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ORIGINAL PAPER

# Role of non-indigenous species in structuring benthic communities after fragmentation events: an experimental approach

**Eva Cacabelos · Ignacio Gestoso · Patrício Ramalhosa · João Canning-Clode**

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**Abstract** Habitat loss and fragmentation, and biological invasions are widely considered the most significant threats to global biodiversity. While marine invasions have already shown dramatic impacts around the world's coasts, many of these habitats are becoming increasingly urbanized, resulting in fragmentation of natural landscape worldwide. This study developed in Madeira (NE Atlantic) aims to understand the synergistic interactions between fragmentation and biological invasions using submerged experimental settlement panels in the field for 3 months. We fragmented crustose coralline habitats, decreasing patch size without an overall habitat loss, and determined its effects on the patterns of abundance of marine fouling organisms across limiting assemblages with or without the presence of non-indigenous species (NIS, considered invaded and non-invaded systems in this study). The presence of crustose coralline algae suppressed the recruitment of some NIS (*Parasmitina alba* and *Botrylloides niger*). Our results also showed that the abundance of NIS (e.g. *B. niger*) could be prompted in highly fragmented habitats, colonizing bare substrates very efficiently. Overall, evidence indicates that fragmentation events modulate biotic interactions and consequently determine the structure of the fouling communities. Future research should address both processes when analyzing biotic resistance to invasion in urban marine habitats.

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E. Cacabelos (✉) · I. Gestoso · P. Ramalhosa · J. Canning-Clode
MARE – Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI), Edifício Madeira Tecnopolo, Piso 0, Caminho da Penteada, 9020-105 Funchal, Madeira, Portugal
e-mail: evacacabelos@yahoo.es

E. Cacabelos
Departamento Ecoloxía e Bioloxía Animal, Facultade de Ciencias Experimentais, Universidade de Vigo, Campus As Lagoas-Marcosende, 36310 Vigo, Spain

I. Gestoso
Department of Biology, Faculty of Marine and Environmental Sciences, University of Cádiz, Puerto Real, Spain

I. Gestoso · J. Canning-Clode
Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037, USA

P. Ramalhosa
OOM – Oceanic Observatory of Madeira, Agência Regional Para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI), Edifício Madeira Tecnopolo, Piso 0, Caminho da Penteada, 9020-105 Funchal, Madeira, Portugal

**Keywords** Macroinvertebrates · Non-indigenous species (NIS) · Recruitment · Disturbance · Marina environment · Biodiversity

## Introduction

Habitat loss and fragmentation, climate change and biological invasions are considered the major anthropogenic stressors threatening biodiversity in marine ecosystems worldwide, imposing significant and permanent changes to the ecology of coastal communities (Myers et al. 2000; Thompson et al. 2002; Fahrig 2003; Reid et al. 2005; Airoldi and Beck 2007; Hutchison 2008; Cole et al. 2012).

Coastal urbanization, a process modifying marine and coastal ecosystems (Airoldi et al. 2015, 2021), affects the complex interactions among biotic and abiotic processes (Matias et al. 2015). Urbanization can be associated with habitat fragmentation, an umbrella term describing the process by which habitat loss results in the division of large, continuous habitats into smaller remnants, isolated from each other by a matrix of different habitats (Didham 2010). There is a longstanding debate within the conservation research community based on the principle postulating that a single patch of habitat holds more species than several small patches of the same total area (the so-called SLOSS debate, Diamond 1975). In coastal areas, fragmentation can alter the quality and connectivity of habitats (Wilcove et al. 1986; Collinge 1996; Gray 1997; Fahrig 2003; Wilson et al. 2016), and through different mechanisms affect the distribution and abundance of organisms, community structure and ecosystem processes (Didham 2010; Dugan et al. 2011; Smoothey 2013; Benedetti-Cecchi and Trussell 2014; Martins et al. 2016; Cacabelos et al. 2016a, b; Bertocci et al. 2017). The relative importance of these mechanisms has raised considerable discussion, highlighting the relevance of clearly discriminating direct versus indirect causal relationships among patch and landscape variables. While habitat fragmentation is a landscape-level phenomenon, patch-level processes (patch area, edge effects and patch shape complexity) can only be understood within a landscape context (isolation and matrix structure) (Didham 2010).

Biological invasions represent a severe threat to marine ecosystems (Halpern et al. 2008; Molnar et al. 2008), and can be exacerbated by fragmentation (Haddad et al. 2015). A successful invasion depends on traits associated with the non-indigenous species (NIS) involved in the invasion process, its propagule pressure (i.e., the number and frequency with which larvae, seeds, juveniles, or adults of a species, arrive at a recipient native community over time) and the invasibility of the recipient community (Vitousek et al. 1997; Lonsdale 1999; Mack et al. 2000; Canning-Clode 2015). According to Elton (1958) the uptake of available resources and the occupation of niches are complete in a species-rich community, preventing invasions. Multiple mechanisms must be considered when investigating biotic resistance hypotheses in marine systems (Caselle et al. 2018). For example, biodiversity loss can facilitate several processes (e.g. provision of bare space) to promote the settlement and expansion of successful invaders (Stachowicz and Byrnes 2006). While disturbed ecosystems can reduce persistence against human-induced impacts (Hooper et al. 2005), 'healthy' native communities have shown greater resistance to invasion (Levine and D'Antonio 1999; Arenas et al. 2006; Giakoumi and Pey 2017). There has been considerable research effort on detection of invasive alien species (EU 2014; Tsiamis et al. 2019), but not much experimental work has been performed to better understand NIS impacts in coastal benthic communities (but see Katsanevakis et al. 2014, and references therein). Further research is still needed to advance the current understanding of which factors determine invasion success (with most studies focused on species traits and both biotic and abiotic characteristics, e.g. Arenas et al. 2006), the underlying processes and mechanisms and how invasions influence biodiversity patterns, with evidence suggesting that propagule pressure is of paramount importance (Simberloff 2009; Brown and Barney 2021).

The different components of global environmental change are often studied and managed independently, but simultaneously multiple stressors may produce synergistic or antagonistic effects (Didham et al. 2007; Crain et al. 2008). Habitat fragmentation strongly interacts with other components of global environmental change, including species invasions, habitat-use intensification and climate change (Hutchison 2008; Didham 2010). Habitat loss and fragmentation may enhance the spread of biological invasions worldwide, partially due to the available bare space provided by the loss of native species, consequences of climate change or the increasing urbanization of coastal environments (With 2004; Megina et al. 2013). Several studies focused on mitigating the effects of loss and fragmentation of coastal urban areas have been developed in recent years, with promising results (e.g. Bulleri 2005; Bishop et al. 2017). The capacity of a fragmented habitat to sustain biodiversity and ecosystem services will hinge upon the total amount and quality of habitat left in fragments, their degree of connectivity, and how they are affected by other human-induced stressors such as invasive species (Haddad et al. 2015). However, little is known on the effects of fragmentation in marine systems (but see Moschella et al. 2005; Goodsell et al. 2007), or how the alteration of landscape structure might promote NIS spread, as well as its ecological consequences (With 2004).

In this context, this study aims to assess the effect of biological invasions in structuring benthic communities and the consequences of fragmentation and generation of free base space on forcing interactions among neighbouring assemblages. Both stressors were simultaneously manipulated to examine their isolated and combined effects on recruitment patterns, and macrofouling assemblages' invasibility. According to theory, fragmented habitats are expected to hold fewer species than a single large patch, while assemblages with NIS in the neighbourhood, i.e. more exposed to invasion, are expected to be more readily colonized by NIS. On the other hand, considering fragmentation as a 'landscape level' disturbance (Hobbs and Huenneke 1992; With 2004), and since disturbance generally promotes invasion (With 2002; Hutchison 2008), we hypothesize that fragmented assemblages will show a higher invasibility than unfragmented (i.e. undisturbed) assemblages.

