The alien octocoral *Carijoa riisei* is a biogenic substrate multiplier in artificial Brazilian shipwrecks

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Abstract Despite the obvious negative effects caused by invasive species, some recent studies have shown that the impacts at local scale are diverse and not necessarily negative. Arborescent benthic organisms such as octocorals form three-dimensional structures capable of increasing the amount of substrate available and providing shelter for epibiont species. We investigated the role of the alien octocoral *Carijoa riisei* on the diversity of benthic communities in three shipwrecks on the north-eastern coast of

Brazil. We expected that (a) the fauna associated with the octocoral are richer and more diverse compared to the adjacent; (b) some species are exclusively associated with *C. riisei*; (c) the species that are present both in the areas with and without *C. riisei* have a greater abundance when associated with the octocoral. For this, we compared the macrobenthic communities associated with *C. riisei* to those found in adjacent areas where the octocoral was absent. Our study showed that the communities associated with the octocoral were 1.5 times richer and 10 times more abundant than adjacent communities, with 29

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exclusive taxa. The dominant taxa were the amphipods *Erichthonius brasiliensis* and *Podocerus brasiliensis* and polychaetes of the family Syllidae. These taxa were present in areas with presence and absence of *C. riisei*, but their abundance was significantly greater where the octocoral was present. Our results reinforce the idea that *Carijoa riisei* acts as an ecosystem engineer in coastal reefs, creating new habitats and increasing diversity at a local scale, even though it is an alien species.

Keywords Soft coral · Non-native species · Non-indigenous species · Epibiosis · Octocorallia · Artificial reefs

Introduction

The introduction of alien species has been considered, at a global scale, as one of the main causes for the loss of diversity (Díaz et al. 2019; IPBES 2019), provoking environmental degradation and accelerating biotic homogenization processes (Olden et al. 2004). Despite the obvious negative effects, mainly through competition with native species and predation interactions (e.g. Riccardi and Giussani 2007), some recent studies have shown that the impacts at a local scale are diverse and, depending on the variables considered, are not necessarily negative [e.g. Ward and Ricciardi (2007); for a revision on this subject see Gallardo et al. (2016)]. Equally, the main focus of studies with bioinvasors has been on the negative effects of alien species, ignoring native biota that profit from the presence of alien species [see Vimercati et al. (2020) and references therein].

Although less studied, positive impacts of invasive species have been registered in the benthic environment. For example, some invasive detritivores in aquatic ecosystems have been demonstrated to induce positive effects on species diversity, mainly among invertebrates and macroalgae (David et al. 2017; Gallardo et al. 2016; Mollot et al. 2017). Positive effects have been recorded, principally, for species that form or modify habitats. These species increase environmental complexity and can provide food, protection and other services that contribute to the increase in local biodiversity (Buhl-Mortensen et al. 2010; Victorero et al. 2018; De la Torriente et al.

2020). Studies with zebra mussels revealed a reduction in planktonic biomass but an increase in benthic biomass (invertebrates, macrophytes, algae and bacteria) due to the increase in substrate availability (Reed et al. 2004; Higgins and Vander Zanden 2010).

Arborescent benthic organisms, such as algae, bryozoans, corals and soft corals, form three-dimensional structures capable of amplifying substrate availability and providing shelter and food for epibiont species (Buhl-Mortensen and Buhl-Mortensen, 2004; Baillon et al. 2014). These species, even when non-native, have the potential of creating or modifying habitat structure and the abundance patterns and composition of native epibiota in a significant way, affecting biodiversity and ecosystem processes. This potential depends on the ability of native epibionts to colonize a non-native species, host specificity, as well as the ability of the non-native organism to increase habitat complexity, providing sustenance and protection to the epibionts (Wikstrom and Kautsky 2004; Buschbaum et al. 2006; Lutz et al. 2019). For seaweeds, the impact of alien species depends on its complexity and epibiont specificity, as several studies have detected differences in native and non-native seaweed community diversities (e.g. Veiga et al. 2014; Dijkstra et al. 2017; Lutz et al. 2019). On the other hand, the impact of non-native octocorals on epibiont communities has been poorly explored. Understanding the effects of non-native species on local biota and ecosystem processes is a significant challenge for ecologists, as well as being fundamental for the conservation of biodiversity (Katsanevakis et al. 2016; Copp et al. 2017).

