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The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea

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Marine Environmental Research

The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea --Manuscript Draft--

Manuscript Number:	MERE-D-21-00590R2
Article Type:	Full Length Article
Keywords:	habitat shift; alga; <i>Ericaria brachycarpa</i> ; epifauna diversity; <i>Cystoseira sensu lato</i> ; rocky shore; Marine Protected Area
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Abstract:	Invasive seaweeds are listed among the most relevant threats to marine ecosystems worldwide. Biodiversity hotspots, such as the Mediterranean Sea, are facing multiple invasions and are expected to be severely affected by the introduction of new non-native seaweeds in the near future. In this study, we evaluated the consequences of the shift from the native <i>Ericaria brachycarpa</i> to the invasive <i>Asparagopsis taxiformis</i> habitat on the shallow rocky shores of Favignana Island (Egadi Islands, MPA, Sicily, Italy). We compared algal biomass and species composition and structure of the associated epifaunal assemblages in homogenous and mixed stands of <i>E. brachycarpa</i> and <i>A. taxiformis</i> . The results showed that the biomass of primary producers is reduced by 90% in the <i>A. taxiformis</i> invaded habitat compared to the <i>E. brachycarpa</i> native habitat. The structure of the epifaunal assemblages displayed significant variations among homogenous and mixed stands. The abundance, species richness and Shannon-Wiener diversity index of the epifaunal assemblages decreased by 89%, 78% and 40%, respectively, from homogenous stands of the native <i>E. brachycarpa</i> to the invasive <i>A. taxiformis</i> . Seaweed biomass was the structural attribute better explaining the variation in epifaunal abundance, species richness and diversity. Overall, our results suggest that the shift from <i>E. brachycarpa</i> to <i>A. taxiformis</i> habitat would drastically erode the biomass of primary producers and the associated biodiversity. We hypothesize that a complete shift from native to invasive seaweeds could ultimately lead to bottom-up effects on rocky shore habitats, with negative consequences for the ecosystem structure, functioning, and the services provided.
Suggested Reviewers:	Antonia Chiarore, PhD Stazione Zoologica Anton Dohrn Napoli antonia.chiarore@szn.it For her scientific skills and publications on the topic of the paper Pedro Augusto Dos Santos Longo, PhD State University of Campinas: Universidade Estadual de Campinas pedro.slongo@gmail.com For his scientific skills and publications on the subject of the paper Javier Urrea Instituto Español de Oceanografía: Instituto Espanol de Oceanografía

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	Valentina Pitacco National Institute of Biology: Nacionalni institut za biologijo valentina.pitacco@mbss.org For her scientific skills and publications on the topic of the paper
Response to Reviewers:	

Highlights:

- Primary producer biomass is 90% lower in *A. taxiformis* than in *E. brachycarpa* habitat.
- From native to invasive seaweeds, epifaunal assemblages lost 40% of their diversity.
- Seaweed biomass was the structural attribute explaining the epifaunal variation.
- We suggest a complete shift from native to invasive seaweeds could impair rocky shore habitats.

1 **The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and**
2
3 **biodiversity of native algal forests in the Mediterranean Sea**

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49 **Abstract**

50 Invasive seaweeds are listed among the most relevant threats to marine ecosystems worldwide.

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52 Biodiversity hotspots, such as the Mediterranean Sea, are facing multiple invasions and are expected
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54 to be severely affected by the introduction of new non-native seaweeds in the near future. In this
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56 study, we evaluated the consequences of the shift from the native *Ericaria brachycarpa* to the
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58 invasive *Asparagopsis taxiformis* habitat on the shallow rocky shores of Favignana Island (Egadi
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60 Islands, MPA, Sicily, Italy). We compared algal biomass and species composition and structure of
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29 the associated epifaunal assemblages in homogenous and mixed stands of *E. brachycarpa* and *A.*
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30 *taxiformis*. The results showed that the biomass of primary producers is reduced by 90% in the *A.*
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31 *taxiformis* invaded habitat compared to the *E. brachycarpa* native habitat. The structure of the
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32 epifaunal assemblages displayed significant variations among homogenous and mixed stands. The
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33 abundance, species richness and Shannon-Wiener diversity index of the epifaunal assemblages
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34 decreased by 89%, 78% and 40%, respectively, from homogenous stands of the native *E. brachycarpa*
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37 shift from *E. brachycarpa* to *A. taxiformis* habitat would drastically erode the biomass of primary
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40 consequences for the ecosystem structure, functioning, and the services provided.
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32 **Keywords:** habitat shift; alga; *Ericaria brachycarpa*; epifauna diversity; *Cystoseira sensu lato*; rocky
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34 shore; Marine Protected Area
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36 37 38 39 **Introduction**

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42 Invasive species are globally recognized among the main drivers of habitat shift in both terrestrial
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44 and marine ecosystems (Gallardo et al., 2016; Mačić et al., 2018). In marine environments, decades
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46 of human activities related to global aquatic trade have enabled the dispersion of invasive species
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48 among distant geographic areas worldwide (Bax et al., 2003; Williams and Smith, 2007; Molnar et
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50 al., 2008; Servello et al., 2019). In addition, the rise in seawater temperature caused by global
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52 warming has allowed non-native species to cross environmental and geographical barriers, facilitating
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54 their expansion and in turn eroding indigenous resistance (Occhipinti-Ambrogi and Galil, 2010; Lo
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56 Brutto et al., 2019). Concerns over ecological and social-economic consequences have led researches
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59 to investigate the effects of invasive species on many marine ecosystems around the world.
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55 Seaweeds are a significant component of marine non-native and invasive species (227 taxa
1 globally), with some of them being responsible for drastic habitat shifts (Williams and Smith, 2007).
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57 Studies have highlighted how invasive seaweeds can negatively impact the recipient habitats by
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78 reducing biomass of primary producers, biodiversity, and nutrient flows, compromising ecosystem
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59 functioning (Boudouresque et al., 2005; Streftaris and Zenetos, 2006; Thomsen et al., 2014; Maggi
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160 et al., 2015; Ramsay-Newton et al., 2017; Geburzi and McCarthy, 2018). Interestingly, the effects of
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61 non-native seaweeds seem to change depending on the complexity of the recipient habitat (Thomsen
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162 et al., 2014). In less structured habitats (e.g. soft bottoms), the introduction of non-native seaweeds
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63 enhances structural complexity that may favor the increase in biodiversity and food web length
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64 (Dijkstra et al., 2017). Conversely, the introduction in well-structured habitats (e.g. seagrass
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65 meadows, algal canopies) may alter the diversity and function, depending on the structural features
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66 of the recipient habitat (Engelen et al., 2013; Veiga et al., 2014, 2018).