## Methods

### Natural assemblages in the study area

Macrobenthic community structure in the shallow rocky subtidal of Madeira are mainly affected by wave exposure, sedimentation, depth and grazing by the sea urchin *Diadema africanum* Rodríguez, Hernández, Clemente & Coppard, 2008 (Bianchi et al. 1998; Alves et al. 2001; Friedlander et al. 2017; Gizzi et al. 2020). Spatial variation among morphofunctional groups is mainly correlated with variation in the density of sea urchins (Sangil et al. 2018). When the density of sea urchins is high ($> 2$–$2.5$ ind. $m^{-2}$), subtidal areas previously covered by erect, fleshy algae are transformed into unproductive overgrazed habitats dominated by crustose coralline algae (CCA), impoverished communities often termed 'urchin barrens' (Hernández et al. 2008; Friedlander et al. 2017; Sangil et al. 2018). A similar phenomenon has been described in other Macaronesian archipelagos and worldwide (see Tuya et al. 2004 and references therein), probably due to increased inshore fishing pressure. Impoverished communities such as these coralline barrens can also be exposed to fragmentation due to physical or biological processes, such as urbanization (habitat modifications occurring at a large spatial scale) or grazing by sea urchins (occurring at smaller spatial scale). Sea urchins can be continually scraping CCA, consuming the surficial layers along with any microalgal films and macroalgal recruits (Chapman 1981), or even 'scrape' the substrate, as has been described for *Arbacia lixula* (Linnaeus, 1758), that has a robust Aristotle's lantern consistently with its preference for crustose algae as food (Bonaviri et al. 2011).

### Building synthetic assemblages

To test the effect of invasions and fragmentation on the forcing of interactions among fouling organisms, we created synthetic assemblages containing bare rock, crustose coralline algae (CCA) and mature marina assemblages with a relevant NIS component, intending to mimic the invasion process. In advance, and to get mature assemblages containing NIS, 7 × 7 × 2 cm basalt panels, the dominant natural volcanic rock in Madeira island, were suspended upside-down 1 m deep from wharves of Quinta do Lorde marina for 14 months (from April 2018 to June 2019) to be fouled with mature assemblages (marina-assemblages with a relevant NIS component, hereafter named 'Invaded'). After 14 months in the field, assemblages colonizing these basalt panels were composed by 62.0 ± 19.6% (mean percent cover ± SE, $n = 10$) of NIS.

In June 2019, small basalt boulders bearing CCA species were collected from natural rock pools in Quinta do Lorde (NW Madeira Island, Portugal) and transported to be cut by a professional stonecutter.

Rock pieces were cut into the experimental size (10 units of 7 × 7 × 2 cm and 40 units of 3.5 × 3.5 × 2 cm) and maintained in the mesocosm system and laboratory facilities of MARE—Marine and Environmental Research Centre, located at Quinta do Lorde Marina, for 24 h until the start of the experiment.

Experimental assemblages were created and attached to main 14 × 14 × 0.3 cm PVC panels with a high-quality adhesive sealant (T-REX Power Turbo, SMX® Polymer-Soudal, 20 min.) and suspended from wharves. Therefore, they consisted of PVC plates where one 7 × 7 × 2 cm or four 3.5 × 3.5 × 2 cm pieces of rock containing CCA were glued, depending on corresponding unfragmented or fragmented treatment. In the case of small rock pieces, they were glued to the four corners of the main PVC panel. Half of the PVC panels, corresponding to the 'invaded' treatment, contained 7 × 7 cm marina-assemblages with a relevant NIS component. Empty basalt panels were used to cover the remaining free space in the PVC panels and complete the configuration (see Fig. 1 and A1.). Synthetic assemblages were then suspended at approx. 50–70 cm depth upside down from wharves in a randomly located position in June 2019.

## Sampling synthetic assemblages

In September 2019, three months after deployment, panels were retrieved from the field and sampled. For this, all fouling organisms were identified to the lowest possible taxonomic level with the aid of a stereomicroscope Leica S8APO, based on scientific literature and then assigned to the categories of 'native', 'non-indigenous species' (NIS), 'cryptogenic' (sensu Carlton 1996) or 'unresolved' (unable to identify to species level) based on scientific literature (e.g., Canning-Clode et al. 2013; Chainho et al. 2015; Marchini et al. 2015; Gestoso et al. 2017; Ramalhosa et al. 2019, 2021) and several current databases (AquaNIS Editorial Board 2015; Ahyong et al. 2018; Fofonoff et al. 2018; WoRMS Editorial Board 2020). All NIS, and not only those included in the marina assemblages' were sampled to include the biological succession on bare rocks and calcareous crusts, which would be influenced by the particular species first arriving at the substratum, an array of direct and indirect species interactions, and physical-environmental change, that dictates that the fouling assemblage generated will follow a range of trajectories with potentially variable endpoints (Jenkins and Martins, 2010).

High-quality photographs were taken from each panel with an Olympus TG-4 camera and analysed using Coral Point Count's image analysis software (CPCe 4.1, Kohler and Gill 2006). In each image, cells containing the unfragmented (one square 7 × 7 cm) and fragmented calcareous crusts (CCA) (four squares 3.5 × 3.5 cm) were selected, and 60 or 15 random points were deployed per cell, respectively (i.e. commensurately with area), resulting in a matrix of 60 randomly distributed points per panel. Similar image analysis was used for sampling the bare rock, and, thus, cells 7 × 7 cm or 3.5 × 3.5 cm were sampled close to unfragmented or fragmented CCA (see Fig. 1 for details). Fouling organisms were visually identified beneath each point, deployed on calcareous crusts and bare rock, up to the highest achievable taxonomic resolution. Organisms present but not falling underneath cross points were recorded as rare and then assigned an arbitrary score of 1%. Obtained data were used to determine the cover of each identified taxa and bare space for specific cells of each panel, total percent cover, and Shannon diversity index.

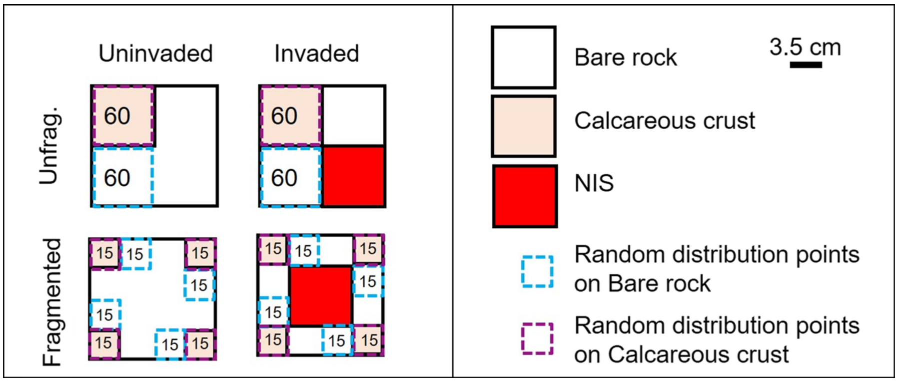

**Fig. 1** Diagram shows the synthetic assemblages, the areas sampled, and the number of random points, after the three months, they were suspended from wharves of Quinta do Lorde marina. Framed in green are points sampled in calcareous crusts, and those sampled on bare rock in blue (see photographs of synthetic assemblages in Supp. Mat.)

## Data analysis

Changes in univariate data, namely abundance (total percent cover of sessile taxa, including both algae and calcified filter feeders, as well as covers of specific status) and diversity index, were analysed using permutational analysis of variance (PERMANOVA) based on Euclidean distances of untransformed data (Anderson 2001). To evaluate NIS settlement success on experimental assemblages/treatments, those categorized as cryptogenic and unresolved were pooled with native species (NCU) for the statistical analysis, as a more conservative approach (e.g., Gestoso et al. 2018; Ramalhosa et al. 2019). Analyses were based on a three-way model, including fragmentation (2 levels: unfragmented and fragmented), invasion (2 levels: uninvaded and invaded), and substrate (2 levels: calcareous crust and bare rock), all of them fixed and orthogonal, with five replicates. In addition, a test for homogeneity of multivariate dispersions (PERMDISP) was performed to complement PERMANOVA (Anderson 2017), and transformations were applied when necessary. Whenever PERMANOVA showed a significant factor or a significant interaction of factors ($p < 0.05$), pair-wise comparisons were done to explore differences among all pairs of levels of the selected factor.