The snowflake octocoral, *Carijoa riisei* (Duchassaing and Michelotti 1860) (Anthozoa: Clavulariidae), is native to the Indo-West Pacific (Concepción et al. 2010) and has achieved ample geographical distribution throughout tropical waters across the world: Atlantic and Caribbean Ocean (Castro et al. 2010; Edwards and Lubbock 1983; Concepción et al. 2010), Indian Ocean (Padmakumar et al., 2011; Dhivya et al. 2012; Yogesh-Kumar et al. 2014; Patro et al. 2015); Indo-Pacific (Raghunathan et al. 2013) and Eastern Pacific (Sánchez and Ballesteros 2014; Quintanilla et al. 2017; Galván-Villa and Ríos-Jara 2018). This species is considered as an invasive alien species in some regions of Hawaii and Columbia, competing with other organisms for food and space and displacing native species (Grigg 2003; Kahng and Grigg

2005; Sánchez and Ballesteros 2014). In Brazil, *C. riisei* is an alien species and is well established from the north of the country down to Santa Catarina State (Castro et al. 2010; Barbosa et al. 2014). The species can be found in coastal reefs, sheltered caves, estuaries, mangroves (Rees 1972; Sánchez 1994; Bruto-Costa et al. 2014), oil platforms (Bull and Kendall Jr. 1994), artificial structures such as jetties, boats and port structures (Cummings 1994; DeFelice et al. 2001), as well as shipwrecks (Baynes and Szmant 1989; Wagner et al. 2009; Amaral et al. 2010; Lira et al. 2010). This habitat plasticity, together with their fouling habit, accelerated branch growth (that can reach up to 1 cm in a week), and rapid sexual maturation (Kahng et al. 2008; Barbosa et al. 2014) explains the ample distribution and invasive potential of the species. On the other hand, its arborescent structure, with branches up to the 6th order, creates a three-dimensional environment (Bayer 1961; Bruto-Costa et al. 2014) capable of housing the diversity of associated fauna (Souza et al. 2007; Neves et al. 2007; Galván-Villa and Ríos-Jara 2018). Thus, even in locations where it is non-native, *C. riisei* may be contributing to an increase in local diversity.

In north-eastern Brazil, *C. riisei* is abundant in several shipwrecks, where it is the only organism with an arborescent structure, offering a three-dimensional structure in these shipwrecks (Amaral et al. 2010; Lira et al. 2010). Shipwrecks have been recognized as oases for benthic fauna, with a consolidated substrate in the midst of the mainly unconsolidated substrate of the sea floor. In this case, the presence of organism substrate multipliers, although non-native, may have a positive effect on diversity. Shipwrecks, as with other coastal artificial structures, are still argued to be potential sources of individuals that can (re)colonize coastal environments that are generally more impacted (Perkol-Finkel et al. 2006). Therefore, this potential depends on several factors associated with the physico-chemical characteristics of the artificial structure, the local community and the connectivity between environments, as well as varying between species (Perkins et al. 2015; Mercader et al. 2017; Ferrario et al. 2016; Sedano et al. 2019 and references therein). On the other hand, shipwrecks can also act as an entry way or provide steppingstone habitats for invasive alien species to expand their distribution into natural habitats (de Oliveira Soares et al. 2020). In cases such as these, the presence of an alien species

can act as a facilitator to other non-native species (for greater discussion on this theme, see Richardson et al. 2000).

Thus, we decided to investigate the role of the alien octocoral *C. riisei* on the diversity of benthic communities in shipwrecks along the coast of north-eastern Brazil. For this, we compared the community of macroinvertebrates present in areas with *C. riisei* and in adjacent areas where *C. riisei* was absent in three shipwrecks. Our hypothesis is that *C. riisei* has a positive effect on local diversity. Thus, we expected that (a) the fauna associated with this octocoral is richer and more diverse compared to the adjacent areas for all the shipwrecks; (b) some species are exclusively associated with *C. riisei*; (c) species that are found both in areas with and without the presence of *C. riisei* have a greater abundance when associated with the octocoral.

Material and methods

Study area (Shipwreck: Servemar X, Taurus and Lupus)

This study was carried out in the Artificial Shipwreck Park of Pernambuco, located on the north-eastern coast of Brazil. The local climate is hot tropical and humid, temperatures have low seasonal variations, with a mean of 25 °C. The average rainfall is 2000 mm/year, with two marked seasons: a rainy season (March–August, > 250 mm/month) and a dry season (September–February, < 100 mm/month) (Cary et al. 2015).

The samples were collected from three shipwrecks: Taurus (− 08°07′13.0000″, − 034°45′11.7600″), Servemar X (− 08°07′19.0000″, − 034°45′46.0000″) and Lupus (− 08°22′11.0000″, − 034°47′28.0000″) (Fig. 1). All the shipwrecks are steel tugboats, sunken at depths of between 20 and 30 m. Servemar X was sunk in 2006 (25 m), Taurus (25 m) and Lupus (26 m) were sunk in 2002 with distances of 15, 13 and 18.1 km from the coast, respectively. In shipwrecks, *C. riisei* is abundant especially in locations of lower luminosity such as the cabin and the ship hold, where its arborescent structure can reach 25 cm in length (Fig. 2).