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Macroalgal complexity plays a significant role in shaping the abundance, richness and structure of
epifaunal assemblages associated with both non-native and native seaweeds (Chemello and Milazzo,
2002; Jormalainen and Honkanen, 2008; Pitacco et al., 2014; Veiga et al., 2014; Maggi et al., 2015;
Dijkstra et al., 2017; Veiga et al., 2018; Chiarore et al., 2019). Algae with a high structural
complexity, expressed as a combination of attributes, such as degree of branching, thallus width and
height, and wet weight, can support well-structured epifaunal communities (Hacker and Steneck,
1990; Chemello and Milazzo, 2002; Jormalainen and Honkanen, 2008; Pitacco et al., 2014; Veiga et
al., 2014; Bitlis, 2019; Chiarore et al., 2019). Studies comparing the epifaunal diversity between
invasive and native seaweeds revealed that, when invasive species are structurally less complex than
native ones, they support low abundance and richness, and a simplified structure of epifaunal
assemblages (Navarro-Barranco et al., 2018; Veiga et al., 2018). However, when native macroalgae
are less complex, the abundance and diversity of epifauna associated with invasive seaweeds may be
higher (Veiga et al., 2014; Dijkstra et al., 2017). This indicates that the effects of invasive seaweeds
on epifaunal assemblages may change depending on both the invasive and the native seaweed

81 structural features. However, other studies have shown that native and invasive seaweeds with similar
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282 morphologies can host either similar (Suárez-Jiménez et al., 2017) or different epifaunal diversity
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583 (Navarro-Barranco et al., 2019). Overall, these contrasting evidences suggest that, apart from
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784 seaweed morphology, other factors can be involved in structuring the associated assemblages.
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1085 In the last decades, the Mediterranean basin has witnessed an increase in the number of non-native
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1286 and invasive seaweeds, with consequent modification of biodiversity and ecosystem functioning of
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1487 coastal areas (Ribera Siguan, 2002; Streftaris et al., 2005; Streftaris and Zenetos, 2006; Piazzini and
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1688 Balata, 2009; Musco et al., 2014; Bulleri et al., 2016; Corriero et al., 2016; Giangrande et al., 2020).
18
1989 In particular, *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon is listed among the 100 worst
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2190 invasive species in this basin (Streftaris and Zenetos, 2006). The earliest reports of its presence in the
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2391 Mediterranean Sea date back to 1798-1801 in Alexandria (Egypt) as a result of trading operations
25
2692 and the opening of the Suez Canal (Verlaque et al., 2015). It was first recorded along the Italian coast
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2893 on the western shore of Sicily, close to the city of Trapani, in May 2000 (Barone et al., 2003). While
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3194 *A. taxiformis* has been suspected of producing harmful effects on native habitats (Barone et al., 2003),
32
3395 as far as we know, only one study assessed its effects on biodiversity, in particular by comparing the
35
3696 vagile macrofauna associated with this species to that of the native *Halopteris scoparia* (Linnaeus)
37
3897 Sauvageau indicating that *A. taxiformis* hosted less diverse epifaunal assemblages compared to native
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4198 algae (Navarro-Barranco et al., 2018).
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43
4499 Along the Italian coast, gametophytes of *A. taxiformis* can colonize coastal areas dominated by
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4600 habitat-forming seaweeds, mainly belonging to the genus *Cystoseira* - recently divided into three
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48101 genera *Cystoseira*, *Gongolaria* and *Ericaria* and hereafter referred to as *Cystoseira sensu lato* to
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5102 include all three genera (Orellana et al., 2019; Molinari Novoa and Guiry, 2020). *Cystoseira sensu*
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53103 *lato* species are important ecological engineers, greatly increasing the habitat surface, complexity and
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5604 productivity in coastal ecosystems from the infra-littoral zone to the upper circalittoral zone.
57
5805 (Giaccone et al., 1994; Bulleri et al., 2002; Falace and Bressan, 2006; Ballesteros et al., 2009;
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6106 Mancuso et al., 2021b). By creating shelter, *Cystoseira sensu lato* species improve the biodiversity
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107 of their related assemblages, leading to the development of well-structured food webs (Schiel and
108 Foster, 2006; Cheminée et al., 2013; Mineur et al., 2015; Mancuso et al., 2021b). According to the
109 European Water Framework Directive (2000/60), they are also considered indicators of good water
110 and environmental quality (European Commission, 2000).

111 In a recent study, we discovered that *A. taxiformis* had a less diverse and less structured molluscan
112 assemblage than *E. brachycarpa*; however, no information about other epifaunal components
113 associated with seaweeds was reported, nor information about intermediate states, such as mixed
114 stands of *E. brachycarpa* and *A. taxiformis* (Mancuso et al., 2021a). Here, we compared the structure
115 of the epifaunal community (amphipods, molluscs and annelids) associated with three plausible
116 alternative states of the transition between the native *Ericaria brachycarpa* (J.Agardth) Orellana &
117 Sansón and the invasive *A. taxiformis*. In particular, we characterized and compared the biomass and
118 the diversity (richness, evenness, structure and composition) of the epifauna associated with the
119 fronds of homogenous and mixed stands of *E. brachycarpa* and *A. taxiformis*. Moreover, we explored
120 the variation of the epifaunal diversity in relation to the structural features of the two algae (dry
121 weight, thallus volume, canopy volume, and interstitial volume). We hypothesize that shifting from
122 habitats dominated by *E. brachycarpa* to those dominated by *A. taxiformis* will have a negative
123 impact on the associated biodiversity, resulting in low abundances and diversity of each epifaunal
124 component.

126 **Materials and Methods**

127 Study area and algal species characteristics

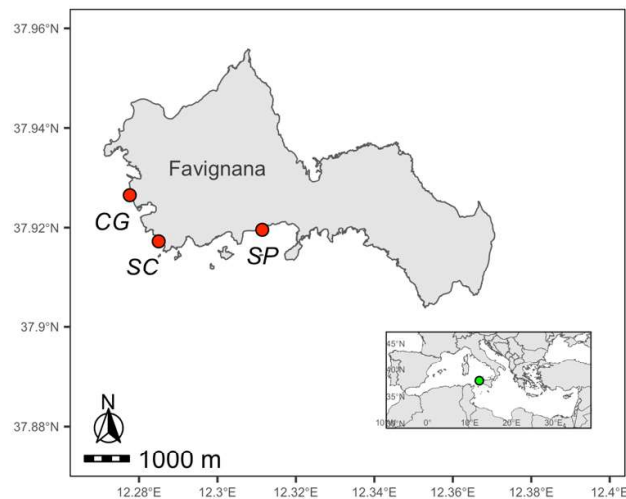
128 The research was performed on the southwestern, shallow rocky shore of Favignana Island
129 (Sicily, Italy), within the Egadi Islands Marine Protected Area (MPA) in June 2011 (Fig. 1). The
130 region consists of gently sloping (5°-10°) carbonate rocky platforms and scattered boulders (Pepe et
131 al., 2018) that provide substrates for well-developed macroalgal vegetation.

132 In this area, *A. taxiformis* was first recorded in 2000 (Barone et al., 2003). Since then, no studies
133 have explored the temporal effects of this invasive species on native habitats. Although today *A.*
134 *taxiformis* is well established in the area, previous surveys allowed the identification of three sites
135 with distinctive habitats corresponding to three possible alternative states of the transition from native
136 to invasive seaweed habitats: “Scoglio Corrente” (37° 55' 2.0778" N, 12° 17' 6.0432" E) characterized
137 by stands of *E. brachycarpa* (100% coverage); “Scoglio Palumbo” (37° 55' 10.4226" N, 12° 18'
138 41.097" E) hosting stands of *A. taxiformis* (100% coverage), and “Cala Grande” (37° 55' 35.385" N,
139 12° 16' 39.514" E) with mixed stands of *E. brachycarpa* (~50% coverage) and *A. taxiformis* (~50%
140 coverage) (Fig. 1). In this study, we decided to use these three sites to compare the epifaunal
141 communities associated with three plausible alternative states of the transition from native to invasive
142 habitats.