Changes in the structure of assemblages, encompassing richness and abundance, were analysed using PERMANOVA performed on square-root transformed data and based on Bray–Curtis similarity matrix (Anderson 2001) and including three factors mentioned above. Non-metric multidimensional scaling (nMDS) was used to visualize multivariate results. To detect what taxa contributed most to similarity within and dissimilarity among groups, an analysis of similarity percentages (SIMPER) was carried out. Analyses of variance based on Euclidean distances was later used to test for differences in the main contributors to these similarities following previously described analysis for univariate data. The software PERMANOVA + for PRIMER (PRIMER-E Ltd, Plymouth, UK) was used for analyses.

## Results

After 3 months suspended from wharves, and due to forcing interactions post fragmentation, the total percentage cover of macrofouling showed significantly lower abundance at unfragmented than on fragmented assemblages (Table 1, Fig. 2). The same effect, although barely non-significant, was observed on the diversity index counting on native, cryptogenic and unresolved status species (Table 1, Fig. 2).

**Table 1** Univariate analysis of variance of macrofouling assemblages across Fragmentation (Fr), Invasion (In) and Substrate (Su) levels after 3 months of panel deployment

| Source | df | Total N | | H | | N-NCU | | H-NCU | | N-NIS | | H-NIS | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | F | MS | F | MS | F | MS | F | MS | F | MS | F |
| Fr | 1 | 902.5 | 6.55* | 0.37 | 1.63 | 58.4 | 0.4 | 0.64 | $3.37^{+}$ | 501.7 | 2.35 | 0.13 | 0.59 |
| In | 1 | 340.3 | 2.47 | 0.01 | 0.04 | 11.7 | 0.1 | 0.18 | 0.96 | 225.6 | 1.06 | 0.29 | 1.27 |
| Su | 1 | 5760.0 | 41.79*** | 0.00 | 0.01 | 2376.7 | 14.8*** | 0.02 | 0.09 | 736.7 | $3.45^{+}$ | 0.11 | 0.50 |
| Fr × In | 1 | 71.1 | 0.52 | 0.31 | 1.37 | 0.1 | 0.03 | 0.28 | 1.49 | 66.74 | 0.31 | 0.02 | 0.09 |
| Fr × Su | 1 | 233.6 | 1.69 | 0.37 | 1.61 | 275.6 | 1.7 | 0.14 | 0.75 | 1.74 | 0.01 | 0.55 | 2.43 |
| In × Su | 1 | 62.5 | 0.45 | 0.00 | 0.00 | 66.7 | 0.4 | 0.03 | 0.17 | 258.4 | 1.21 | 0.00 | 0.00 |
| Fr × In × Su | 1 | 134.4 | 0.98 | 0.57 | 2.50 | 95.1 | 0.6 | 0.30 | 1.58 | 3.4 | 0.02 | 0.30 | 1.32 |
| Res | 32 | 4411.1 | | 0.23 | | 160.1 | | 0.19 | | 213.3 | | 0.23 | |
| Total | 39 | | | | | | | | | | | | |
| PERMDISP | | 0.714 | | 0.624 | | 0.009 | | 0.329 | | 0.167 | | 1 | |

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $^{+}p = 0.07$

*N*, total percentage cover (excluding dead and alive calcareous crusts and bare rock); H, Shannon diversity index; NCU, native, cryptogenic and unresolved species; NIS, non-indigenous species. Analyses were performed on untransformed data. *P*-values are indicated in Table 4

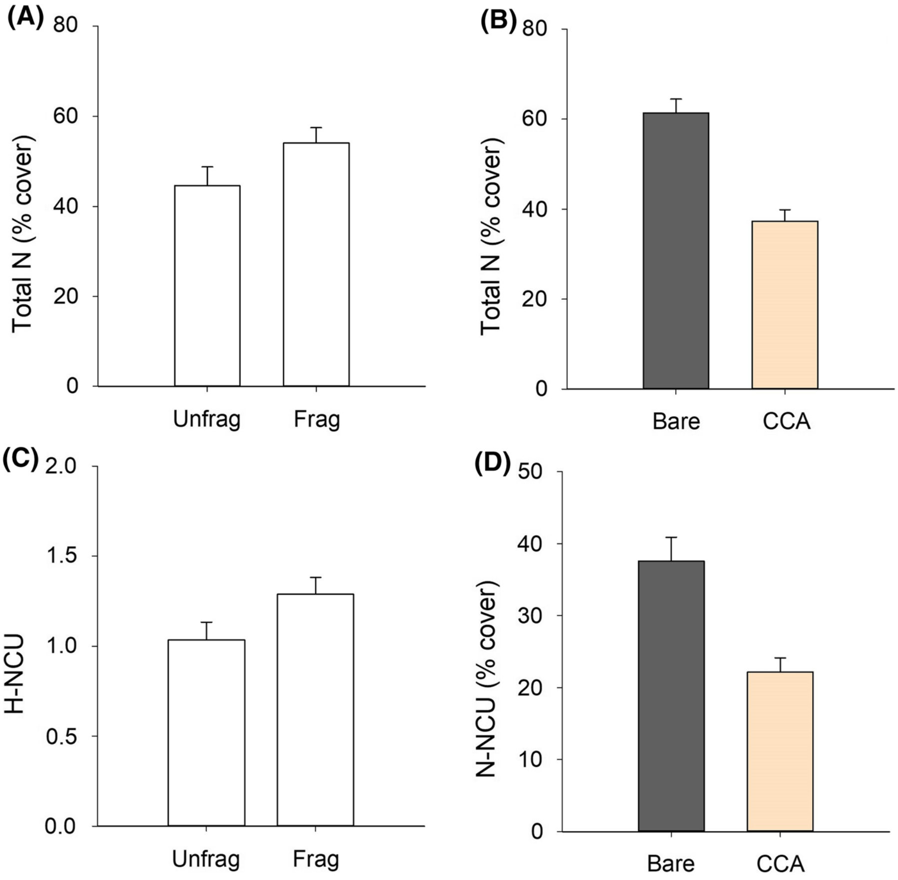

**Fig. 2** Mean (+SE, per panel) total cover of fouling organisms across fragmentation (**A**) and substrates (Bare = Bare rock, CCA = Calcareous crust) (**B**), diversity index of native, cryptogenic and unresolved species (NCU) across fragmentation levels (**C**) and the cover of NCU species across substrates (**D**) ($n = 5$)

Thus, although invaded treatments have greater cover and biodiversity of biofouling organisms than non-invaded treatments, invasion treatment did not significantly affect the percentage cover of benthic organisms or biodiversity (Table 1). On the other hand, the percentage cover of total macrofouling and native, cryptogenic, and species with unresolved status was significantly lower on calcareous crust substrate than bare rock (Table 1, Fig. 2).

The factor 'substrate' affected the structure of macrofouling assemblages significantly, with assemblages settled on bare rock differing from those settled on the calcareous crust (Table 2, Fig. 3). SIMPER analysis revealed that while *Spirorbis* sp., *Salmacina dysteri* and the NIS *Botrylloides niger*, *Parasmittina alba* and *Distaplia corolla* recruited more on bare rock, the bryozoan *Crisia* sp. presented greater cover on top of the calcareous crust (Table 6). The structure of macrofouling assemblage also changed significantly with 'fragmentation', but depending on the 'invasion' level (i.e. a significant interaction Fr x Inv, Table 2, Fig. 3). The variability among replicates did not significantly contribute to these differences (PERMDISP = 0.561, $p > 0.05$). SIMPER analysis indicated that NIS contribution to unfragmented and uninvaded habitats was dominated by *Cradoscrupocellaria bertholletii* and *B. niger* (accumulating 33.9% similarity) (Table 7, showing up to 75% similarity, dissimilarities are indicated in Table 8). The polychaete *Spirorbis* sp. was especially abundant in these unfragmented treatments, contributing for more than 37% to the similarity in both invaded and uninvaded treatments. The NIS *D. corolla* and *P. alba* contributed to 19% similarity in unfragmented and invaded habitats. In contrast, in the case of fragmented habitats, NIS contribution to similarity within treatments was higher in invaded than in uninvaded treatments, with both *B. niger* and *D. corolla* contributing up to 33% similarity in invaded treatment *versus* previously cited NIS and *P. alba* accounting for 19.5% cumulative similarity in uninvaded treatment.