Fig. 1 Geographical localization of shipwrecks on the north-eastern coast of Brazil: Servemar X (25 m depth), Taurus (25 m depth) and Lupus (36 m depth)

Collection procedures and analysis of biological samples

The sample collections were performed using SCUBA in two surveys in July and December 2018. The samples (15 × 15 cm) were defined with PVC squares, and the substrate was scratched, with the help of a spatula, into a plastic bag to avoid the loss of epibionts. Samples were collected randomly and independently in each survey (not marked plots), from all sectors of the shipwreck where the octocoral was present (mainly cabin and the ship hold). In these sectors, at each shipwreck during each survey, 20

samples were collected, ten in the areas where the octocoral *Carijoa riisei* was present (CP) and ten in the adjacent areas within the same sectors, where the octocoral was absent (CA). Samples were collected at least 1 m apart to reduce the probability of sampling the same colony and to ensure independent samples. For the majority of the areas where *C. riisei* was absent, the surface of the shipwreck was covered with algae and sponges. The samples were fixed with 4% formalin in the field. In the laboratory, the samples were washed successively in a sieve of 250 µm to remove the fragile fauna and to retain the macrofauna, which was conserved in plastic pots with 70% alcohol

Fig. 2 *Carijoa riisei* colonies from Servemar X shipwreck. **a**, **b** details of *C. riisei* colonies branching and **c** *C. riisei* in the ship's hold. Colonies are between 15 and 25 cm in length

and was then sorted, counted and identified to the lowest taxonomic level possible, with the aid of specific identification guides and consultations with specialists. The colonial organisms were not quantified, only classified as present or absent and used for richness and some beta diversity measures.

Data analysis

The ecological indices of Abundance (N), Richness (S or total number of taxa), Pielou's evenness (J' using $\log e$) and Shannon–Wiener Diversity (H' using $\log e$) were calculated using the absolute abundance values of each sample using the DIVERSE routine. For the average Taxonomic Distinctness (Δ^+), as a measure of the taxonomic amplitude of a sample, the data were transformed into presence and absence, where colonial organisms were also included.

Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations (if the number of permutation was lower than 100, the Monte Carlo permutation was used) was performed to test the significance of the effect of the factors *Carijoa riisei* (fixed, two levels: *C. riisei* present—CP and *C. riisei* absent—CA) and Sampling events (random, two levels: July and December) for each index (N, S, H' , J' , Δ^+). In case a significant effect was found, pairwise tests were carried out.

For the multivariate analyses, the macrofauna abundance data were transformed with $\log(x + 1)$, added to the dummy variable (+d) and converted into a Bray–Curtis similarity matrix. PERMANOVA was used to test the possible differences between macrobenthic communities associated with substrates with and without the presence of *C. riisei* (fixed factor, 2 levels: CP and CA) during Sampling events (random factor, 2 levels: July and December). The homogeneity of the dispersions between sample groups was tested using a PERMDISP routine (Anderson 2006). When the main PERMANOVA test detected significant differences, pairwise PERMANOVA tests were performed. The significant results of the PERMANOVA were then represented using non-metric multidimensional scaling (nMDS) (Anderson et al. 2008).

To investigate whether the beta diversity differs between-areas and within-areas with and without the presence of *C. riisei*, PERMDISP was performed (Anderson et al. 2006). Jaccard dissimilarity based on presence/absence data was used.

The SIMPER analysis was performed to identify which species contributed to the dissimilarity in the presence and absence of *C. riisei*, using the value of 80% as a cut-off point. All the tests were carried out using a significance level of $\alpha = 0.05$, and the data analyses were performed using the program PRIMER

version 6.0 + PERMANOVA (Clarke and Gorley 2006; Anderson et al. 2008).

Results

Composition of macrofauna

During the study, 54 taxa were found in the area where *C. riisei* was present (29 exclusive), whereas in the area where *C. riisei* was absent, we found 36 taxa (12 exclusive taxa). A total of 2924 individuals were counted, of these 2762 were found in the areas where *C. riisei* was present and 162 individuals where the octocoral was absent, where the individuals were associated with sponges, seaweeds, sand and the steel of the shipwrecks. The most abundant groups were Crustacea (1945 individuals) and Polychaeta (827 individuals) (Table 1).

Ecological indices

There was a significant difference between the areas where *Carijoa riisei* was present and absent for Abundance and Richness (PERMANOVA, $P < 0.05$) (PERMDISP: $P = 0.002$ and 0.7558 , respectively) (Fig. 3; Table 2). No significant differences were observed between Sampling events in Abundance, Richness, Pielou's evenness, Shannon–Wiener Diversity or average Taxonomic Distinctness (PERMANOVA, $P < 0.05$).

