measure the effect of *I. bicolor* on the abundance of the native species over time on the Saco da Pedra reef, detected variations in the abundances of Ulvales sp., *M. solisianus*, *E. ziczac*, *V. irregulares*, and *C. corniculatum*, but no relation was observed with the experimental treatment (Figure 6).

Different species showed different growth and dominance patterns. *M. solisianus*, *C. clavulatum*, and *F. clenchi* were more abundant in the control quadrats (with *I. bicolor*). *M. solisianus* was more abundant in April and September, the algae *C. clavulatum* was more abundant in May and August, and *F. clenchi* was more abundant in December and August. *C. aerea*, *T. stalactifera*, and *V. irregulares* were more abundant in quadrats where the invader was absent. Compared to the other months, the alga *C. aerea* showed higher densities from April to September, and *T. stalactifera* was most abundant in March and July. On Saco da Pedra Reef, the alga *C. corniculatum* was highly abundant in the control quadrats, especially from March to June. The other native species of Saco da Pedra Reef showed similar patterns of variations in both control and treatment quadrats (Figure 7).

4 | Discussion

Our results indicate that *I. bicolor* significantly influences benthic community structure by altering the composition, abundance, richness, and diversity of native species. On Sereia Reef, we observed a greater richness and diversity of native species where *I. bicolor* was not removed than where *I. bicolor* was