**Table 2** Permulational multivariate analysis of variance (PERMANOVA) of total assemblage across Fragmentation (Fr), Invasion (In) and Substrate (Su) levels based on Bray–Curtis similarity matrix

| Source | df | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|
| Fr | 1 | 7020.4 | 4.828 | 0.001 |
| In | 1 | 2012.6 | 1.384 | 0.232 |
| Su | 1 | 9530.0 | 6.554 | 0.001 |
| Fr × In | 1 | 3634.8 | 2.500 | 0.009 |
| Fr × Su | 1 | 1738.0 | 1.195 | 0.331 |
| In ×Su | 1 | 981.1 | 0.675 | 0.717 |
| Fr x In × Su | 1 | 1196.4 | 0.823 | 0.579 |
| Res | 32 | 1454.1 | | |
| Total | 39 | | | |
| Transf | Sq root | | | |
| PERMDISP | P(perm) | 0.561 | | |
| *Pair-Wise tests* | | t | P(perm) | |
| Term ’Fr ×In’ for pairs of levels of factor Fragmentation | | | | |
| Within Uninvaded | Unfrag, Fragmented | 2.062 | 0.003 | |
| Within Invaded | Unfrag, Fragmented | 1.765 | 0.007 | |
| Term ’Fr × In’ for pairs of levels of factor Invasion | | | | |
| Within Unfragmented | Uninvaded, Invaded | 1.624 | 0.023 | |
| Within Fragmented | Uninvaded, Invaded | 1.111 | 0.303 | |

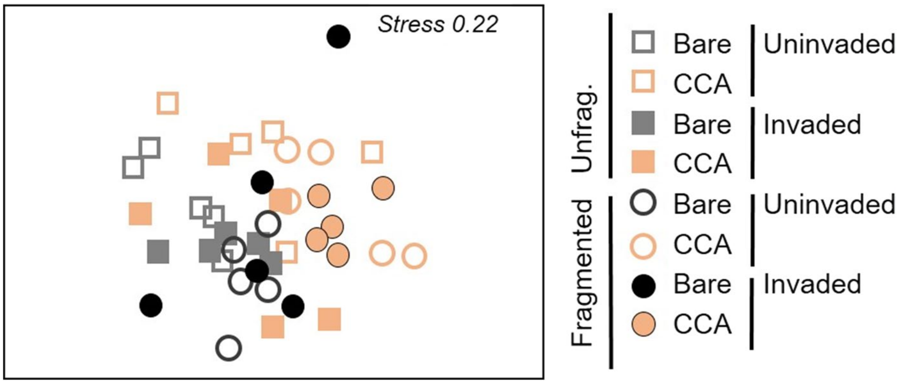

**Fig. 3** Non-metric multidimensional scaling (nMDS) representing the assemblage structure between fragmentation (squares vs. circles) and invasion levels (full vs. empty figures) across substrate levels (Bare = Bare rock, CCA = Calcareous crust). nMDS is based Bray–Curtis similarities on square-root transformed (for further details, see Table 2)

Univariate analysis performed on the percentage cover of these key species clarifies these results. *Spirorbis* sp. showed significantly higher abundance on unfragmented than fragmented habitats (Table 3, Fig. 4a). It was also negatively affected by calcareous crust, which recruited much lower individuals than bare rock (Fig. 4b). The same substrate effect was observed for *S. dysteri* and *P. alba* (Table 3, Figs. 4c and d, respectively). On the other hand, percentage cover of NIS *C. bertholletii* and *D. corolla* were affected by invasion, but *C. bertholletii* showed greater abundance on uninvaded habitats, whereas *D. corolla* showed the inverse trend (Table 3, Fig. 4e and f, respectively). *B. niger* and *Crisia* sp. were both affected by fragmentation, but inconsistently across invasion levels. The NIS *B. niger* was more abundant in invaded treatments on fragmented habitats, while the opposite tendency was observed on unfragmented conditions. *Crisia* sp. showed the opposite trend, and while it was more abundant on uninvaded treatments of fragmented habitats, its cover was higher on invaded and unfragmented treatments (Table 3, Fig. 4g and h, respectively).

**Table 3** Univariate analysis of variance of relevant macrofouling taxa across Fragmentation (Fr), Invasion (In) and Substrate (Su) levels after 3 months of panel deployment

| Source | df | *Spirorbis* sp. | | *S. dysteri* | | ***P. alba*** | | ***C. bertholletii*** | | ***D. corolla*** | | ***B. niger*** | | *Crisia* sp. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | F | MS | F | MS | F | MS | F | MS | F | MS | F | MS | F |
| Fr | 1 | 736.7 | 10.6** | 111.1 | 4.6 | 0.1 | 0.0 | 1.7 | 0.2 | 0.3 | 0.0 | 513.6 | 4.2* | 122.5 | 3.4$^+$ |
| In | 1 | 0.1 | 0 | 0.3 | 0.0 | 3.4 | 0.1 | 66.7 | 6.5* | 202.5 | 4.1* | 90.0 | 0.7 | 13.6 | 0.4 |
| Su | 1 | 1120.1 | 16.1*** | 302.5 | 12.6*** | 293.4 | 9.8** | 20.1 | 2.0 | 10.0 | 0.2 | 111.1 | 0.9 | 80.3 | 2.2 |
| Fr × In | 1 | 116.7 | 1.7 | 1.1 | 0.0 | 0.6 | 0.0 | 3.4 | 0.3 | 27.8 | 0.6 | 360.0 | 2.9$^+$ | 217.8 | 6.1** |
| Fr ×Su | 1 | 43.4 | 0.6 | 111.1 | 4.6 | 5.6 | 0.2 | 3.4 | 0.3 | 22.5 | 0.5 | 27.8 | 0.2 | 27.8 | 0.8 |
| In × Su | 1 | 20.1 | 0.3 | 2.5 | 0.1 | 8.4 | 0.3 | 15.6 | 1.5 | 22.5 | 0.5 | 62.5 | 0.5 | 1.1 | 0.0 |
| Fr × In × Su | 1 | 241.7 | 3.5$^+$ | 4.4 | 0.2 | 5.6 | 0.2 | 5.6 | 0.5 | 1.1 | 0.0 | 0.3 | 0.0 | 2.5 | 0.1 |
| Res | 32 | 69.4 | | 24.1 | | 29.8 | | 10.2 | | 49.2 | | 122.6 | | 35.8 | |
| Total | 39 | | | | | | | | | | | | | | |
| PERMDISP | | 0.433 | | 0.011* | | 0.027* | | 0.254 | | 0.343 | | 0.183 | | 0.040* | |