Community structure

Significant differences were found between Sampling events and between areas where *Carijoa riisei* was present and absent. Additionally, the PERMANOVA tests revealed a significant *Carijoa riisei* $\times$ Sampling events interaction. (PERMANOVA results, Table 3). The PERMDISP test did not indicate significant differences in the dispersion between sampling events and the presence of *C. riisei* (Table 3). The pattern visualized in nMDS showed clear differences between the communities associated with *C. riisei* to those found in adjacent areas where the octocoral was absent (Fig. 4).

Beta diversity significantly differed between the areas where *Carijoa riisei* was present and absent ($F = 2.51$; $P = 0.001$). The area without *C. riisei*

showed greater variability in species composition. The average Jaccard distance-to-centroid is about 54% for areas with *C. riisei* and 64% for areas where the octocoral was absent. No significant differences were observed within the areas (CP: $F = 1.22$; $P = 0.325$ and CA: $F = 0.19$; $P = 0.698$).

The SIMPER analysis showed the taxa which were responsible for the dissimilarity between the areas where *C. riisei* was present and absent. The amphipods *Erichthonius brasiliensis* and *Podocerus brasiliensis* and the polychaetes from the Syllidae family dominated the areas where *C. riisei* was present (Table 4; Fig. 5). Regarding the feeding habits and the habitat/motility of these dominate groups, it was observed those most are deposit or suspension feeders, tube-dwelling, sessile or have low motility (Table 5).

Discussion

Our results reinforce the importance of the octocoral *C. riisei* as a habitat-forming species, sheltering rich and diverse-associated fauna. The community associated with the octocoral in the shipwrecks was 1.5 times richer than the adjacent community with 29 exclusive taxa. Thus, the presence of the species in the shipwrecks increased the local diversity. Furthermore, some taxa were favoured by the presence of the octocoral, presenting higher abundances when associated with it. Thus, despite being an alien species, *C. riisei* was able to establish interactions with native species, contributing to an increase in diversity in the shipwrecks.

These results were expected, since habitat-forming species can provide structural complexity, food and other services, which contribute to an increase in diversity. These species modify environmental parameters, reducing predation intensity and increasing the availability of ecological niches (Jones et al. 1994; Bruno and Kennedy 2000). The presence of *C. riisei* in the shipwrecks provided a three-dimensionality which was not available in the surroundings. Even the species of macroalgae or sponges present did not have the erect structure of the octocoral, whose colonies can reach up to 30 cm in height (Bayer 1961).

Although the alpha diversity was higher in the area with the presence of *C. riisei*, the beta diversity was higher in the area where the octocoral was absent. This was also expected since in areas without the presence

Table 1 Macroinvertebrates in areas with presence (CP) and absence (CA) of *Carijoa riisei* in shipwrecks in December 2018 (CPD and CAD) and July 2018 (CPJ and CAJ) surveys; *n. ident.* no identified, *X* presence

TAXA	CPD	CPJ	CAD	CAJ
<i>Porifera</i>				
<i>Demospongiae</i>				
<i>Haliclona</i> sp.	x	x		
<i>Tedania ignis</i> (Duchassaing and Michelotti, 1864)	x	x		
<i>Cnidaria</i>				
<i>Hydrozoa</i>				
<i>Corydendrium parasiticum</i> (Linnaeus, 1767)	x	x		
<i>Halopteris glutinosa</i> (Lamouroux, 1816)	x	x		
<i>Halopteris verwoorti</i> Galea, 2008		x		
<i>Plumularia strictocarpa</i> Pictet, 1893	x	x		
<i>Platyhelminthes</i>				
<i>Turbellaria</i>	44	28	1	1
<i>Mollusca</i>				
<i>Gastropoda</i>				
<i>Alaba incerta</i> (d'Orbigny, 1841)		2		
<i>Alvania auferiana</i> (d'Orbigny, 1842)		1	2	
<i>Astarys lunata</i> (Say, 1826)		1	1	
<i>Bittium varium</i> (Pfeiffer, 1840)		2	2	
<i>Cerithiopsis gemmulosa</i> (Adams, 1850)			1	
<i>Cerithiopsis greenii</i> (Adams, 1839)		1		1
<i>Cerithium atratum</i> (Born, 1778)				1
<i>Cerithium eburneum</i> Bruguière, 1792				1
<i>Cerithium litteratum</i> (Born, 1778)		1	1	
<i>Coralliophila aberrans</i> (Adams, 1850)		1		
<i>Coralliophila caribaea</i> Abbott, 1958	1	3	1	
<i>Eulithidium pterocladicum</i> (Robertson, 1958)				1
<i>Gabrielona sulcifera</i> Robertson, 1973	1	7	2	2
<i>Mitrella ocellata</i> (Gmelin, 1791)		1	1	
<i>Nassarius consensus</i> (Ravenel, 1861)			5	
<i>Natica menkeana</i> Philippi, 1851				1
<i>Olivella minuta</i> (Link, 1807)		1		
<i>Sigatica carolinensis</i> (Dall, 1889)			1	
<i>Steironepion minus</i> (Adams, 1845)		1		
<i>Vexillum moisei</i> McGinty, 1955				1
<i>Volvarina avena</i> (Kiener, 1834)			1	
<i>Bivalvia</i>				
<i>Barbatia domingensis</i> (Lamarck, 1819)			2	
<i>Botula fusca</i> (Gmelin, 1791)			1	
<i>Musculus lateralis</i> (Say, 1822)	2	5		1
<i>Annelida</i>				
<i>Polychaeta</i>				
Ampharetidae Malmgren, 1866		1		
Chrysopetalidae Ehlers, 1864		2		
Dorvilleidae Chamberlin, 1919	2	2		