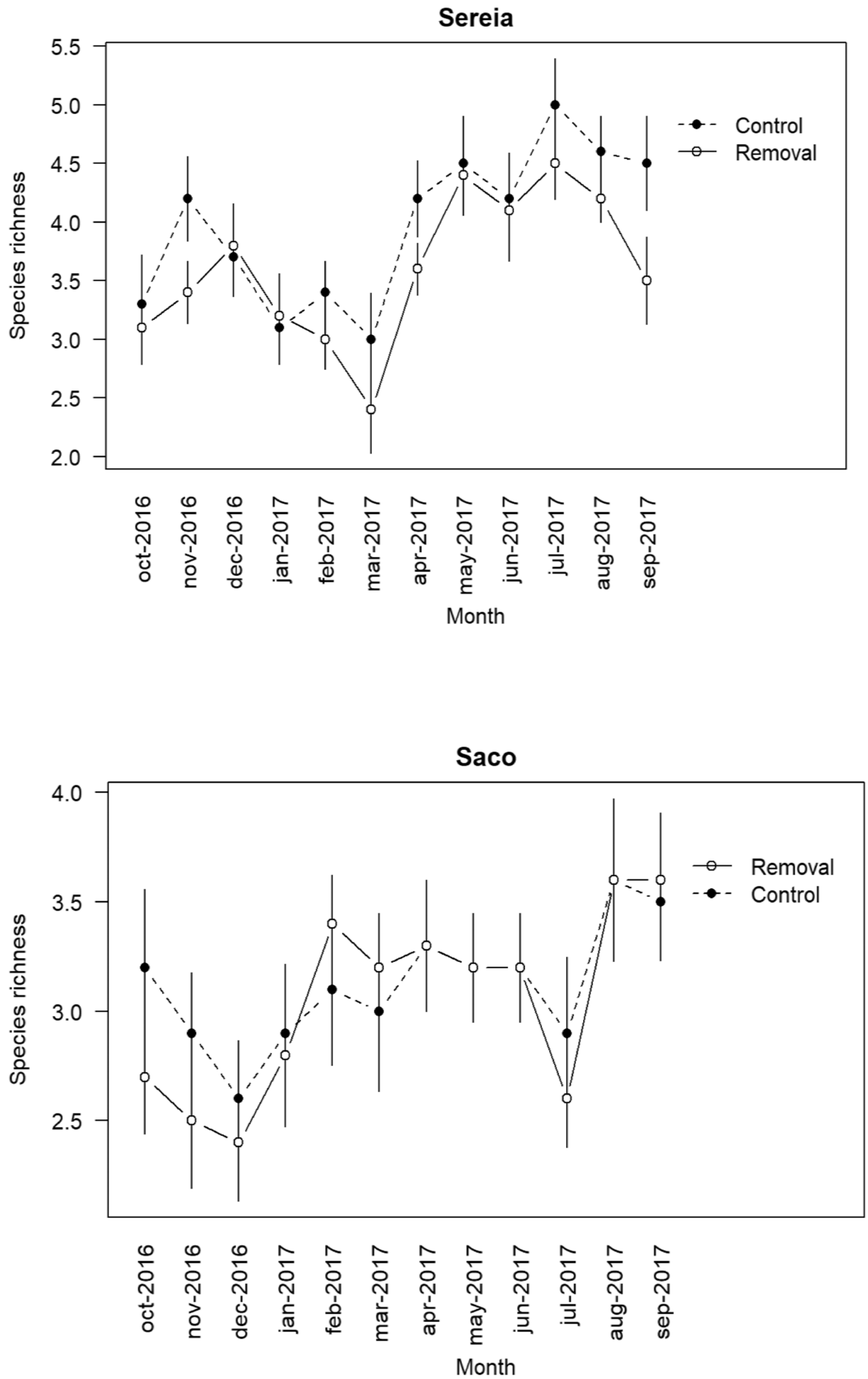

FIGURE 2 | Variation of species richness in the sandstone reefs of Sereia and Saco da Pedra over the months. The points represent the average number of species and the bars represent the standard error in the different collection months in the treatment (with removal) and in the control (without removal).

removed. However, on Saco da Pedra Reef, the removal of the invasive bivalve seemingly had no effect on the richness and diversity of the native species. These results most likely reflect the differences existing in both reefs that, despite being made of sandstone, have some important differences.

The differences between the native biota of the two reef areas may have influenced the behavior of the bioinvader and, consequently, the response of the reef community to the introduction of the invasive species (Table 1). On Sereia reef, the invader forms dense banks, potentially creating a substrate more complex than that produced by native species. This was also observed for the exotic oyster *Crassostrea gigas* (Thunberg, 1793), which also creates a more complex substrate than the native species in areas it colonizes (Kochmann et al. 2008). Similarly, the invasive bivalve *Corbicula fluminata* (Müller, 1774) can considerably increase the availability of hard surfaces for species that prefer structured habitats (Werner and Rothhaupt 2007).