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, $^+p = 0.07$

NIS are highlighted in bold. *P*-values are indicated in Table 5

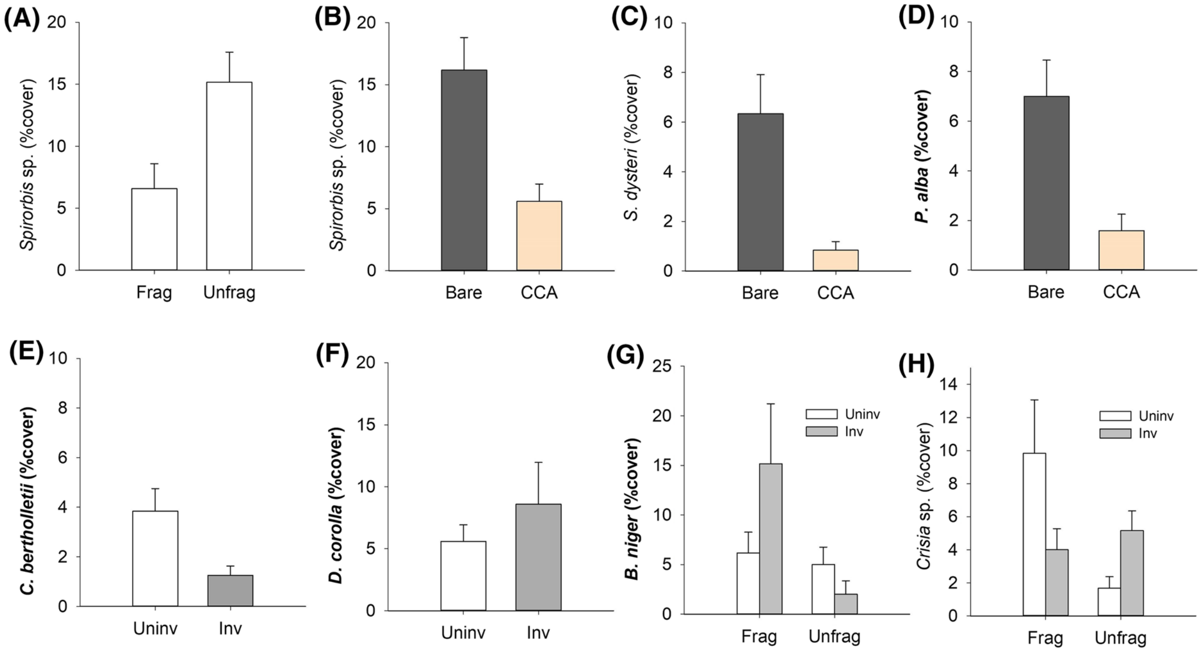

**Fig. 4** Mean (+SE, per panel) cover of relevant species across fragmentation, invasion (Invaded in light grey) and substrates levels (Bare = Bare rock, CCA = Calcareous crust) (*n* = 5). NIS are highlighted in bold

## Discussion

In this study, we investigated the role of the fragmentation of crustose coralline habitats in determining the diversity patterns (i.e. species richness and abundance) of marine fouling organisms across assemblages with or without the presence of non-indigenous species in Madeira Island. Despite limitations related to the increase of richness and percentage cover in invaded treatments, which could mask invasion effects, our results indicate that both fragmentation and substrate affected the abundance of fouling species, with the structure of fouling assemblages differing strongly between bare rock and calcareous crust. Moreover, fragmentation and invasion may interact and affect the composition of assemblages by modulating the recruitment and successful establishment of species.

Although the effects on some species were mostly negligible, opposite responses were observed on some non-indigenous species (NIS) versus native species (e.g. *B. niger* vs *Crisia* sp.), with previously invaded habitats facilitating NIS spread after fragmentation. Different NIS can aid one another in different ways, with numerous idiosyncratic interactions described in the literature (e.g. Simberloff and Von Holle 1999 and references therein). On some occasions, interactions may be synergistic, and these interactions among invaders may accelerate impacts on native ecosystems—an invasional 'meltdown' process (Simberloff and Von Holle 1999). Facilitation can be significant among invasive species and occur between invasive and native species, where the invader may act as either the facilitated or the facilitating species (see Gallien and Carboni 2016 and references therein). The relative importance of competition and facilitation is likely to vary along environmental gradients associated with disturbance (Gallien and Carboni 2016), forcing interactions among species such as the fragmentation event performed in the present study.

Sea urchin barren grounds, habitats dominated by encrusting coralline algae, are considered stable-state systems (Chapman 1981; Filbee-Dexter and Scheibling 2014), and various feedback mechanisms have been cited to enable them to persist or resist to minor disturbances. Firstly, sea urchins themselves can contribute to the resilience of these systems, preventing kelp recruitment by continuously scraping calcareous crusts (Chapman 1981; Filbee-Dexter and Scheibling 2014). However, the persistence of the coralline crustose algae in our experimental panels is not related to this mechanism as they were suspended from wharves, and therefore inaccessible to benthic fauna like sea urchins. On the other hand, as chemical cues, some characteristics of the crustose coralline algae can induce fouling or contrarily suppress settlement of marine organisms larval and spores. Furthermore, larvae can use those biotic cues to select attachment sites. For example, in the north shore of Moorea, French Polynesia, Price (2010) found corals recruited more frequently to one species of CCA, experiencing increased growth and survivorship on top of 'preferred' CCA. Other authors detected similar responses, showing that CCA can reduce settlement of potential competitors (see Bulleri et al. 2002, and references therein) or structure coral reef communities through suppressions of macroalgae (Vermej et al. 2011). In the present study, we found suppression in recruiting some species on top of CCA compared to those colonizing the neighbouring bare rock. More importantly, some of them, such as *P. alba* and *B. niger*, are categorized as NIS, supporting the capacity of CCA as key players in determining the colonization process of macrofoulers and, consequently, on the biotic resistance or resilience of these systems. Thus, our findings suggest that the mechanism that helps prevent recruitment on top of calcareous crusts may be highly relevant in determining the stability and invasibility of these systems (Gestoso et al. 2017).

Habitat fragmentation positively affected the native biodiversity and total cover of the sampled fouling assemblages. Our result contrasts with broader literature as fragmentation: (i) does not affect the number of species nor the structure of benthic assemblages (Matias et al. 2015 and references therein), or (ii) leads to lower abundances (biomass) and species richness, in agreement with the 'SL > SS' principle postulated by Diamond (1975), proposing that a single large patch of habitat (SL) holds more species than several small patches (SS) of the same total area). Although species richness has been a standard measure of diversity in disturbance studies, as species losses may be coupled with immigration, a global decrease in species richness does not necessarily result in local decreases in species richness (Elo et al. 2016). The mechanism where a disturbance event (such as fragmentation) affects species diversity depends on both community assembly processes (e.g. dispersal) and on whether disturbance disrupts the processes or not (Elo et al. 2016). For example, building coastal defences results in the loss and fragmentation of sedimentary habitats, and their replacement by artificial rocky habitats that become colonised by algae and marine animals (Moschella et al. 2005).

While habitat loss typically occurs concurrently with habitat fragmentation (Collinge 2009), and the impact of edge proximity is exacerbated by fragmentation (showed for vegetated habitats, see Colomer and Serra 2021 for references), we follow the proxy of fragmentation established in Matias et al. (2015), i.e., decreasing patch size without an overall habitat loss. For example, Matias et al. (2015) found that fragmentation did not significantly affect the assemblages of macroinvertebrates, suggesting that fragmentation effects may be limited when associated with habitat reduction. However, these effects may well be positive through habitat complexity enhancement (Bertolini et al. 2020), determining species composition and predation risks while altering effects that have been frequently analysed in vegetated habitats (Colomer and Serra 2021). Changes in connectivity among patches depend on their spatial scale and configuration, the organisms' perception of changes in spatial patterns, the surrounding matrix and dispersal among patches (see Matias et al. 2015 and references therein). Fragmentation increases the edge-to-area ratio of patches, potentially affecting the intensity of the wave action and the local nearshore hydrodynamics and biota recruitment, and although there is a growing body of literature on the responses of animals to increases in edge habitat (i.e. 'edge effects'), no consistent evidence have been found about the net effect in aquatic systems (Boström et al. 2011). In addition, abiotic effects at these edges can also create abrupt changes in the transition zone between the fragment and surrounding matrix habitats (as widely explored in terrestrial environments or marine seagrass meadows, Cadenasso et al. 2003, Colomer and Serra 2021). In the present study, the structural conditions at the CCA side do not strongly differ from adjacent bare rocks. Even so, the forcing of interactions among assemblages after habitat fragmentation could influence the obtained positive response, as in the case of *Spirorbis* sp., favoured in fragmented treatments, or *B. niger*, favoured in fragmented treatments when NIS are present but favoured in unfragmented treatments when they are absent. Many species avoid edge habitats, while others have their proliferation favoured by less predation and/or increased resource availability (Wirth et al. 2008), depending on if resources are concentrated around edged or divided between habitats (Ries and Sisk 2004), and can therefore exert a direct influence on the benthic community.