Table 1 continued

TAXA	CPD	CPJ	CAD	CAJ
Eunicidae Berthold, 1827	10	17	1	2
Hesionidae Grube, 1850	1	2		1
Lumbrineridae Schmarda, 1861	47	36	5	6
Nereididae Blainville, 1818	8	1		1
Phyllodocidae Örsted, 1843		1	1	
Alciopini Ehlers, 1864		1		
Polynoidae Kinberg, 1856	1			
Sabellidae Latreille, 1825	42	34	4	9
Serpulidae Rafinesque, 1815	1			
Sigalionidae Kinberg, 1856	1	1		
Spionidae Grube, 1850			3	
Syllidae Grube, 1850	330	205	28	20
<i>Arthropoda</i>				
<i>Crustacea</i>				
Ostracoda	3	16	3	7
<i>Malacostraca</i>				
<i>Amphipoda</i>				
Amphipoda n. ident	5	7	1	
Ischyroceridae				
<i>Erichthonius brasiliensis</i> (Dana, 1853)	250	670	8	26
Podoceridae				
<i>Podocerus brasiliensis</i> (Dana, 1853)	189	458		3
Stenithoidae				
<i>Stenothoe</i> sp.	87	65	1	5
<i>Decapoda</i>				
<i>Palaemonidae</i>				
Palaemonidae n. ident.	2	2		
<i>Periclimenaeus</i> sp.	5	1		
<i>Mithracidae</i>				
<i>Mithrax</i> sp.	3	1		
<i>Xanthidae</i>				
<i>Paractaea rufopunctata</i> (Milne Edwards, 1834)	1			
Xanthidae n. ident.		1		
<i>Inachidae</i>				
<i>Podochela brasiliensis</i> Coelho, 1972	3			
<i>Alpheidae</i>				
<i>Synalpheus</i> sp.	1	2		
<i>Isopoda</i>				
<i>Janiridae</i>				
<i>Carpas</i> sp.	7	7		
<i>Stenetriidae</i>				
<i>Hansenium occidentale</i> (Hansen, 1905)*	20	4		
<i>Stenetrium</i> sp.	23	4	4	
<i>Janiroidea</i>				
<i>Joeropsis</i> sp.			1	

Table 1 continued

TAXA	CPD	CPJ	CAD	CAJ
<i>Tanaidacea</i>				
<i>Leptochellidae</i>				
<i>Chondrochelia dubia</i> (Krøyer, 1842)	16	16		
<i>Chondrochelia</i> sp1	1			
<i>Chondrochelia</i> sp2	9			
<i>Paratanaidae</i>				
<i>Paratanaid coelhoi</i> Araujo-Silva and Larsen, 2012		1		
<i>Echinodermata</i>				
<i>Ophiuroidea</i>				
<i>Ophiactidae</i>				
<i>Ophiactis savignyi</i> Müller and Troschel, 1842	9	23	1	1
Total	1125	1636	83	91
Richness	37	43	27	20

*Taxonomy under revision (see Bruce and Buxton 2013)

of *C. riisei*, the substrate was covered by different taxa (e.g. algae, sponges) resulting in greater environmental heterogeneity, which can promote greater variation in the composition of the biota (Hewitt et al. 2005).

In general, the most abundant groups were polychaetes and amphipods, both associated with the presence and absence of *C. riisei*. However, the total abundance of these groups in areas where the octocoral was present was approximately 20 times greater. This is due, mainly, to the increase in representatives of the family Syllidae (11 × higher) among the polychaetes and the species *Podocerus brasiliensis* (215 × higher) and *Erichthonius brasiliensis* (27 × higher) among the amphipods. Although they were not exclusive taxa, they were more numerous when associated with *C. riisei*, mainly in the July sample, possibly associated with the increment of nutrient transport and sediment from the continent during the rainy season (Bastos et al. 2011). Particles in suspension are retained in the branches of *C. riisei* favouring some organisms (Bruto-Costa et al. 2014).