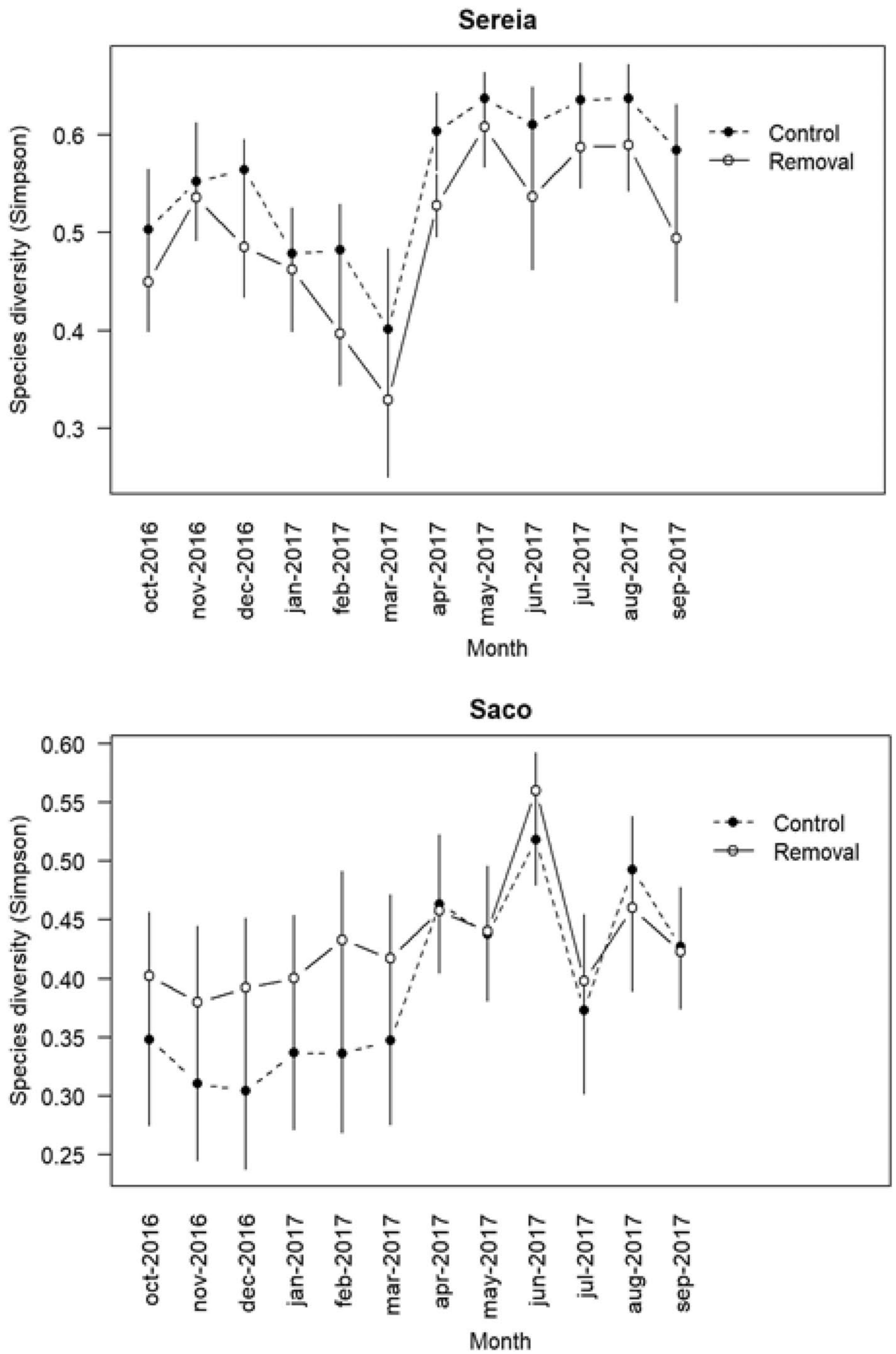

FIGURE 3 | Variation of species diversity (Simpson) in the sandstone reef of Sereia and Saco da Pedra over the months. The points represent the mean diversity and the bars represent the standard error in the different collection months in the treatment (with removal) and control (without removal).

More generally, mussels may increase the complexity of benthic communities, as well as the richness and diversity of species in the intertidal zone (Robinson et al. 2007). Thus, some bivalve species, when introduced, may increase habitat heterogeneity, leading to higher native species and richness (Crook 2002).

The presence of invasive species may often result in an increase in the abundance or biomass of native species. According to Rodriguez (2006), this increase depends on the ecological context and the ecology of the introduced species. Such “facilitating interactions” may sometimes be as frequent as other interspecific interactions, including competition, predation, and parasitism (Bruno et al. 2003). However, increases in the density and richness of invertebrates after bivalve invasions are typically associated with a decrease and even extirpation of other native species (Souza et al. 2006). Thus, invasive habitat-forming species can affect the components of a native community in several different and context-dependent ways (Gribben et al. 2013). Since percent cover was estimated using photographs, there may be limitations in analyzing abundance over time if there is a large amount of algae cover, as this may underestimate the abundance of small organisms. In Figure 7, for example, the reduction in