143 *Ericaria brachycarpa* is a brown seaweed (Fucales) characterized by caespitosus thalli up to 20-
144 25 cm in height with several perennial axes, up to 2-6 cm in height, connected to the substratum by a
145 more or less compact discoid base formed by haptera (Molinari Novoa and Guiry, 2020). The apices
146 of the axes are flattened, smooth and not very prominent. Branches are cylindrical with smooth bases,
147 or covered with tiny spinose appendages that are typically fertile in the spring-summer season
148 (Gómez-Garreta et al., 2002; Mannino and Mancuso, 2009; Cormaci et al., 2012). Like other
149 *Cystoseira sensu lato* species, *E. brachycarpa* displays seasonal differences in vegetative
150 development (Gómez-Garreta et al., 2002). At the study sites, new branches of *E. brachycarpa* grow
151 from the perennial axes in spring (May-June) providing new substrate and shelter for colonizing
152 fauna, while in autumn (September-October) *E. brachycarpa* starts to become quiescent, losing
153 almost all branches, leaving perennial axes that persist throughout the cold winter season.

154 *Asparagopsis taxiformis* is a red alga (Bonnemaisoniales) common in the tropics and subtropics
155 across the globe. The species experiences a heteromorphic life cycle, with an erect gametophyte
156 alternating with a filamentous sporophyte known as *Falkenbergia hillebrandii* (Bornet) Falkenberg
157 (Andreakis et al., 2004; Ní Chualáin et al., 2004). The gametophytes are characterized by sparsely

158 branched, creeping stolons and erect shoots from which several side branches grow in all directions.
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159 The latter ramifies over and over again giving the thallus a plumose appearance. In the study area, *A.*
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160 *taxiformis* develops in the upper sublittoral zone of the rocky substrate or as an epiphyte of other algal
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6 species. The gametophytes are present during all seasons with a maximum occurrence in spring
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162 (Barone et al., 2003).



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166 **Fig. 1** Location of the three study sites (red dots) along the rocky-shore of Favignana Island MPA
167 (green dot), Trapani, Sicily, Italy. **SC** = Scoglio Corrente, **SP** = Scoglio Palumbo, **CG** = Cala Grande.

169 Sampling and analysis of epifauna

170 Samples were collected by scuba diving at a depth of 5-7 m. For each site (hereafter referred to
171 as habitat), two areas (5 x 5 m) were haphazardly selected. For each area, 10 thalli of *E. brachycarpa*
172 from homogenous stands (100% algal coverage), 10 thalli of *E. brachycarpa* from mixed stands and
173 10 gametophytes of *A. taxiformis* from homogenous stands (100% algal coverage) were collected (n
174 = 20 per habitat). Thalli were collected 50cm apart to avoid spatial autocorrelation among samples.
175 Underwater, each thallus and the associated epifauna were enveloped in a plastic bag, then the alga
176 was detached from the substrate and the plastic bag was immediately closed to prevent the escape of
177 vagile fauna. After collection, each sample was carefully drained of seawater in order to prevent

178 escape of small epifauna and stored at -20°C until laboratory analysis. In the laboratory, each thallus
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179 of *E. brachycarpa* and gametophytes of *A. taxiformis* were transferred into buckets abundantly rinsed
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180 under running water, allowing the associated fauna to detach from the algae. Then, the water was
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181 sieved through a 1 mm mesh. After sorting, molluscs, amphipods, and annelids were stored in 70%
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182 seawater ethanol solution and subsequently counted and identified to species, or the nearest possible
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183 taxonomic level. Taxonomy and nomenclature were updated according to the World Register of
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184 Marine Species database (WoRMS Editorial Board (2021)).
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186 Seaweed structural attributes

187 For each thallus of *E. brachycarpa* and gametophyte of *A. taxiformis* collected, we measured 4
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2488 structural features (thallus volume, canopy volume, interstitial volume, and biomass), to explore their
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289 relationships with the diversity indices calculated for the epifaunal assemblages. Thallus volume was
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290 measured as the variation of volume, in ml, after the immersion of a thallus into a graduated cylinder
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3492 (1990). The canopy volume (*CV*, the volume, in ml, created by the overall dimension of a
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394 thallus submerged in seawater) was defined as the volume of a theoretical cylinder ($CV = \pi \times r^2 \times$
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4496 *h*), where $\pi = 3.14$, *h* is the length of the thallus from the base to its apical portion of the thallus,
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497 including epiphytes, and *r* is the radius calculated as an average measure of the radius of the thallus
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199 Finally, the biomass of the macroalgae was calculated as dry weight (*DW*, gr) after drying in a
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200 stove at 60 °C for 48 h (Stein-Taylor et al., 1985). Biomass was used as a proxy for the primary
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201 production of each habitat.
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203 Data analysis

204 For each epifaunal species, we calculated total abundance (N), frequency (F%; the percentage of
1 samples in which a particular species is present) and dominance index (D%; the percentage of the
205 rate between the percentage of individuals of a particular species and the total number of individuals
3 within the sample) (Magurran, 1988). The epifaunal assemblages of each habitat were characterized
4 according to total abundance of individuals (N), rarefied species richness (S), Shannon-Wiener
5 diversity index (H') and Pielou's Evenness index (J). A two-way analysis of variance (ANOVA) was
6 used to test differences in the epifaunal indices (N, S, H', J) between habitats (fixed with 3 levels: *E.*
7 *brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*) and areas (random and nested within
8 habitat with 2 levels: area 1 and area 2). Cochran's test was used to check for the homogeneity of
9 variances (Underwood 1997). Tukey's HSD procedure was used to separate means (at $\alpha = 0.05$)
10 following significant effects in the ANOVAs (Underwood, 1996). The hierarchical structure of the
11 taxonomic classifications of the epifaunal assemblages of *E. brachycarpa*, *E. brachycarpa* in mixed
12 stands, and *A. taxiformis* was visualized using the "heat_tree" function in the "Metacoder" R- package
13 (Foster et al., 2017).

14 SIMPER analysis (Clarke, 1993) was performed to identify those taxa that contributed to the
15 dissimilarity of the epifaunal assemblages between habitats ($\delta_i\%$). The ratio $\delta_i/SD_{(\delta_i)}$ was used to
16 measure the consistency of the contribution of a particular taxon to the average dissimilarity in the
17 comparison between habitats. A cut-off value of 70% was used to exclude low contributions.