Polychaetes and crustaceans were also found to be associated with *C. riisei* in the Port of Manzanillo, Mexican Pacific (Galván-Villa and Ríos-Jara 2018). However, the composition and structure of the community differed notably from that found in this study. In Mexico, the most abundant species was the sabellid polychaete *Branchiommia bairdi* (McIntosh 1885). Among the crustaceans, Decapoda was the best represented, with a small abundance of Amphipoda.

On the other hand, an elevated abundance was registered for Ophiuroidea, with four species, whereas in this study, only *Ophiactis savignyi* was found to be associated with *C. riisei* in the shipwrecks. Despite the differences in community composition, among the taxa associated with *C. riisei* filter organisms, suspension feeders and detritivores were predominant (Table 5). The increased habitat tridimensionality provided by *C. riisei* could be especially beneficial to species filtering the water column (see examples below).

The composition of the epibiont fauna of *C. riisei* varied with the surroundings, where 12 species were found to be exclusive. Also, results showed clear distinction in community structure between these areas in both sampling events. This is different from other habitat-forming species, such as the zebra mussel, whose invasion has been noted to cause an increase in the abundance of benthic invertebrates; however, the community composition was not found to significantly change (Haynes et al. 1999). Thus, it appears that *C. riisei* has a greater specificity in terms of its associated community, differing between the surrounding habitats and between other locations where the octocoral occurs. This reflects the ability of *C. riisei* to associate with a wide diversity of taxa, establishing interactions with both native and exotic species. Although the taxa that most contributed to dissimilarity are present in areas with and without the presence of the octocoral, the much lower abundance

values in areas without *C. riisei* indicate an occasional occurrence, while the same taxa are dominant in the community associated with the octocoral.

The arborescent stolonial structure of *C. riisei* allows for the retention of suspended particles in its branches (Bruto-Costa et al. 2014), serving as food for detritivorous organisms such as the tanaidacean *Chondrochelia dubia* (Ortiz and Lalana 2019), which was found to be exclusively associated with the octocoral. *Podocerus brasiliensis*, very abundant in our study, cannot build tubes, but frequently captures empty tubes of other taxa (inquilism). Due to its feeding habit (deposit or suspension feeder), *P. brasiliensis* seeks the highest part of the environment when possible, spreading its antennae in the form of a net in the water column (Barnard et al. 1988). The great difference in abundance of this amphipod associated with the octocoral, in our study, may indicate that *C. riisei* provides higher sites that optimize its feeding. In the same way, the other species dominant in the community associated with the octocoral are tube-dwelling or sessile and deposit/suspension feeders (see Table 5). So, they also can be favoured with the elevation provided by colonies of *C. riisei*.

Several studies have shown that structural complexity has a direct relation to the richness and composition of associated fauna (De Cipelle et al. 2015; Nogueira et al. 2015). Some polychaetes, found to be associated with species of octocorals, have been considered as commensal species, benefitting from associations without negatively affecting their hosts (Serpetti et al. 2017). On the other hand, representatives of the family Syllidae, which were well represented in this study, are commonly found to be associated with sponges and octocorals in commensal or parasitic relationships (Lattig and Martin 2009). Molluscs of the genus *Coralliophila* (Family Muricidae) were found to be exclusively associated with *C. riisei*. Species of this genus, which predate upon scleractinian corals and octocorals and in some areas, have shown preferences for the latter due to their availability and ease of manipulation (Del Monaco et al. 2010).

Studies evaluating the role of corals as biogenic substrates have increased greatly, especially for cold water species (Krieger and Wing 2002; Roberts and Hirshfield 2004; Buhl-Mortensen and Mortensen 2004, 2005; Metaxas and Davies 2005; Buhl-

Mortensen et al. 2010; De Cipelle et al. 2015; Molodtsova et al. 2016). Several species of octocorals establish a large variety of associations with microorganisms, invertebrates and vertebrates, including host-specific interactions and, in some cases, include parasitism, commensalism and mutualism (Buhl-Mortensen and Mortensen 2004; Watling et al. 2011; Montano et al. 2017). However, establishing the type of interaction that exists between the host and epibiont is not always possible. It is likely that due to its arborescent structure and high branching rate, *C. riisei* acts as an ecosystem engineer (Jones et al. 1994), providing not only substrate and food resources, but also altering local hydrodynamics. Many invasive ecosystem engineer organisms have been associated with positive impacts both in terrestrial and aquatic ecosystems (Vimercati et al. 2020).