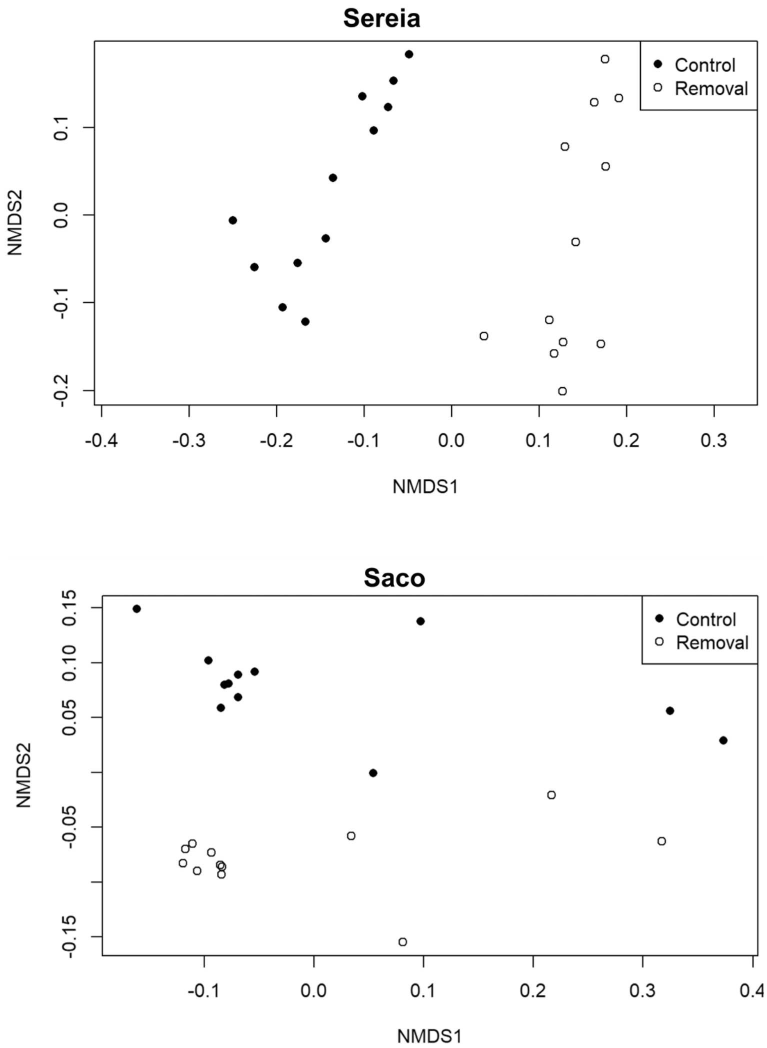

FIGURE 4 | Representation of the differences in the structure and composition of the native community in the squares where the invasive species *I. bicolor* was removed (removal) and in the squares where this species was present (control) in the sandstone reef of Sereia and Saco da Pedra, result of an NMDS applied to the Bray–Curtis distance matrix (stress: 0.07 in the Sereia reef and 0.05 in the Saco da Pedra reef).

the density of *M. solisianus* is accompanied by an increase in foliaceous green algae, which may have covered these small bivalves. Those events, however, were not frequent, and our field observations during the photographs were made it unlikely that this could impact our main results and conclusions.

Similar results for the relationship between the abundance of *I. bicolor* and the diversity of the native biota on Saco da Pedra Reef were reported by Aranha (2010). Depending on the ecological context, an invader may change, increase, decrease, or have no effect on the richness, abundance, or structure of the native community (Thomsen et al. 2016). A study on the bivalve *Mytilus galloprovincialis* (Lamarck, 1819) reported a negative influence on the abundance and biomass of the cirripedia *Chthamalus dentatus* (Krauss, 1848); however, there were no changes in the diversity, richness, or abundance of the native biota (Hanekom 2008). An experimental study on the invasive ascidean *Ciona robusta* (Hoshino and Tokioka, 1967) also showed no effect on the richness, diversity, or composition of the native community in one of the environments studied (Robinson et al. 2017).

The different abiotic conditions of the studied reefs might have also contributed to the different observed of results for the removal of the biological invader in the native community in both environments. The Saco da Pedra reef is longer than the Sereia reef; in addition, it is exposed for more time during low tide, and for this reason, it is a drier reef. On the other hand, the Sereia reef is more humid, has more algae, and is less exposed at low tide. Therefore, the direction and magnitude of the impacts of the invasion may depend on the properties associated with the invasive species (e.g., size, sex, and density), native biota (e.g., community structure), resource levels (e.g., nutrient levels), and abiotic conditions (e.g., sedimentation) (Thomsen et al. 2011).

