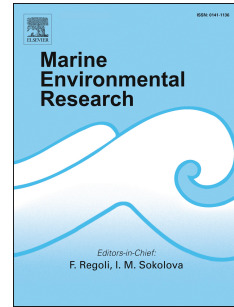


# Journal Pre-proof

The invasive *Asparagopsis taxiformis* hosts a low diverse and less trophic structured molluscan assemblage compared with the native *Ericaria brachycarpa*

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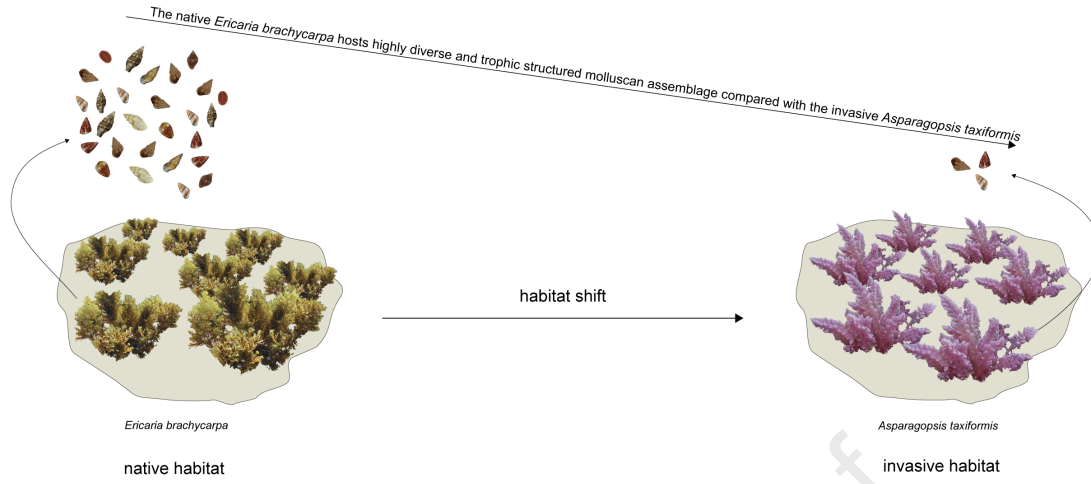
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Journal Pre-proof



1 **The invasive *Asparagopsis taxiformis* hosts a low diverse and less trophic**  
2 **structured molluscan assemblage compared with the native *Ericaria brachycarpa***

3  
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12  
13 **Abstract**

14 Invasive seaweeds threaten biodiversity and socio-economics values of worldwide marine  
15 ecosystems. Understanding to what extent invasive seaweeds can modify local biodiversity is one  
16 of the main priorities in conservation ecology. We compared the molluscan assemblage of the  
17 invasive *Asparagopsis taxiformis* with that of the native *Ericaria brachycarpa* and explore if  
18 variation in the molluscan assemblage diversity was related to the substrate attributes (biomass, and  
19 thallus, canopy, and interstitial volumes) of the algae. Results showed that *A. taxiformis* harboured  
20 lower diversity and trophic structure of the molluscan assemblage compared to *E. brachycarpa*.  
21 Biomass was the variable that better explained the variation of abundance and number of species as  
22 well as the multivariate structure of the molluscan assemblage. Overall, our results suggest that a  
23 complete habitat shift from native to invasive species can potentially trigger bottom-up effects in  
24 rocky shores habitats, reducing the biodiversity and the services provided by the invaded habitat.

25

26 **Keywords:** molluscs diversity; trophic guilds; *Cystoseira sensu lato*; *Ericaria brachycarpa*;  
27 *Asparagopsis taxiformis*; Mediterranean Sea

28

## 29 **1. Introduction**

30 Invasive seaweeds are one of the major threats to biodiversity and human livelihoods of  
31 worldwide marine ecosystems (Williams and Smith, 2007; Maggi et al., 2015). The causes of  
32 seaweeds introductions have been mainly attributed to anthropogenic activities related to global  
33 marine trade (introduction through ballast waters and hull fouling, but also other activities such as  
34 aquariology, aquaculture, fishing gear, the building of artificial channels connecting different  
35 environments), that in the last century have exponentially increased the introduction of invasive  
36 species (Bax et al., 2003; Williams and Smith, 2007). At the same time, the increase of seawater  
37 temperatures, caused by global warming, may enhance the ability of invasive species to overcome  
38 environmental and geographical barriers facilitating their spread, while simultaneously eroding the  
39 resistance of native communities (Occhipinti-Ambrogi and Galil, 2010).