It is important to note that in Brazil, coral fauna has an elevated endemism, however, different to other areas, there are few branching species (Mies et al. 2020). In natural or artificial reef environments, only representatives of the genus *Millepora* (Hydrozoa) and some octocorals are branched and provided more complex habitats. As such, they shelter a rich diversity of associated fauna (Souza et al. 2007; Neves et al. 2007; Garcia et al. 2008, 2009; Pérez and Gomes 2012) and play a fundamental role in the diversification of benthic communities. *Carijoa riisei* stands out for its high abundance and multiplicity of habitats that it can occupy, consequently it has become of interest to compare the communities associated with the octocoral in these different environments. In addition, species of the genus *Millepora* have shown high susceptibility to bleaching and difficulty in recovery, resulting in high mortality (Ferreira et al. 2021). In this perspective, the octocoral *C. riisei* can play a fundamental role in providing habitats and maintaining complexity in Brazilian reefs, due to its three-dimensionality. However, it is important to note that due to the absence of calcareous skeleton, it does not contribute to reef construction.

The two most abundant taxa associated with *C. riisei*, the amphipods *Ericthonius brasiliensis* and *Podocerus brasiliensis*, were originally described in Rio de Janeiro and are considered to be native to Brazil. *E. brasiliensis* is capable of associating itself with various species including seagrass (Lewis III and Stoner 1983), sponges and octocorals and is generalist with its host (Wendt et al. 1985). This amphipod, as

Fig. 3 Mean values ($\pm$ SD) of univariate community attributes in relation to octocoral *Carijoa riisei* (CP *C. riisei* present, CA *C. riisei* absent) and Sampling events (July and December 2018)

with *C. riisei*, is part of the fouling community which may explain its association with the octocoral and favouring its dispersion. Indeed, *E. brasiliensis* has a wide distribution in the Atlantic and Mediterranean (Myers and McGrath 1984) and is one of the most successful invaders around the world (Zettler 2021). In a study on the coast of California (USA), where this species is considered non-native (Cohen et al. 2005), *E. brasiliensis* was found to be abundant in the communities located on oil platforms but rare or absent in natural reefs (Page et al. 2007). Other identified species such as *Astyris luneta* and *Musculus lateralis* are also generalists, using various species as

hosts (Wendt et al. 1985). These generalist epibionts may be less influenced by the invasion of non-native species compared to specialist epibionts, since they can prioritize hosts which provide greater protection or higher quality habitats in a determined time and space (Buschbaum et al. 2006; Bates and DeWreede 2007).

The shipwrecks of our study are close to the coastal zone (distances of up to 18 km) where natural reefs occur. Thus, it is possible that there is a connectivity among the populations of *C. riisei* and the epibiont species between these environments, particularly for those less specialized species. Despite depending on

Table 2 Results of a 2-factor PERMANOVA for effect of the factors *Carijoa riisei* (C) (*C. riisei* present and *C. riisei* absent) and Sampling events (SE) (July and December 2018) and with interactions, on the Abundance (N), Richness (S), Pielou's evenness (J'), Shannon–Wiener Diversity (H') and Average Taxonomic Distinctness (AvTD, Δ^+) (df degrees of freedom, MS mean sum of squares)

Source	Variation Source	df	MS	Pseudo- F	P (MC)
S	C	1	11,068	62.665	0.0267
	SE	1	26.638	9.1217E-2	0.8683
	C $\times$ SE	1	176.62	0.60482	0.4634
	Residuals	97	292.02		
N	C	1	17,154	38.8	0.038
	SE	1	916.41	5.3334	0.0664
	C $\times$ SE	1	442.1	2.573	0.0879
	Residuals	97	171.82		
J'	C	1	505.2	30.488	0.0922
	SE	1	3.3687	0.23433	0.6296
	C $\times$ SE	1	16.57	1.1526	0.2896
	Residuals	97	14.376		
H'	C	1	106.04	1.1455	0.478
	SE	1	0.67714	3.2866E-2	0.8763
	C $\times$ SE	1	92.573	4.4932	0.0584
	Residuals	97	20.603		
Δ^+	C	1	16.541	3.1317	0.3171
	SE	1	9.2317	0.17458	0.6891
	C $\times$ SE	1	5.2817	9.988E-2	0.6744
	Residuals	97	52.88		

Table 3 Results of a 2-factor PERMANOVA and PERMDISP testing differences between the macrobenthic communities in Sampling events (SE) (July and December 2018), and *Carijoa*

riisei(C) (*C. riisei* present and *C. riisei* absent) and with interactions (df degrees of freedom, MS mean sum of squares, ECV per cent estimated components of variation)

PERMANOVA						PERMDISP	
Variation Source	df	MS	Pseudo- F	P (MC)	ECV	F	P (perm)
C	1	38,987	94.692	0.0013	26.7	11.132	0.301
SE	1	5981.7	31.961	0.0054	9.2	0.2971	0.607
C $\times$ SE	1	4117.3	21.999	0.0369	9.6		
Residuals	97	18.154			43.3		
Total	100						

the biological requirements of species, their dispersion can be facilitated by the dispersion of *C. riisei* through the fouling community, since this species fixes itself in diverse types of natural and artificial substrates (Sánchez 1994; DeFelice et al. 2001; Bull and Kendal Jr. 1994; Lira et al. 2010). The comparison with the communities associated with *C. riisei* in coastal reefs may contribute to the comprehension of the role of

shipwrecks as shelters, as well as the role of this non-native octocoral in the diversity of these ecosystems.