18 Differences in the epifaunal community structure (which takes into account species identity and
19 relative abundance) and composition (presence/absence, which only takes into account species
20 identity) among habitats and areas were assessed by Permutational Multivariate Analysis of Variance
21 (PERMANOVA). The analyses were based on a Bray-Curtis distance matrix of square-root
22 transformed epifaunal abundances (structure) and on a Jaccard distance matrix of presence/absence
23 data (composition) using 9999 permutations. PERMANOVA was also performed separately for each
24 component of the epifauna (molluscs, annelids and amphipods). Permutational analysis of
25 multivariate dispersion (PERMDISP) was used to test differences in multivariate dispersion

230 (Anderson et al., 2008). A principal coordinate analysis (PCoA) plot was generated to visualize the
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231 variation of the epifaunal community structure (based on a Bray-Curtis distance matrix) and
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232 composition (based on a Jaccard distance matrix).
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233 Differences in each of the structural attributes (*CV*, *IV*, *TV*, *DW*) among habitats and areas were
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234 analyzed by two-way ANOVAs according to the above mentioned design. Cochran's test was used
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235 to check for the homogeneity of variances (Underwood, 1996).
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236 Linear regression (LM) analysis was used to test which algal structural attributes explained better
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237 the variation of total abundance (N), rarefied species richness (S), Shannon-Wiener diversity (H')
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238 and Pielou's Evenness (J) of the whole epifaunal assemblages and its individual components
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239 (molluscs, annelids and amphipods). If a non-linear relationship between response and depended
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240 variables was detected, we examined the significance of applying a quadratic term in the model. In
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241 addition, a distance-based redundancy analysis (dbRDA, Legendre and Anderson, 1999) was used to
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242 investigate the relationship between structural attributes and the epifaunal multivariate structure.
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243 Since dbRDA is susceptible to multicollinearity (i.e. high correlation between environmental
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244 variables), draftsman plots were used to verify skewness or identify clear correlations between
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245 structural attributes. A $\log(x + 1)$ transformation was used to correct the right-skewness of thallus
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246 volume (*TV*) and biomass (*DW*). Moreover, due to the high correlation between canopy volume (*CV*)
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247 and interstitial volume (*IV*) we removed *CV* from the subsequent analyses. Then, the structural
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248 attributes were normalised using a z-score transformation due to their varying measurement scales.
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249 Finally, forward selection was used to identify the structural properties that mostly contributed to the
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250 heterogeneity in the multivariate structure of the epifaunal assemblages.
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251 Statistical analyses were performed using R open access statistical software 3.5.1 (R Core Team,
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252 2018). See the "*Data availability and reproducible research*" section for further details.
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254 **Results**

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255 Epifauna

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256 Overall, we identified 5676 individuals of epifauna belonging to 199 taxa (74 molluscs, 50
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257 amphipods, and 75 annelids). Of these, 46 and 38 taxa were exclusively found on homogenous and
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258 mixed stands of the native *E. brachycarpa* respectively, while the invasive *A. taxiformis* hosted only
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259 12 unique taxa (Fig. 2, Table S1-S2). Syllidae (annelids) and Rissoidae (molluscs) were the most
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260 species rich families (35 spp. and 21 spp. respectively), while all the other families contained less
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261 than 10 species each (Fig. 2, Table S1). Among molluscs, the most abundant species were *Eatonina*
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262 *cossurae* (Calcara, 1841) on both *E. brachycarpa* (186 ind.) and *A. taxiformis* (12 ind.) and *Setia*
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263 *ambigua* (Brugnone, 1873) on *E. brachycarpa* from mixed stands (161 ind.). The most abundant
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264 species among amphipods were *Ampithoe ramondi* on *E. brachycarpa* (164 ind.), *Apherusa*
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265 *alacris* (Krapp-Schickel, 1969) on *E. brachycarpa* from mixed stands (253 ind.) and *Caprella*
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266 *acanthifera* (Leach, 1814) on *A. taxiformis* (33 ind.). Finally, annelids were mostly represented by
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267 *Amphiglena mediterranea* (Leydig, 1851) on *E. brachycarpa* (457 ind.) and *Syllis prolifera* (Krohn,
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268 1852) on both *E. brachycarpa* in mixed stands (171 ind.) and *A. taxiformis* (17 ind.) (Fig. 2, Table
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269 S1).

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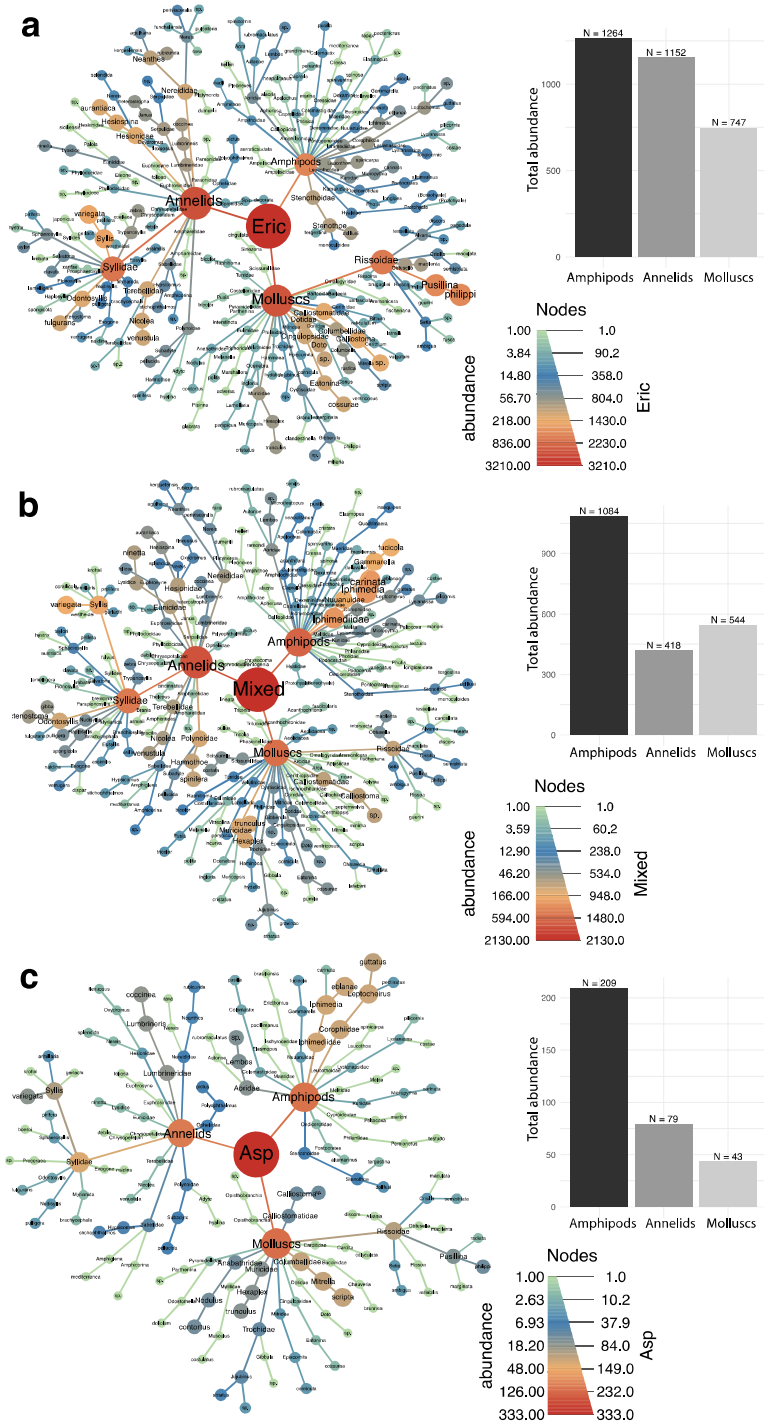


Fig. 2 Differences in the epifaunal assemblages among habitats. Heat trees show the abundances of taxa classified at the lowest taxonomic level possible on *E. brachycarpa* (a), *E. brachycarpa* in mixed stands (b) and *A. taxiformis* (c). Bar charts show the total abundance of amphipods, annelids, and molluscs for each habitat.