40 At the population level, the ecological impact of an invasive species can be perceived as  
41 “harmful” or “useful” depending on the stakeholder or on the effects that an invasive species can  
42 have on a particular ecosystem service (Simberloff et al., 2013). Different studies have highlighted  
43 that invasive seaweeds can modify the biodiversity, energy and nutrient flows along the food chain,  
44 compromising the functioning pattern of the ecosystems (Boudouresque et al., 2005; Streftaris and  
45 Zenetos, 2006; Geburzi and McCarthy, 2018). However, studies on the effects of the same invasive  
46 species on native habitats have highlighted contrasting results. For example, Veiga et al. (2018)  
47 found that the invasive *Sargassum muticum* (Yendo) Fensholt hosted a low diverse faunal  
48 assemblage compared to the native *Sargassum flavifolium* Kützinger. These results were in contrast  
49 with previous studies which suggested only a weak impact of the introduction of *S. muticum* upon  
50 native faunal diversity (Wernberg et al., 2004; Buschbaum et al., 2006; Gestoso et al., 2010;  
51 Engelen et al., 2013; Bedini et al., 2014; Veiga et al., 2014; Rubal et al., 2018). This suggests that

52 the effects of the same invasive seaweeds could change depending on the invaded habitat or the  
53 location investigated.

54 The Mediterranean basin is among the world's most vulnerable areas to the introduction of  
55 seaweeds, which pose a growing threat to biodiversity, modifying ecosystem functioning (Ribera  
56 Siguan, 2002; Streftaris et al., 2005; Streftaris and Zenetos, 2006; Piazzì and Balata, 2009;  
57 Giangrande et al., 2020). Among invasive seaweeds, *Asparagopsis taxiformis* (Delile) Trevisan de  
58 Saint-Léon has been recognized among the 100 worst invasive seaweed in the Mediterranean Sea  
59 (Streftaris and Zenetos, 2006). First claims of its presence in this area date back 1798-1801 at  
60 Alexandria (Egypt) as a consequence of shipping activities and the opening of the Suez Canal  
61 (Delile, 1813). Along the Italian coasts, it was first reported on May 2000 at the western shore of  
62 Sicily, near the city of Trapani (Barone et al., 2003). Although the presence of *A. taxiformis* has  
63 been related to negative effects on native community, for example by replacing habitats previously  
64 occupied by species of *Cystoseira* C. Agardh (Barone et al., 2003), to our knowledge only one  
65 study has evaluated its effects on biodiversity, by comparing the mobile macrofauna inhabiting this  
66 species to the dominant native species *Halopteris scoparia* (Linnaeus) Sauvageau (Navarro-  
67 Barranco et al., 2018). The results of this study show that *A. taxiformis* hosted a lower diverse  
68 epifaunal assemblage in comparison to that associated with the native seaweed (Navarro-Barranco  
69 et al., 2018). Understanding the effects of invasive seaweeds on the epifaunal assemblage  
70 associated with recipient habitats can allow to understand the possible consequence of changing  
71 habitats and predict potential bottom-up effects on rocky shores.

72 Along the Italian coasts, gametophytes of *A. taxiformis* can colonize coastal areas dominated by  
73 important habitat-forming seaweeds of the genus *Cystoseira*. Recently this genus was divided into  
74 three genera *Cystoseira*, *Carpodesmia* (transferred to the genus *Ericaria* according to Molinari  
75 Nova and Gury, 2020), and *Treptacantha* (Orellana et al., 2019). In this paper, we decided to refer  
76 to as *Cystoseira sensu lato* to include all the three genera. *Cystoseira* species *sensu lato* are essential  
77 ecosystem engineers, significantly enhancing the habitat surface, complexity, and productivity of

78 coastal communities from the infralittoral zone down to the upper circalittoral zone (Giaccone et al.,  
79 1994; Bulleri et al., 2002; Falace and Bressan, 2006; Ballesteros et al., 2009; Mancuso et al., 2021).  
80 By providing habitat, *Cystoseira* species *sensu lato* increase the biodiversity of their associated  
81 assemblages, creating well-structured food webs (Schiel and Foster, 2006; Cheminée et al., 2013;  
82 Mineur et al., 2015; Mancuso et al., 2021). They are also considered useful indicators of ecosystem  
83 quality according to the Water Framework Directive (2000/60) (European Commission, 2000).

84 Decline or loss of *Cystoseira* populations *sensu lato* has been reported from many rocky coasts  
85 particularly close to urban areas due to combined effects of anthropogenic impacts and climate-  
86 change (Benedetti-Cecchi et al., 2001; Thibaut et al., 2005; Arevalo et al., 2007; Mangialajo et al.,  
87 2008; Strain et al., 2014; Mineur et al., 2015; Mancuso et al., 2018; Blanfuné et al., 2019). In this  
88 context, the introduction of invasive seaweeds may add further stress on these vulnerable habitats  
89 facilitating their shift towards less diverse and less structured assemblages (Navarro-Barranco et al.,  
90 2018). Thus, facilitating the decrease in essential ecosystem services (Mineur et al., 2015; Buonomo  
91 et al., 2018) and the economic value of coastal areas (De La Fuente et al., 2019).