Surprisingly, we found that habitat fragmentation negatively affected NIS cover in uninvaded systems, mainly because of the great abundance of *C. bertholletii* in unfragmented (and uninvaded) systems. Many studies provide clear evidence of substantial and typically degrading impacts of habitat fragmentation on biodiversity and ecological processes across world environments (see, e.g. Hagen et al. 2012; Haddad et al. 2015; Pardini et al. 2017). Habitat fragmentation implies decreasing habitat size and connectivity, although having the same habitat across fragmentation levels. Thus, specific disturbance patterns would benefit good colonizers, predicted to spread better in landscapes where disturbances are small and dispersed (i.e., fragmented habitats) (With 2004). Some taxa colonizing the fragmented habitats are successful invaders of natural communities (as botryllids, Sheets et al. 2016). Although not analysed in this study, the deployment time can also have a relevant role in the succession of assemblages. For example, although spatially variable across Madeira island, settlement of *B. niger* showed maximum values on bare plates deployed in April in the study area (compared to January or September deployments, Ramalhosa et al. 2021).

In addition, fragmentation can affect particular species interactions and marine food webs (Hagen et al. 2012). For instance, fragments of surviving coral surrounded by reef pavement and coral rubble created by coral bleaching can have consequences for top-down control as average food chains shorten, generalist species proliferate, and phase shifts may occur (Hughes 1994). Our results indicate that habitat fragmentation negatively affected the system by increasing the NIS potential for spreading. We found different effects of habitat fragmentation across invasion levels (i.e. a significant interaction), which became more apparent in the fragmented habitats exposed to invaders. Inadequate dispersers may spread better in landscapes in which disturbances are concentrated in space, whereas good dispersers (as typically invasive species are) are predicted to spread better in landscapes, where disturbances are small and dispersed (i.e., fragmented habitats) (With 2004). It is important to highlight that our experiment mimicked the invasion process by taxa with NCU status at panel scale, and our experimental results must be interpreted with caution. If invasive species spread primarily through disturbed landscape areas, fragmentation can have more substantial consequences in invaded habitats, as previously established NIS can proliferate in fragments (see e.g. *B. niger* behaviour). When unfragmented, the system should have more chances to activate a kind of biotic resistance against NIS dispersion, and therefore invasion could be controlled (remember that NIS on unfragmented and invaded systems accounted for 3.65 average percent cover and 19.5% similarity, whereas it rose to 4.8 average percent cover and 33% similarity in fragmented and invaded habitats (Av ab., sq root transformed data). Accordingly, we assume that our result was likely attributed to the strong effect of fragmentation on biotic resistance, in agreement with previously reported effects of other global stressors known to reduce population sizes and biodiversity and that is exacerbated by fragmentation (see Haddad et al. 2015 and references therein).

In regions experiencing anthropogenic alteration, particularly habitat fragmentation and biotic homogenization, such as coastal habitats, critical connectivity thresholds may be required to maintain the ecological integrity of native communities (Howeth 2017). This study represents an additional contribution to the general understanding of interactive effects between specific global change drivers, namely habitat fragmentation and biological invasions. This experiment revealed changes only 3-months after fragmentation, but understanding the relationship between short and long-term dynamics is a substantial challenge that ecologists must tackle, mainly in the current human scenarios where fragmentation and biological invasions will continue (Haddad et al. 2015). Our findings suggest that both fragmentation and invasion perspectives synergistically aid in managing biological invasions and conservation actions on marine ecosystems. Both processes deserve consideration when analysing biotic resistance to invasion in urban marine habitats. The change in the importance of NIS across an invasion gradient suggests that conservation priorities for unfragmented habitats should be established when considering management issues. Using Madeira Island as a model system, this study contributes to a better understanding of the ecology of invasive spread across fragmented landscapes.

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**Authors' contributions** EC: Conceptualization, Investigation, Data curation, Formal analysis, Writing—original draft, Writing—review and editing. IG: Conceptualization, Methodology, Investigation, Data curation, Writing—review and editing. PR: Methodology, Investigation, Data curation, Writing—review and editing. JC-C: Funding acquisition, Writing—review and editing.

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**Availability of data and material** Data available on request from the authors.

## Declarations

**Conflicts of interest** The authors declare no conflict of interest.

## Appendix

See Fig. 5.

See Tables 4, 5, 6, 7, 8.

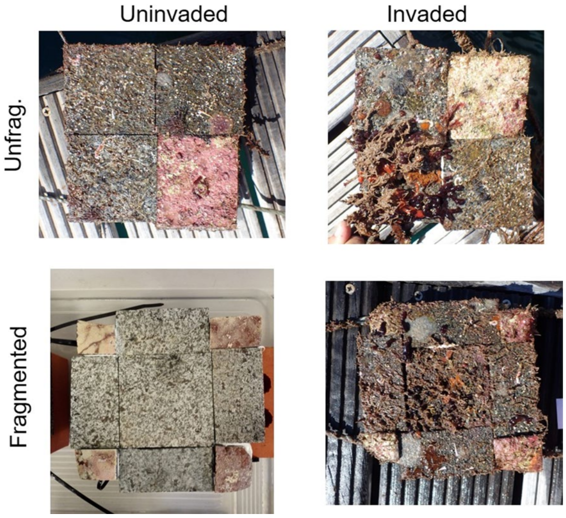

**Fig. 5** Photogras showing real synthetic assemblages (see Photographs in Fig. 1.)

**Table 4** P-values of the univariate analysis of variance of macrofouling assemblages across Fragmentation (Fr), Invasion (In) and Substrate (Su) levels after 3 months of panel deployment (Results in Table 1)

| Source | df | Total N | H | N-NCU | H-NCU | N-NIS | H-NIS |
|---|---|---|---|---|---|---|---|
| Fr | 1 | 0.01 | 0.0986 | 0.56 | 0.0794 | 0.123 | 0.469 |
| In | 1 | 0.144 | 0.8757 | 0.764 | 0.334 | 0.32 | 0.271 |
| Su | 1 | 0.001 | 0.2537 | 0.001 | 0.7649 | 0.081 | 0.475 |
| Fr × In | 1 | 0.487 | 0.1195 | 0.989 | 0.2352 | 0.577 | 0.764 |
| Fr × Su | 1 | 0.213 | 0.0851 | 0.2 | 0.3939 | 0.928 | 0.124 |
| In × Su | 1 | 0.515 | 0.9307 | 0.54 | 0.6762 | 0.276 | 0.977 |
| Fr × In × Su | 1 | 0.345 | 0.8108 | 0.46 | 0.2174 | 0.9 | 0.243 |
| Res | 32 | | | | | | |
| Total | 39 | | | | | | |

*N*, total percentage cover (excluding dead and alive calcareous crusts and bare rock); H, Shannon diversity index; NCU, native, cryptogenic and unresolved species; NIS, non-indigenous species. Analyses were performed on untransformed data

**Table 5** *P*-values of the univariate analysis of variance of relevant macrofouling taxa across Fragmentation (Fr), Invasion (In) and Substrate (Su) levels after 3 months of panel deployment (Results in Table 3)

| Source | Df | *Spirorbis* sp. | *S. dysteri* | ***P. alba*** MS | ***C. bertholletii*** | ***D. corolla*** | ***B. niger*** | *Crisia* sp |
|---|---|---|---|---|---|---|---|---|
| Fr | 1 | 0.002 | 0.033 | 0.96 | 0.694 | 0.945 | 0.064 | 0.05 |
| In | 1 | 0.974 | 9.17E-01 | 0.741 | 0.016 | 0.045 | 0.428 | 0.599 |
| Su | 1 | 0.001 | 0.003 | 0.003 | 0.179 | 0.672 | 0.38 | 0.149 |
| Fr × In | 1 | 0.214 | 0.823 | 0.876 | 0.582 | 0.461 | 0.085 | 0.006 |
| Fr × Su | 1 | 0.455 | 0.041 | 0.653 | 0.576 | 0.506 | 0.645 | 0.408 |
| In × Su | 1 | 0.599 | 0.755 | 0.588 | 0.209 | 0.526 | 0.514 | 0.877 |
| Fr × In x Su | 1 | 0.072 | 0.703 | 0.646 | 0.463 | 0.881 | 0.962 | 0.863 |
| Res | 32 | | | | | | | |
| Total | 39 | | | | | | | |