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Total abundance (**N**) and rarefied species richness (**S**), differed significantly among habitats, with values that were higher in *E. brachycarpa* compared to *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. 3, Table S3). Shannon-Wiener diversity (**H'**) varied significantly across habitats, with *E. brachycarpa* and *E. brachycarpa* in mixed stands exhibiting closer and higher values than *A. taxiformis*.

Conversely, Pielou's evenness (**J**) was higher in *A. taxiformis* compared to the other two habitats, which showed comparable values (Fig. 3, Table S3).

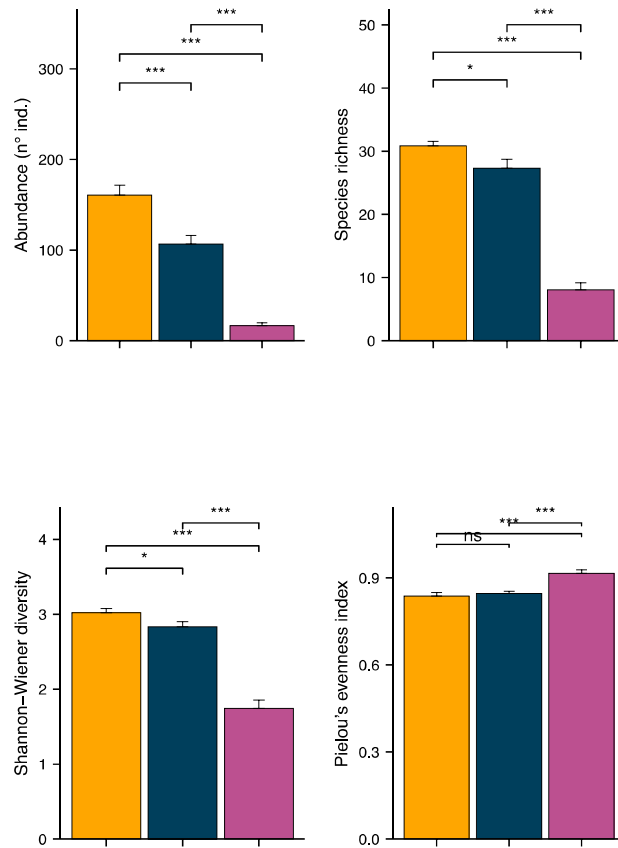
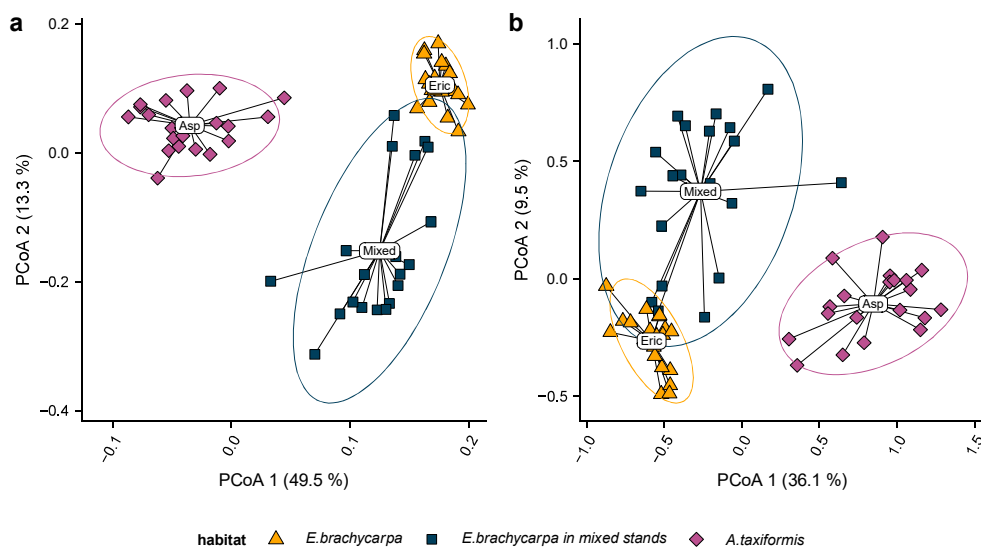


Fig. 3 Comparison of the alpha diversity indices among habitats. Abundance (a), rarefied species richness (b), Shannon-Wiener diversity (c), and Pielou's evenness index (d) of the epifaunal

292 assemblage associated with *E. brachycarpa*, *E. brachycarpa* in mixed stands, and *A. taxiformis*. Bar
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 293 plots show mean \pm 1 standard error (n = 20). Significant codes: *** $p \leq 0.001$, * $p \leq 0.05$, ns
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 294 $p > 0.05$. See Table S3 for further details.
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 296 PERMANOVA showed that the structure and composition of the epifaunal assemblages
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 11 differed significantly among habitats (Table S4). PERMDISP analysis revealed a high dispersion of
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 13 samples within habitats, especially for *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. 4).
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309 **Fig. 4 Structure (a) and composition (b) of the epifaunal assemblages associated with the three**

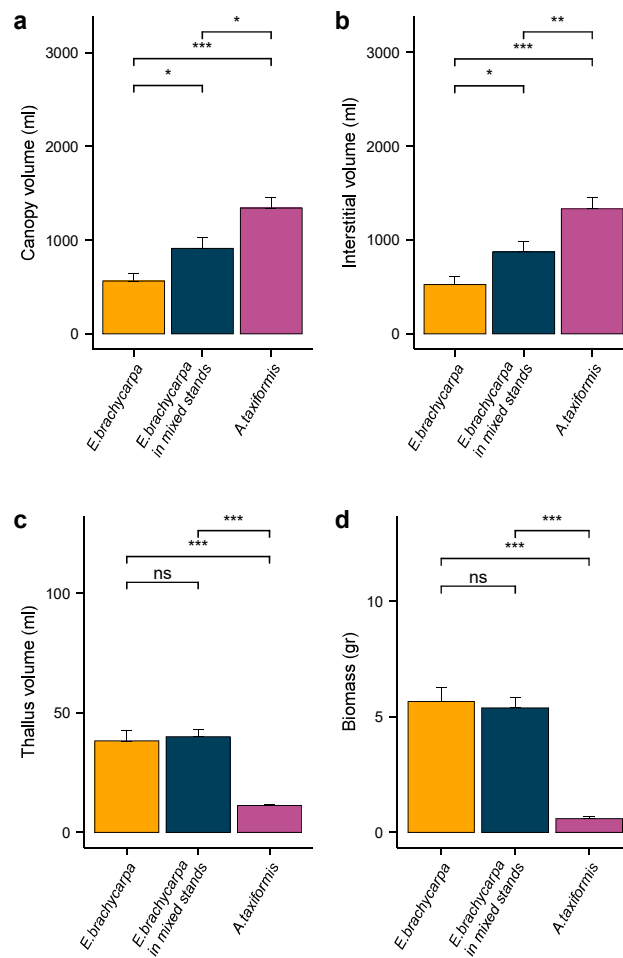
310 **habitats.** The Principal coordinate analysis plot (PCoA) based on a Bray-Curtis distance matrix of
311 square-root transformed relative abundances (structure) or on a Jaccard distance matrix of
312 presence/absence data (composition). The circles show the 90% confidence interval for each seaweed.