92 Macroalgal complexity together with the seasonal variation of the alga and presence of chemical  
93 defences can critically shape the diversity of their associated assemblage (Chemello and Milazzo,  
94 2002; Jormalainen and Honkanen, 2008; Pitacco et al., 2014; Veiga et al., 2014; Chiarore et al.,  
95 2019). Algae with high structural complexity expressed as a combination of substrate attributes  
96 (such as degree of branching, thallus width and height, and wet weight), can support well-structured  
97 molluscs communities (Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Bitlis, 2019).  
98 Macroalgal complexity is one of the main drivers that can explain the variation in the fauna  
99 associated with native and invasive seaweeds (Veiga et al., 2014, 2018; Dijkstra et al., 2017).  
100 Comparisons between invasive and native seaweeds revealed that, when the invasive species have  
101 lower structural complexity than native species, the invasive species alga show a low abundance,  
102 richness and structure of epifaunal assemblage compared to native one (Navarro-Barranco et al.,  
103 2018; Veiga et al., 2018). Conversely, when native macroalgae are less complex, the abundance and

104 diversity of epifauna is higher in the invasive seaweeds (Veiga et al., 2014; Dijkstra et al., 2017).  
105 These results suggest that the effects of invasive seaweeds would also change according to the  
106 morphological differences between invasive and native seaweeds. However, other studies have  
107 shown that native and invasive seaweeds with similar morphologies can host either similar (Suárez-  
108 Jiménez et al., 2017) or different epifauna diversity (Navarro-Barranco et al., 2019). These  
109 contrasting results suggest that apart from seaweeds morphology, other factors can be involved in  
110 such ecological process.

111 Among the different taxa inhabiting macroalgae, molluscs represent one of the main groups,  
112 usually characterized by high numbers of species and trophic guilds (Milazzo et al., 2000; Chemello  
113 and Milazzo, 2002; Urrea et al., 2013; Pitacco et al., 2014; Lolas et al., 2018; Piazzini et al., 2018;  
114 Bitlis, 2019; Chiarore et al., 2019; Poursanidis et al., 2019; Mancuso et al., 2021). Molluscs  
115 associated with seaweeds have an important role in aquatic ecosystems as consumers as well as  
116 prey and are considered an important food source for higher trophic levels (Martin et al., 1992;  
117 Heck et al., 2003). Thus, studying how invasive seaweeds affects the molluscan assemblage in the  
118 invaded habitats can contribute to understanding the possible consequence of changing habitats and  
119 their potential trigger bottom-up effects in rocky shores habitats.

120 In this study, we investigated the effects of the invasive *Asparagopsis taxiformis* in shaping the  
121 diversity of their associated molluscan assemblage compared to the native *E. brachycarpa*  
122 (J.Agardth) Molinari & Guiry. In particular, we characterized the diversity (in terms of  
123 composition, structure and trophic guilds) of the phytal molluscs associated with the fronds of *E.*  
124 *brachycarpa* and *A. taxiformis*. Moreover, we explored if the variation of the molluscan assemblage  
125 diversity was related to the substrate attributes of the algae (biomass, thallus volume, canopy  
126 volume, and interstitial volume).

127

## 128 **2. Materials and Methods**

### 129 2.1. Study area and species



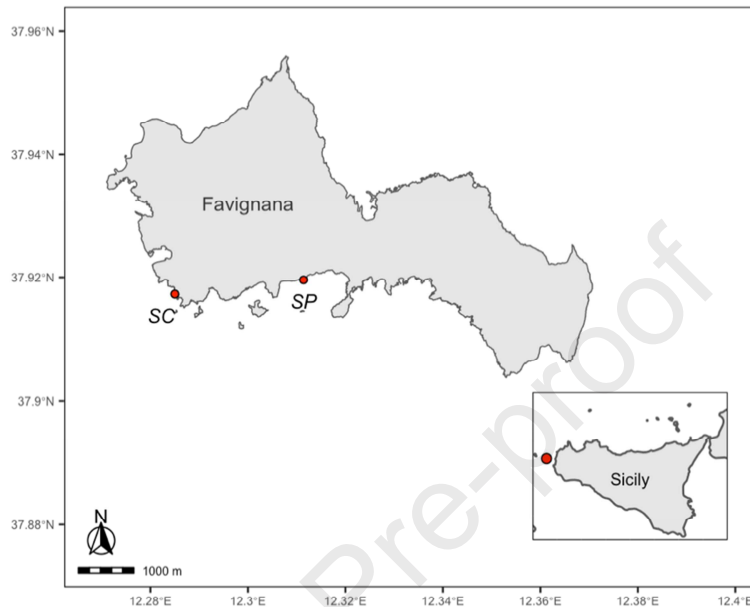
130 The study was carried out at the southwest shallow rocky shore of the Favignana island (Egadi  
131 Islands MPA, Sicily, Italy) in June 2011 (Fig. 1). The area consists of gently sloping (5°-10°)  
132 carbonate rock platforms and scattered boulders (Pepe et al., 2018) that provide substrates for well-  
133 developed macroalgal vegetation. Previous surveys in the area allowed us to identify two sites with  
134 distinctive habitats. The site Scoglio Corrente (37° 55' 2.0778" N, 12° 17' 6.0432" E) is  
135 characterized by the presence of stands of *E. brachycarpa* (100 % coverage), while the site Scoglio  
136 Palumbo (37° 55' 10.4226" N, 12° 18' 41.097" E) hosts stands of *A. taxiformis* (100 % coverage)  
137 (Fig. 1).