NIS are highlighted in bold

**Table 6** SIMPER analysis on transformed data (sq root) showing the contribution of taxa to the average Bray–Curtis similarity between Substrate levels (B, bare rock and CCA, calcareous crust)

| Status | B (Sim. 46.45%) | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| U | *Spirorbis* sp. Daudin, 1800 | 3.7 | 14.74 | 1.78 | 31.73 | 31.73 |
| **NIS** | ***Parasmittina alba*** Ramalho, Muricy & Taylor, 2011 | 2.22 | 6.8 | 1.17 | 14.63 | 46.36 |
| **NIS** | ***Botrylloides niger*** Herdman, 1886 | 2.11 | 4.6 | 0.66 | 9.91 | 56.27 |
| N | *Salmacina dysteri* (Huxley, 1855) | 1.9 | 4.28 | 0.74 | 9.22 | 65.48 |
| N | *Spirobranchus triqueter* (Linnaeus, 1758) | 1.45 | 4.21 | 0.88 | 9.07 | 74.56 |
| U | *Crisia* sp. Lamouroux, 1812 | 1.36 | 3.24 | 0.76 | 6.98 | 81.53 |

| | CCA (42.80%) | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| U | *Crisia* sp. Lamouroux, 1812 | 2.26 | 10.67 | 1.36 | 24.92 | 24.92 |
| U | *Spirorbis* sp. Daudin, 1800 | 1.88 | 7.57 | 0.87 | 17.68 | 42.6 |
| U | Amphipod sp. | 1.4 | 5.1 | 0.9 | 11.92 | 54.52 |
| U | Unknown | 1.3 | 3.97 | 0.78 | 9.27 | 63.79 |
| **NIS** | ***Distaplia corolla*** Monniot F., 1974 | 1.35 | 3.95 | 0.65 | 9.24 | 73.03 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** (Audouin, 1826) | 1.27 | 3.93 | 0.59 | 9.18 | 82.21 |

| | B and CCA (Diss. 62.37%) | Group B Av.Abund | Group CCA Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|---|
| U | *Spirorbis* sp. Daudin, 1800 | 3.7 | 1.88 | 7.27 | 1.27 | 11.66 | 11.66 |
| **NIS** | ***Botrylloides niger*** Herdman, 1886 | 2.11 | 1.57 | 6.71 | 0.95 | 10.75 | 22.42 |
| **NIS** | ***Parasmittina alba*** Ramalho, Muricy & Taylor, 2011 | 2.22 | 0.66 | 5.75 | 1.44 | 9.23 | 31.64 |
| U | *Crisia* sp. Lamouroux, 1812 | 1.36 | 2.26 | 5.37 | 1.25 | 8.62 | 40.26 |
| N | *Salmacina dysteri* (Huxley, 1855) | 1.9 | 0.48 | 5.15 | 1.19 | 8.26 | 48.52 |
| **NIS** | ***Distaplia corolla*** Monniot F., 1974 | 1.49 | 1.35 | 4.8 | 1.07 | 7.7 | 56.21 |
| U | Amphipod sp. | 1.1 | 1.4 | 4.01 | 1.25 | 6.43 | 62.64 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** (Audouin, 1826) | 0.96 | 1.27 | 3.9 | 1.2 | 6.25 | 68.89 |
| N | *Spirobranchus triqueter* (Linnaeus, 1758) | 1.45 | 0.62 | 3.85 | 1.3 | 6.17 | 75.06 |

Average similarities (Sim.) and dissimilarities (Diss.) are indicated in brackets. Non-indigenous species are highlighted in bold

**Table 7** SIMPER analysis on transformed data (sq root) shows taxa's contribution to the average Bray–Curtis similarity between Fragmentation and Invasion levels

| Status | Unfrag-Uninv (Sim. 43.58%) | Av.Abund | Av.Sim | Sim/SD | Contrib.% | Cum.% |
|---|---|---|---|---|---|---|
| U | *Spirorbis* sp. | 3.69 | 17.9 | 1.52 | 41.08 | 41.08 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** | 1.8 | 9.23 | 1.14 | 21.17 | 62.25 |
| **NIS** | ***Botrylloides niger*** | 1.75 | 5.53 | 0.82 | 12.7 | 74.95 |
| N | *Spirobranchus triqueter* | 1.12 | 2.8 | 0.68 | 6.42 | 81.37 |
| | Unfrag-Inv (Sim. 47.98%) | Av.Abund | Av.Sim | Sim/SD | Contrib.% | Cum.% |
| U | *Spirorbis* sp. | 3.49 | 17.97 | 2.45 | 37.45 | 37.45 |
| U | *Crisia* sp. | 2.07 | 10.1 | 1.47 | 21.06 | 58.5 |
| **NIS** | ***Distaplia corolla*** | 2.11 | 6.02 | 0.84 | 12.55 | 71.06 |
| **NIS** | ***Parasmittina alba*** | 1.54 | 3.31 | 0.65 | 6.9 | 77.95 |
| | Frag-Uninv (Sim. 44.06%) | Av.Abund | Av.Sim | Sim/SD | Contrib.% | Cum.% |
| U | *Crisia* sp. | 2.69 | 10.06 | 1.21 | 22.83 | 22.83 |
| U | Amphipod sp. | 1.6 | 5.52 | 1.1 | 12.52 | 35.35 |
| U | *Spirorbis* sp. | 1.82 | 5.34 | 1.14 | 12.11 | 47.45 |
| **NIS** | ***Botrylloides niger*** | 1.88 | 4.38 | 0.69 | 9.93 | 57.39 |
| **NIS** | ***Distaplia corolla*** | 1.31 | 3.72 | 0.84 | 8.45 | 65.84 |
| **NIS** | ***Parasmittina alba*** | 1.52 | 3.55 | 0.65 | 8.07 | 73.91 |
| N | *Salmacina dysteri* | 1.61 | 2.9 | 0.52 | 6.58 | 80.49 |
| | Frag-Inv (Sim. 41.76%) | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
| **NIS** | ***Botrylloides niger*** | 3.11 | 9.77 | 0.89 | 23.39 | 23.39 |
| U | Amphipod sp. | 2.05 | 6.8 | 1.23 | 16.29 | 39.67 |
| U | *Spirorbis* sp. | 2.16 | 5.06 | 0.81 | 12.13 | 51.8 |
| U | *Crisia* sp. | 1.6 | 4.61 | 0.87 | 11.04 | 62.84 |
| **NIS** | ***Distaplia corolla*** | 1.71 | 3.97 | 0.88 | 9.5 | 72.34 |
| U | Unknown | 1.28 | 2.98 | 0.52 | 7.14 | 79.49 |

Average similarities (Sim.) are indicated in brackets. NIS are highlighted in bold