313
314 The SIMPER analysis revealed that 28 taxa contributed 70% to the dissimilarity between *E.*
315 *brachycarpa* and *A. taxiformis*; 37 taxa contributed 70% to the dissimilarity between *E. brachycarpa*
316 and *E. brachycarpa* in mixed stands; and 30 taxa contributed 70% to the dissimilarity between *E.*
317 *brachycarpa* in mixed stand and *A. taxiformis* (Fig. S1, Table S5). Most of the species contributing
318 to the dissimilarities belonged to amphipods. The polychaete *Amphiglena mediterranea* (Leydig,
319 1851) was the species mostly contributing to the differences observed between both *E. brachycarpa*
320 and *A. taxiformis* and between *E. brachycarpa* and *E. brachycarpa* in mixed stands, contributing
321 respectively to 8% and 6% of the observed differences. The amphipod *Apherusa alacris* Krapp-
322 Schickel, 1969 was the species most contributing to the differences (7%) between *E. brachycarpa* in
323 mixed stands and *A. taxiformis*. In addition, the gastropod *Obtusella macilenta* (Monterosato, 1880)
324 was the species that contributed consistently (higher $\delta_i/SD(\delta_i)$ values) to the difference between *E.*
325 *brachycarpa* and *A. taxiformis* (Fig. S1, Table S5), while the amphipod *Stenothoe monoculoides*
326 (Montagu, 1813) and the gastropod *Eatonina cossurae* (Calcara, 1841) were the species that
327 contributed consistently to the differences between *E. brachycarpa* in mixed stands and *E.*
328 *brachycarpa*, and between *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. S1, Table S5). The
329 polychaete *S. prolifera* was among the first 5 species contributing to the differences between each
330 couple of habitats (Fig. S1, Table S5).

331 Multivariate analyses conducted separately for the three dominant epifaunal groups (molluscs,
332 annelids, and amphipods) revealed patterns of variation comparable to those of the whole epifaunal
333 assemblage (Table S6). Only, amphipods showed less variability among habitats (Table S6).

335 Seaweed structural attributes and relationships with the epifaunal assemblages.

336 Canopy volume (CV) and interstitial volume (IV) differed significantly among habitats with
337 higher values in *A. taxiformis* compared to *E. brachycarpa* in mixed stands and *E. brachycarpa* (Fig.
338 5 a-b, Table S7). Biomass (DW) and thallus volume (TV) showed similar values between *E.*
339 *brachycarpa* and *E. brachycarpa* in mixed stands and were significantly higher compared to those of
340 *A. taxiformis* (Fig. 5 c-d, Table S7).



342
343 **Fig. 5 Differences in structural attributes among habitats.** Canopy volume (CV), interstitial
344 volume (IV), thallus volume (TV) and biomass (expressed as dry weight, DW) of the epifaunal
345 assemblages associated with *E. brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*. Bar

346 plots show mean \pm 1 standard error (n = 20). Significant codes: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq$
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347 0.05, ns $p > 0.05$. See Table S7 for further details.
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349 The linear regression analysis revealed that biomass (DW) was the attribute that explained better the
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350 variation in abundance ($R^2_N = 0.51$), rarefied species richness ($R^2_S = 0.58$), Shannon-Wiener diversity
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351 ($R^2_{H'} = 0.54$) and Pielou's evenness index ($R^2_J = 0.2$) of the epifaunal assemblages (Table S8). The
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352 variance explained by algal biomass increased if we considered a quadratic relationship between
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353 those variables (Fig. 6). The relationship was positive for N, S and H' , while J presented and opposite
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354 pattern of variation (Fig. 6). Otherwise, canopy volume (CV) interstitial volume (IV) and thallus
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355 volume (TV) explained less variation (and it was significant for N, S and H' but not for J) of the
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356 epifaunal attributes (R-squared < 0.5 , Table S8). The analysis conducted separately on the three
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357 dominant epifaunal groups (molluscs, annelids, and amphipods) revealed similar results however for
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358 amphipods and annelids the relationship between assemblage parameters and algal biomass was
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359 weaker (annelids: $R^2_N = 0.35$, $R^2_S = 0.52$, $R^2_{H'} = 0.49$, $R^2_J = 0.03$; amphipods: $R^2_N = 0.23$, $R^2_S = 0.43$,
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360 $R^2_{H'} = 0.31$, $R^2_J = 0.01$) although remaining the most important explanatory variable for both groups.
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361 Meanwhile, molluscs revealed patterns of variation similar to the whole assemblage ($R^2_N = 0.5$, R^2_S
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362 $= 0.53$, $R^2_{H'} = 0.48$, $R^2_J = 0.12$) (Table S8). As for the other algal structural features, annelids showed
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363 a weaker and not significant relationship with the canopy and interstitial volumes, differing from
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364 amphipods and molluscs (Table S8).
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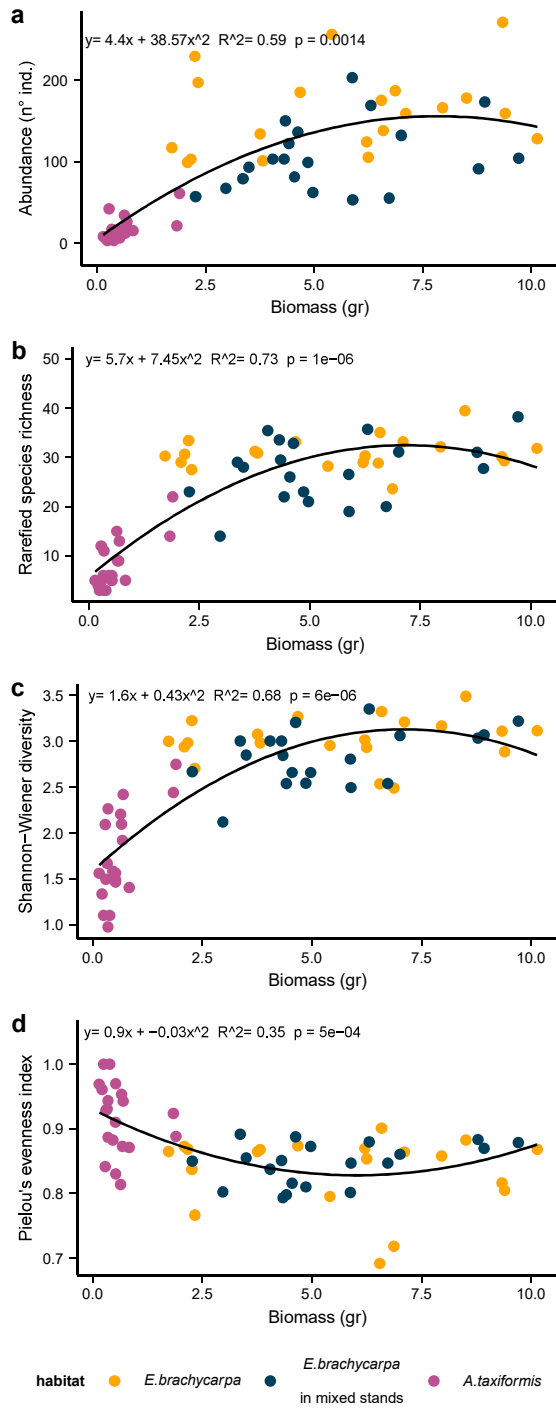


Fig. 6 Relationship between seaweed structural attributes and epifaunal diversity. Results of the linear regression analysis (LM) between the algal biomass (expressed as dry weight, DW) and the abundance (a), rarefied species richness (b), Shannon-Wiener diversity (c) and Pielou's evenness index (d) of the epifaunal assemblages.