Our results reinforce the idea that *C. riisei* acts as an ecosystem engineer in coastal reef environments, creating new habitats and increasing species richness at a local scale. A similar effect was observed in the alien ascidian species *Pyura praeputialis*, which create novel mid-intertidal habitats in the rocky shores

Fig. 4 Non-metric multidimensional scaling (nMDS) plots of the macrobenthic community structure in areas with presence (CP—blue symbols) and absence (CA—green symbols) of the octocoral *Carijoa riisei*. Sampling events are indicated by

numbers 1 (July 2018) and 2 (December 2018). Data were $\text{Log}(x + 1)$ transformed and were used in the calculation of Bray–Curtis similarities. (Color figure online)

Table 4 Contribution percentages of the main macrofauna taxa for the average dissimilarity (δ) (Bray–Curtis Index) between areas with presence (CP) and absence (CA) of *Carijoa riisei*

Taxa	Average abundance		Contribution to the average Bray–Curtis dissimilarity ($\delta = 87.20$)	
	CP	CA	Contribution %	Cumulative %
<i>Ericthonius brasiliensis</i>	2.12	0.29	19.13	19.13
<i>Podocerus brasiliensis</i>	1.61	0.10	13.66	32.78
Syllidae	1.49	0.54	12.54	45.32
<i>Stenothoe</i> sp.	0.85	0.09	6.45	51.78
Sabellidae	0.53	0.16	5.15	56.93
Lumbrineridae	0.41	0.13	4.23	61.16
<i>Chondrochelia dubia</i>	0.30	0.00	4.10	65.26
Turbellaria	0.50	0.03	3.89	69.15
Ostracoda	0.20	0.18	2.65	71.80
<i>Gabrielona sulcifera</i>	0.13	0.07	2.44	74.24
<i>Stenetrium</i> sp.	0.20	0.06	2.09	76.33
<i>Hansenium occidentale</i>	0.17	0.00	1.90	78.24
Eunicidae	0.24	0.06	1.67	79.91
Amphipoda	0.18	0.00	1.44	81.35

of Chile and increase species richness at local and seascape scales (Castilla et al. 2004). Alien species can reduce or increase ecosystem attributes, such as

biomass or species diversity, causing positive or negative environmental impacts. Evaluating only the negative effects can result in a simplification or even

Fig. 5 Non-metric multidimensional scaling (nMDS) bubble plots showing the five taxa with substantial contributions to dissimilarity between areas with presence (grey bubbles) and

absence (black bubbles) of the octocoral *Carijoa riisei* on shipwrecks (stress = 0.18). The size of each bubble represents an untransformed abundance data

misunderstanding of impact dynamics (Goodenough 2010; Boltovskoy et al. 2018). Thus, including analyses on the positive effects of alien species is fundamental for the more ample understanding of alterations provoked in the functioning of ecosystems. It is important to highlight that the recognition of positive impacts on the presence of a non-native

species, as observed in this study for the octocoral *C. riisei*, should not be understood as compensation for the deleterious effects of non-native taxa, but rather as additional information to scientists, management and decision-makers (for a review of this topic, see Vimercati et al. 2020).

Table 5 Feeding habit and the habitat/motility of the main taxonomic groups dominating areas with the presence of *C. riisei* on shipwrecks from the coast of Pernambuco, Brazil

Taxa	Habitat/motility	Feeding habit	References
<i>Erichthonius brasiliensis</i>	Tube-dwelling	Deposit/suspension feeders	Dixon and Moore (1997) and Guerra-García et al. (2014)
<i>Podocerus brasiliensis</i>	Inquiline tube-dwelling	Deposit/suspension feeders	Barnard et al. (1988) and Guerra-García et al. (2014)
Syllidae	Motile to discreetly motile	Predators/parasites (omnivorous)	Jumars et al. (2015)
<i>Stenothoe</i> sp.	Motile to discreetly motile	Suspension feeders/carnivorous	Guerra-García et al. (2014)
Sabellidae	Sessile	Suspension feeders	Jumars et al. (2015)

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Availability of data and materials Data will be made available upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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