**Table 8** SIMPER analysis on transformed data (sq root) shows taxa's contribution to the average Bray–Curtis similarity between Fragmentation and Invasion levels

| | Unfrag_Uninv and Unfrag_Inv (Diss. 58.52%) | Unfrag_ Uninv Av.Abund | Unfrag_Inv Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|---|
| **NIS** | ***Distaplia corolla*** | 0.55 | 2.11 | 6.49 | 1.13 | 11.09 | 11.09 |
| U | *Spirorbis* sp. | 3.69 | 3.49 | 6.18 | 1.15 | 10.56 | 21.65 |
| **NIS** | ***Botrylloides niger*** | 1.75 | 0.63 | 5.72 | 1.19 | 9.77 | 31.42 |
| U | *Crisia* sp. | 0.88 | 2.07 | 5.33 | 1.3 | 9.1 | 40.53 |
| **NIS** | ***Parasmittina alba*** | 1.31 | 1.54 | 5.15 | 1.22 | 8.8 | 49.33 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** | 1.8 | 0.74 | 5.04 | 1.29 | 8.61 | 57.94 |
| N | *Spirobranchus triqueter* | 1.12 | 1.2 | 3.94 | 1.23 | 6.74 | 64.68 |
| N | *Salmacina dysteri* | 0.62 | 1.09 | 3.8 | 1.16 | 6.5 | 71.18 |
| C | *Diplosoma listerianum* (Milne Edwards, 1841) | 0.87 | 0.5 | 3.31 | 0.74 | 5.66 | 76.83 |
| | Unfrag_Uninv and Frag_Uninv (Diss. 62.62%) | Unfrag_ Uninv Av.Abund | Frag_Uninv Av.Abund | Av.Diss | Diss/SD | Contrib.% | Cum.% |
| U | *Spirorbis* sp. | 3.69 | 1.82 | 7.8 | 1.3 | 12.45 | 12.45 |
| U | *Crisia* sp. | 0.88 | 2.69 | 7.19 | 1.15 | 11.48 | 23.93 |
| **NIS** | ***Botrylloides niger*** | 1.75 | 1.88 | 5.41 | 1.27 | 8.64 | 32.57 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** | 1.8 | 1.22 | 4.81 | 1.31 | 7.69 | 40.26 |
| **NIS** | ***Parasmittina alba*** | 1.31 | 1.52 | 4.79 | 1.18 | 7.65 | 47.91 |
| N | *Salmacina dysteri* | 0.62 | 1.61 | 4.79 | 1.06 | 7.65 | 55.56 |
| U | Amphipod sp. | 0.57 | 1.6 | 4.14 | 1.3 | 6.61 | 62.17 |
| **NIS** | ***Distaplia corolla*** | 0.55 | 1.31 | 3.91 | 1.19 | 6.25 | 68.42 |
| N | *Spirobranchus triqueter* | 1.12 | 0.93 | 3.45 | 1.21 | 5.5 | 73.92 |
| C | *Diplosoma listerianum* | 0.87 | 0.72 | 3.27 | 1.01 | 5.22 | 79.13 |
| | Unfrag_Inv and Frag_Uninv (Diss. 57.24%) | Unfrag_Inv Av.Abund | Frag_Uninv Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| U | *Spirorbis* sp. | 3.49 | 1.82 | 6.14 | 1.28 | 10.73 | 10.73 |
| **NIS** | ***Botrylloides niger*** | 0.63 | 1.88 | 5.21 | 1.14 | 9.1 | 19.83 |
| **NIS** | ***Distaplia corolla*** | 2.11 | 1.31 | 5.09 | 1.21 | 8.9 | 28.73 |
| U | *Crisia* sp. | 2.07 | 2.69 | 4.91 | 1.16 | 8.58 | 37.31 |
| N | *Salmacina dysteri* | 1.09 | 1.61 | 4.65 | 1.34 | 8.13 | 45.44 |
| **NIS** | ***Parasmittina alba*** | 1.54 | 1.52 | 4.65 | 1.25 | 8.13 | 53.56 |
| U | Amphipod sp. | 0.79 | 1.6 | 4.01 | 1.28 | 7 | 60.56 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** | 0.74 | 1.22 | 3.69 | 1.08 | 6.45 | 67.01 |
| N | *Spirobranchus triqueter* | 1.2 | 0.93 | 3.46 | 1.22 | 6.05 | 73.07 |
| **NIS** | ***Virididentula dentata*** (Lamouroux, 1816) | 0.47 | 0.94 | 3.18 | 0.92 | 5.55 | 78.62 |
| | Unfrag_Uninv and Frag_Inv (Diss. 63.96%) | Unfrag_ Uninv Av.Abund | Unfrag_ Uninv Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| **NIS** | ***Botrylloides niger*** | 1.75 | 3.11 | 8.5 | 0.95 | 13.29 | 13.29 |
| U | *Spirorbis* sp. | 3.69 | 2.16 | 8.32 | 1.27 | 13.01 | 26.31 |
| U | *Amphipod* sp. | 0.57 | 2.05 | 5.22 | 1.52 | 8.16 | 34.47 |
| **NIS** | ***Distaplia corolla*** | 0.55 | 1.71 | 4.88 | 1.1 | 7.63 | 42.1 |
| **NIS** | ***Parasmittina alba*** | 1.31 | 1.4 | 4.88 | 1.18 | 7.62 | 49.73 |

**Table 8** (continued)

| | Unfrag_Uninv and Frag_Inv (Diss. 63.96%) | Unfrag_ Uninv Av.Abund | Unfrag_ Uninv Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|---|
| N | *Salmacina dysteri* | 0.62 | 1.44 | 4.62 | 0.91 | 7.22 | 56.95 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** | 1.8 | 0.72 | 4.62 | 1.35 | 7.22 | 64.17 |
| U | *Crisia* sp. | 0.88 | 1.6 | 4.28 | 1.21 | 6.7 | 70.86 |
| U | Unknown | 0.13 | 1.28 | 4.11 | 0.99 | 6.42 | 77.29 |
| | Unfrag_Inv and Frag_Inv (Diss. 60.31%) | Unfrag_Inv Av.Abund | Frag_Inv Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| **NIS** | ***Botrylloides niger*** | 0.63 | 3.11 | 9.59 | 1 | 15.9 | 15.9 |
| U | *Spirorbis* sp. | 3.49 | 2.16 | 6.85 | 1.31 | 11.36 | 27.26 |
| **NIS** | ***Distaplia corolla*** | 2.11 | 1.71 | 5.66 | 1.17 | 9.38 | 36.64 |
| U | Amphipod sp. | 0.79 | 2.05 | 4.89 | 1.4 | 8.11 | 44.76 |
| **NIS** | ***Parasmittina alba*** | 1.54 | 1.4 | 4.87 | 1.25 | 8.07 | 52.83 |
| N | *Salmacina dysteri* | 1.09 | 1.44 | 4.58 | 1.15 | 7.6 | 60.42 |
| U | *Crisia* sp. | 2.07 | 1.6 | 3.97 | 1.16 | 6.58 | 67.01 |
| U | Unknown | 0.26 | 1.28 | 3.91 | 1.09 | 6.48 | 73.48 |
| N | *Spirobranchus triqueter* | 1.2 | 0.9 | 3.49 | 1.19 | 5.79 | 79.28 |
| | Frag_Uninv and Frag_Inv (Diss. 57.05%) | Frag_Uninv Av.Abund | Frag_Inv Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| **NIS** | ***Botrylloides niger*** | 1.88 | 3.11 | 7.45 | 0.98 | 13.07 | 13.07 |
| U | *Crisia* sp. | 2.69 | 1.6 | 5.47 | 1.1 | 9.6 | 22.66 |
| U | *Spirorbis* sp. | 1.82 | 2.16 | 5.08 | 1.2 | 8.9 | 31.56 |
| N | *Salmacina dysteri* | 1.61 | 1.44 | 5.06 | 1.16 | 8.87 | 40.43 |
| **NIS** | ***Parasmittina alba*** | 1.52 | 1.4 | 4.54 | 1.25 | 7.96 | 48.39 |
| **NIS** | ***Distaplia corolla*** | 1.31 | 1.71 | 3.9 | 1.11 | 6.84 | 55.23 |
| U | Unknown | 0.93 | 1.28 | 3.78 | 1.23 | 6.62 | 61.84 |
| U | Amphipod sp. | 1.6 | 2.05 | 3.64 | 1.27 | 6.38 | 68.22 |
| **NIS** | ***Cradoscrupocellaria bertholletii*** | 1.22 | 0.72 | 3.51 | 1.1 | 6.15 | 74.37 |
| N | *Spirobranchus triqueter* | 0.93 | 0.9 | 3 | 1.12 | 5.25 | 79.62 |

Average dissimilarities (Diss.) are indicated in brackets. NIS are highlighted in bold

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