Biomass (DW) was also the structural attribute selected for constrained db-RDA, explaining 24.7% of the variation in the structure of the epifaunal assemblages (Table S9). The first two axes of the dbRDA plot explained 15.6% of the total variance of the multivariate structure of the epifaunal assemblages, with 12.4% for axis 1 and 3.2% for axis 2 (Fig. 7).

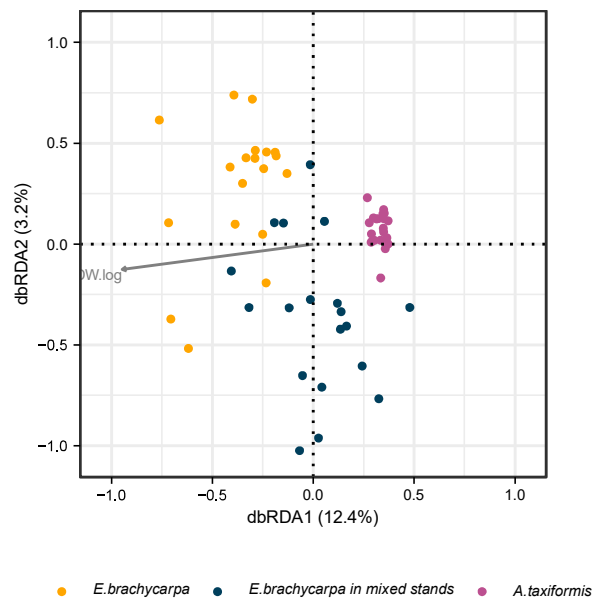


Fig. 7 Relationship between structural attributes and the multivariate structure of the epifaunal assemblages associated to the three habitats. The distance-based redundancy (dbRDA) plot illustrates the structural attribute better explaining the multivariate structure of the three habitats.

DW.log = seaweed biomass (log + 1).

388 **Discussion**

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389 The biodiversity and the socio-economic value of marine ecosystems are threatened by biological
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390 invasions around the world (Bax et al., 2003; Molnar et al., 2008). Understanding how invasive
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391 seaweeds modify the functioning of recipient ecosystems may allow us to better understand large
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392 scale effects on native rocky shore habitats. Here we investigated the effects of the invasive *A.*
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393 *taxiformis* on the native *E. brachycarpa* by comparing the epifaunal assemblage associated with three
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394 alternative states of the transition between native and invasive seaweeds, homogenous and mixed
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395 stands of the two seaweeds. Our results showed differences in abundance and diversity of the
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396 epifaunal assemblages between three alternative states of the transition from native *E. brachycarpa*
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397 to invasive *A. taxiformis*. In particular, *A. taxiformis* hosted almost 6 times less epifaunal individuals
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398 compared to *E. brachycarpa* in mixed stands, and 10 folds less individuals compared to homogenous
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399 stands of *E. brachycarpa*. Also, the number of epifaunal species was more than 4 folds lower in the
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400 invasive compared to the native habitat, while diversity reduced by half. These results confirm that
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401 generally invasive seaweeds exhibit a less diverse epifaunal component compared to native seaweeds
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402 (Guerra-García et al., 2012; Janiak and Whitlatch, 2012; Maggi et al., 2015; Navarro-Barranco et al.,
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403 2018; Veiga et al., 2018).