The geomorphological differences between the two reefs studied may cause the invasive species to affect the benthic community in different ways, since according to Mello-Rafter et al. (2021), there are significant differences in species composition between communities on different substrates. The Sereia Reef has species such as the mollusk *Fissurella clenchi*, the arthropods *Chthamalus bisinuatus*, and *Tetraclita stalactifera*, the cyanobacteria *Oscillatoriales*, and algae such as *Chaetomorpha*

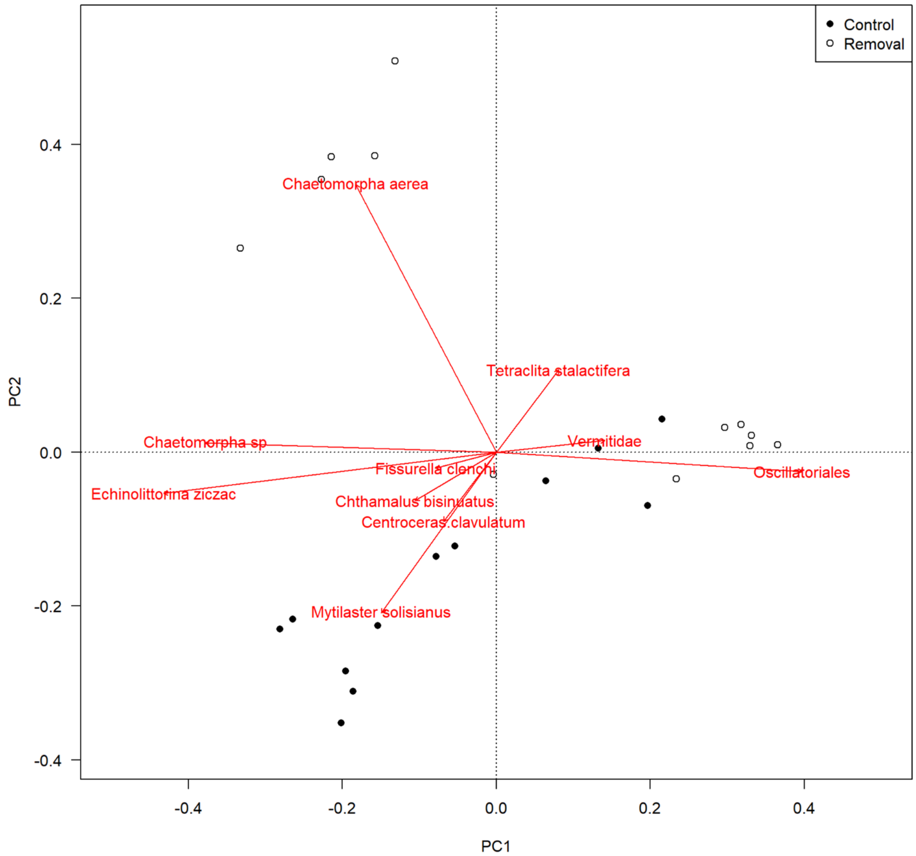

FIGURE 5 | *Biplot* of the PCAs of the densities of the native species of the Sereia over time and the relation with the experimental squares of treatment (with the removal of *I. bicolor*) and control (without the removal of the invading bivalve). The full dots represent the control quadrats and the empty points the removal quadrats. PC1 and PC2 explain 47.91 and 15.71% of the variation, respectively (adding 63.62%).

spp. According to Feldmann (1937) and Giaccone et al. (1993), there is a close relationship between the presence of some algae and the types of rock; in addition, the increased water movement increases the availability of nutrients for seaweeds (Ballesteros 1989). The Saco da Pedra Reef has species such as the mollusk *Lottia subrugosa*, poriferans, and cnidarians such as *Cliona celata*, *Bunodosoma cangicum*, and *Zoanthus sociatus* that require a rigid and stable surface for attachment (Beazley et al. 2013; Kazanidis et al. 2019).

Annual Rainfall on Praia da Sereia, in Maceió, varies throughout the year. The months of April to July represent the period of greatest rainfall, while the least rainy period is established between the months of October and January (Firmino et al. 2024). Regarding species richness and diversity on the Sereia reef, during the months of greatest rainfall, we had a decrease only in the month of June, which suggests that this decrease is probably not related to the annual rainfall of this reef. The municipality of Marechal Deodoro, where Praia do Saco is located, has little rainfall, with a dry summer and rainfall in the fall and winter; that is, between the months of March and August (Bezerra 2010). Species richness and diversity decreased in the months of March, May, and July, months in which rainfall occurs on this reef, but there were other decreases in species richness in the months of November and December and in species diversity in the months of September and November, which also suggests that this decrease in species richness is probably not related to the annual rainfall that occurs on this reef.