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404 We found that variation in diversity and multivariate structure of the epifaunal assemblages was
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405 related to changes in algal structural features. In particular, biomass was the variable better explaining
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406 the variation in abundance, number of species, and the multivariate structure of the epifaunal
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407 assemblages. The role of macroalgal complexity in shaping the associated biota has been highlighted
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408 in several studies, with complex algae hosting a larger abundance and diversity of epifauna than
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409 simpler ones (Chemello and Milazzo, 2002; Pitacco et al., 2014; Veiga et al., 2014; Lolas et al., 2018;
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410 Veiga et al., 2018; Bitlis, 2019; Chiarore et al., 2019; Poursanidis et al., 2019; Mancuso et al., 2021b).
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411 In general, studies have highlighted that invasive seaweeds host lower (Guerra-García et al., 2012;
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412 Navarro-Barranco et al., 2018; Rubal et al., 2018; Veiga et al., 2018) or higher (Veiga et al., 2014)
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413 epifaunal abundance, species richness, and diversity, depending on whether their structural
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414 complexity is respectively lower or higher compared to native seaweeds. Navarro-Barranco et al.
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415 (2018) showed that *A. taxiformis* had low fractal complexity and hosted an impoverished faunal
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416 assemblage compared to native seaweeds. Guerra-García et al., (2012) found that *A. armata* had low
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417 algal volume and showed lower abundance, species richness, and diversity of associated isopods
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418 fauna compared to the native *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders.
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419 Moreover, lower dry weight and fractal dimension in the invasive *S. muticum* compared to native
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420 seaweeds have been shown to play a major role in shaping the associated faunal assemblages (Veiga
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421 et al., 2014, 2018). Likewise other studies (Janiak and Whitlatch, 2012; Veiga et al., 2014; Rubal et
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422 al., 2018), our results indicated that the quantity of habitat (biomass) was the best predictor variable
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423 explaining variation in terms of abundance, species richness, as well as multivariate structure of the
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424 associated epifauna.
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425 Interestingly, our results highlight that *A. taxiformis* affected each component (molluscs, annelids,
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426 and amphipods) of the epifaunal assemblages in the same way. However, in the available literature
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427 on the epifaunal assemblages of invasive seaweeds, we can find distinct responses among epifaunal
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428 components (Schmidt and Scheibling, 2006; Gestoso et al., 2010; Guerra-García et al., 2012; Bedini
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429 et al., 2014; Veiga et al., 2018; Navarro-Barranco et al., 2019). For example, species richness,
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430 Shannon diversity and total abundance of isopods were significantly lower in *A. armata* compared to
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431 native algae (Guerra-García et al., 2012). Bedini et al. (2014) found that the invasive *Lophocladia*
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432 *lallemandii* (Montagne) F. Schmitz hosted a higher abundance of amphipods, isopods, and
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433 polychaetes, while native habitats harbored a greater abundance of molluscs and decapods. Bivalves
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434 associated with the invasive *S. muticum* were more abundant compared to native seaweeds, which, in
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435 contrast, hosted more gastropods (Veiga et al., 2018), and Gestoso et al. (2010) found that isopods
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436 and amphipods were more abundant in *S. muticum* than in native seaweeds. Moreover, the invasive
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437 *Codium fragile* subsp. *fragile* (Suringar) Hariot supported higher densities of nematodes, bivalves,
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438 and specialist herbivores compared to fronds of the native kelp, which, in contrast, supported greater
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439 densities of gastropods and asteroids (Schmidt and Scheibling, 2006). Other authors revealed that
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440 differences between invasive and native seaweeds in single components of epifaunal assemblages
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441 changed depending on the site and the identity of the algal species (Navarro-Barranco et al., 2019).
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442 The fact that in our study, the *A. taxiformis* habitat showed lower abundance, species richness, and
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443 diversity values for all the epifaunal organisms, regardless of the groups investigated in this study
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444 (molluscs, amphipods and annelids), led us to hypothesize that a potential shift from the native (i.e.
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445 *E. brachycarpa*) to the invasive (i.e. *A. taxiformis*) habitat could cause large negative cascade effects
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446 on the benthic ecosystem.
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447 Although differences in the epifaunal assemblages among native and invasive seaweeds have
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448 been largely explored, our results also suggest that the presence of *A. taxiformis* affects the epifaunal
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449 assemblages associated with *E. brachycarpa* in mixed stands. This result could be explained by other
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450 attributes that differed between native and invasive seaweeds, such as the amount of epiphytes and/or
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451 the presence of chemical defenses, that have been related to the ability of seaweeds to shape their
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452 associated fauna (Hay et al., 1987; Viejo, 1999; Paul et al., 2006; Cacabelos et al., 2010; Máximo et
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453 al., 2018; Gache et al., 2019). Invasive seaweeds can release secondary metabolites (e.g. halogenated
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454 compounds) able to act as deterrents against epiphytes, and herbivores (Paul et al., 2006; Cacabelos
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455 et al., 2010; Vega Fernández et al., 2019). Secondary metabolites released by *A. taxiformis* can affect
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456 the survival of fish in the post-larval stages, eventually leading to alteration of the grazing pressure
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457 on the surrounding habitat (Máximo et al., 2018; Gache et al., 2019). Other studies suggest that
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458 invasive seaweeds can alter the trophic web by changing the composition of epiphytes which reduces
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459 suitable habitat for many epifaunal species (Viejo, 1999; Wikström and Kautsky, 2004). Several
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460 authors suggested that the amount of epiphytes could explain the higher species richness found in the
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461 invasive *S. muticum* compared to native seaweeds (Viejo, 1999; Cacabelos et al., 2010). In our study,
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462 *A. taxiformis* had no or fewer epiphytes compared to *E. brachycarpa* (R.C. personal observation). As
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463 epifauna is mostly represented by microalgae grazers, we can hypothesize that differences in the
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464 abundance of epiphytes between *A. taxiformis* and *E. brachycarpa* could contribute to the variation
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465 in epifaunal assemblages observed in this study. It is therefore arguable that further studies analyzing
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466 the direct and indirect role of epiphyte abundance and secondary metabolites released by *A. taxiformis*
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467 in structuring its associated epifauna would allow us to better clarify the effects of this seaweed on
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468 the recipient habitats.
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469 Moreover, as suggested by other authors (Navarro-Barranco et al., 2019), landscape features
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470 could be another key aspect explaining the effect of *A. taxiformis* on *E. brachycarpa* associated
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471 assemblages in mixed stands. In fact, the presence of invasive seaweeds may contribute to the
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472 fragmentation of native habitats, reducing the patch size of native seaweeds, and at the same time
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473 increasing their isolation (Roberts and Poore, 2006; Lanham et al., 2015). It has been observed that
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474 the reduction in patch size of *Cystoseira sensu lato* habitats reduces the diversity of associated faunal
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475 assemblages (Mancuso et al., 2021b). Thus, we can hypothesize that the presence of *A. taxiformis* in
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476 mixed stands can act as a physical barrier to the dispersal of vagile fauna, reducing connectivity on a
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477 small scale and ultimately eroding the diversity of native habitats (Lanham et al., 2015). However,
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478 another possibility to consider is that some epifaunal groups may be able to disperse through the
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479 different seaweeds (Taylor, 1998) in mixed stands. In this case, the lower epifaunal abundance and
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480 diversity observed on *E. brachycarpa* from mixed stands could be because part of this diversity may
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481 have preferentially dispersed to the *A. taxiformis* portion of these mixed stands. Our study, however,
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482 cannot address the effects of epifauna movement among seaweeds on the observed results, and more
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483 studies are necessary to understand the possible role of mobile epifaunal assemblage movement
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484 patterns within mixed stands of *E. brachycarpa*.
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485 One inherent weakness of this study concerns the impossibility of separating the effects of *A.*
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486 *taxiformis* from natural spatial variability. This should be accounted for by using more interspersed
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487 sites for each condition (mono and mixed stands of native and invasive seaweeds). Unfortunately, we
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488 were not able to find more interspersed sites in the area of study. However, the three sites selected
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489 had the same average values of different environmental variables (surface temperature, salinity,
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490 nitrate and phosphate concentrations, dissolved oxygen, chlorophyll and photosynthetic active
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491 radiation, Table S10), indicating that spatial variability had little effect. Then, we think that the data
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492 presented in this study is still valuable, albeit with its limitations, for understanding epifaunal
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493 community changes between plausible alternative states of the transition between *E. brachycarpa*
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494 and *A. taxiformis*.
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496 In summary, our study suggests that shifting from native to invasive habitats may pose a serious
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497 threat to biodiversity in coastal areas (Martin et al., 1992; Heck et al., 2003), potentially leading to
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498 bottom-up effects on rocky shore ecosystems. In addition, the low biomass supplied by the herein
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499 studied invasive species suggests that the shift from native canopy-forming algae to the invasive *A.*
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500 *taxiformis* habitat would also drastically reduce the biomass of primary producers in affected coastal
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501 areas. Predicting the ecological effects of invasive seaweeds is one of the main goals in the study of
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502 biological invasions. Previous research has highlighted the context-dependent effects of invasive
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503 seaweeds, with larger impact caused by invasive species exerting a different functional role compared
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504 to native habitat forming species (Ricciardi and Atkinson, 2004; Ricciardi et al., 2013; Navarro-
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505 Barranco et al., 2019). Our results not only remark the negative effect of *A. taxiformis* on *E.*
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506 *brachycarpa* epifaunal assemblages, but also suggest that invasive species are able to affect native
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507 habitats in a transitional phase (mixed stands) of the habitat shift, facilitating fragmentation and
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508 isolation. Further studies aimed at understanding the effects of the habitat shift from native to invasive
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509 seaweeds should include multiple transitional phases (different percentage coverage), as well as the
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510 analysis of changes in the trophic structure of the associated epifaunal assemblages.
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512 **Declarations**

513 Not applicable
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Conflicts of interest/Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability and reproducible research

The repository with all the data and the scripts used to reproduce the research in this paper is available at <http://dx.doi.org/10.17632/h3r8ygnjfd.1>

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Author Contributions

Conceptualization, C.R., M.M. and D.R.; Methodology, C.R. and M.M.; Investigation, D.R.; Formal Analysis, M.F.P.; Data curation, M.F.P.; Writing – Original Draft Preparation, M.F.P.; Writing – Review & Editing, M.F.P., M.M., C.R., B.F., M.L., M.B., L.B.S.; Visualization, M.F.P.; Validation, M.F.P.; Supervision, C.R.; Project Administration, C.R.; Funding Acquisition, C.R.; Resources, C.R.; molluscs identification, C.R., D.R.; amphipods identification , L.B.S; annelids identification ; B.F., M.B., M.L.

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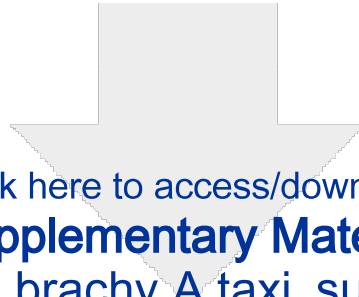
Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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