We conclude that the establishment of the invasive bivalve *I. bicolor* on the consolidated substrates of sandstone reefs can change the structure of the benthic community, altering the composition, abundance, richness, and diversity of native species. The invasive bivalve *I. bicolor* was found to increase the richness and diversity of native species on one of the reefs, but on another, the presence of the invasive mollusk apparently had no effect on the native biota, suggesting that the composition of native species and the abiotic conditions of the reef may influence the impact of invasive species, resulting in different responses of the native community. The species *M. solisianus, E. ziczac*, and *Chaetomorpha* spp., *C. clavulatum, C. bisinuatus*, and *F. clenchi* were more abundant in the presence of the invader, indicating that they may be benefiting from the presence of the mollusk. However, the species *C. aerea, Oscillatoriales, T. stalactifera, and V. irregulares* were more abundant in the absence of the mollusk, suggesting that these species were the most impacted by the presence of this invader. The invasive mollusk *I. bicolor* has demonstrated a high invasive potential and should be considered a new threat to coastal biodiversity. Future research is needed to test how this species damages native communities in other environments, such as coral reefs of the infralittoral, artificial reefs, and hypersaline rivers. Studies on larger spatial and temporal

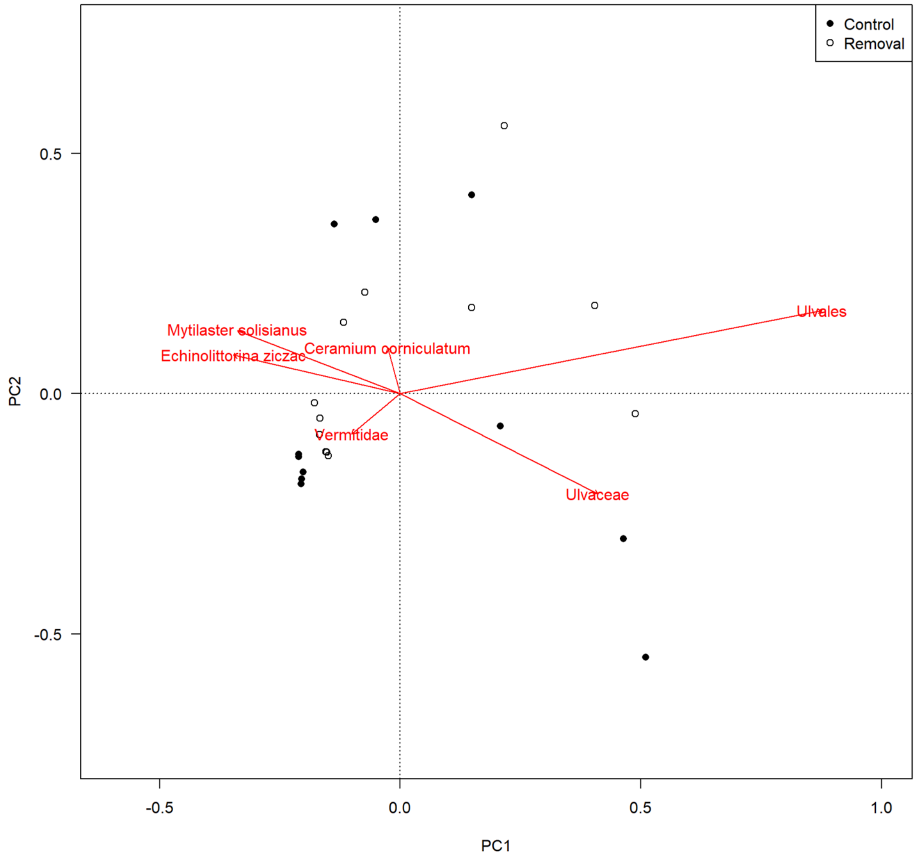

FIGURE 6 | Biplots of the PCAs of the densities of the native species of Saco da Pedra over time and the relation with the experimental squares of treatment (with the removal of *I. bicolor*) and control (without the removal of the invading bivalve). The full dots represent the control quadrats and the empty points the removal quadrats. PC1 and PC2 explain 81.15% and 7.76% of the variation, respectively (adding 88.90%).

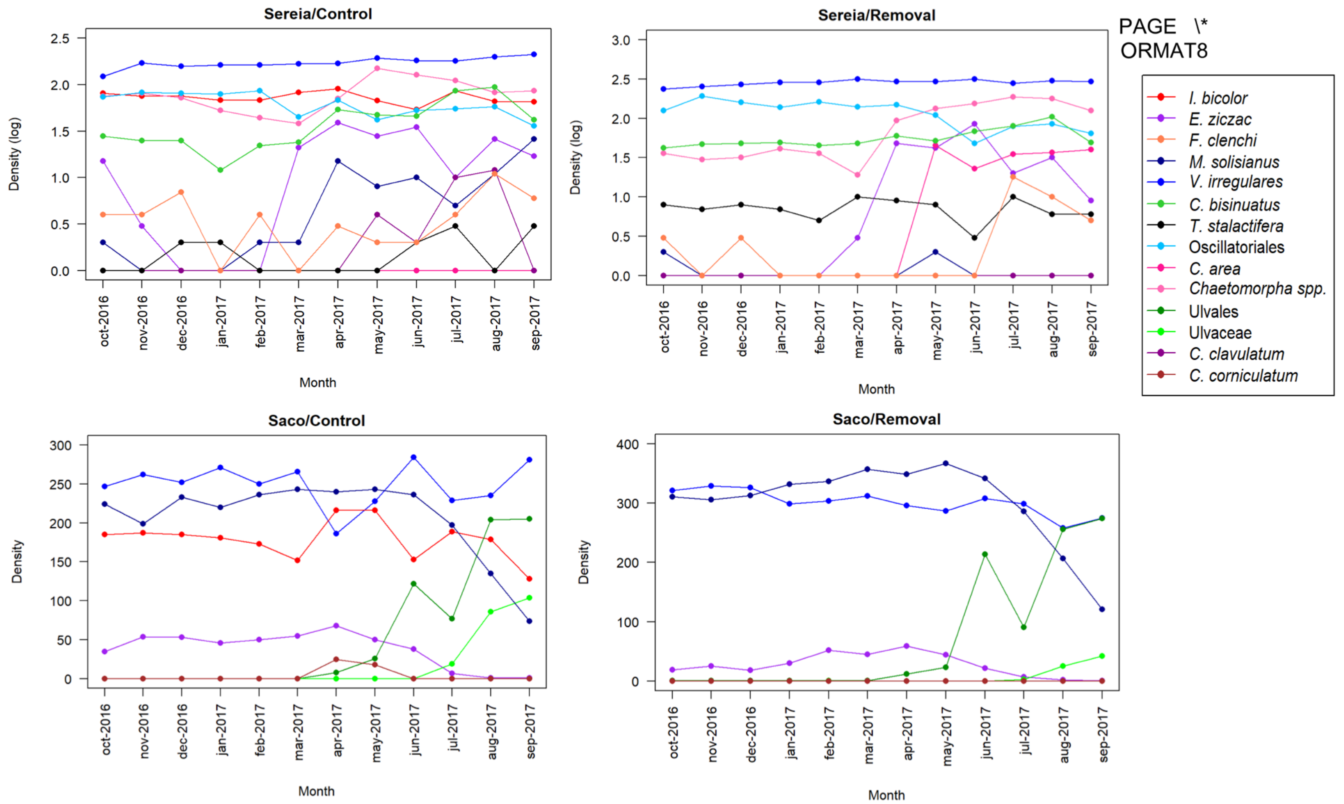

FIGURE 7 | Variation of densities of native species and invasive species in the sandstone reefs of Sereia and Saco da Pedra during the months and the relation with the experimental squares of treatment (with the removal of *I. bicolor*) and control (without the removal of the bivalve invader).

scales are also essential for long-term monitoring. Knowledge about interactions between biotic invaders and native species is of extreme importance for assessing the impacts that these species can have on ecosystems. Such information can also be used in the development of control and eradication strategies to mitigate environmental degradation and prevent future invasions.

Acknowledgements

This study was partially funded by the Brazilian National Council for Scientific and Technological Development (CNPq) and the Coordination for the Improvement of Higher Education Personnel (CAPES).

Data Availability Statement

The authors have nothing to report.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S11–S3:** maec70052-sup-0001-FigureS11–S3;.docx.