138 *Ericaria brachycarpa* is a brown seaweed (Fucales) characterized by thalli high up 20-25 cm,  
139 with multiple perennial axes (caespitose) up to 2-6 cm in height, attached to the substratum by a  
140 more or less compact discoid base formed by haptera. Apices of the axes are not very prominent,  
141 flattened and smoothed, from which primary branches branch off. Branches are cylindrical with  
142 smooth bases or covered by small spinose appendages that are usually fertile in spring-summer  
143 (Gómez-Garreta et al., 2002; Mannino and Mancuso, 2009; Cormaci et al., 2012). Like other  
144 *Cystoseira* species *sensu lato*, *E. brachycarpa* exhibits seasonal variations in the vegetative growth  
145 (Gómez-Garreta et al., 2002). At the study sites, new branches of *E. brachycarpa* grow from the  
146 perennial axes in spring (May-June) providing new substratum and shelter for colonizing fauna,  
147 while in autumn (September-October) *E. brachycarpa* starts to become quiescent losing almost the  
148 totality of their branches leaving perennial axes that persists during the cold winter season.

149 *Asparagopsis taxiformis* is a red alga (Bonnemaisoniales) widespread in the tropics and the  
150 subtropics around the globe. The species exhibits a heteromorphic life cycle, where the erect  
151 gametophyte alternates with a filamentous sporophyte referred to *Falkenbergia hillebrandii*  
152 (Bornet) Falkenberg (Andreakis et al., 2004; Ní Chualáin et al., 2004). The gametophytes are  
153 characterized by sparsely branched, creeping stolons and erect shoots from which numerous side  
154 branches develop in all directions. The latter ramify over and over again giving the thallus a  
155 plumose appearance. At the study area, thalli of *A. taxiformis* grow in the upper sublittoral zone on

156 the rocky substrate or as epiphyte of other algal species. The gametophytes are present during all  
 157 seasons with a maximum occurrence in spring (Barone et al., 2013).

158



159  
 160 **Fig. 1.** Location of the two study sites (red dots) at the rocky-shore of the Favignana island (MPA),  
 161 Trapani, Sicily, Italy. **SC** = Scoglio Corrente, **SP** = Scoglio Palumbo.

162

## 163 2.2. Sampling and molluscan analysis

164 Samples were collected by scuba diving at a depth of 5-7 m. For each habitat, two areas (5 x 5  
 165 m) were haphazardly selected. Then, 10 thalli of *E. brachycarpa* and 10 gametophytes of *A.*  
 166 *taxiformis* were collected (n = 20 per habitat). Underwater, each thallus and associated fauna were  
 167 enveloped with a 500 µm nylon mesh bag, to prevent the escape of mobile fauna, then the alga was  
 168 carefully scraped off the substratum using a hammer and chisel. At the surface, each sample was  
 169 drained from seawater and stored at -20°C until laboratory analysis. In the laboratory, each thallus  
 170 of *E. brachycarpa* and *A. taxiformis* were rinsed under tap water and the associated fauna was  
 171 sieved through a 1 mm mesh. Molluscs were separated from the other fauna and stored in a solution  
 172 of 70% ethanol and seawater. Molluscs were sorted out under a stereomicroscope and determined to

173 the lowest possible taxonomic level. They were subsequently counted, listed according to the  
174 updated taxonomy and nomenclature of the World Register of Marine Species database (see  
175 <http://www.marinespecies.org>, accessed November 2020).

176 Each species was classified into trophic guilds. A trophic guild can be defined as a group of  
177 species with similar size, mobility, and structure of their feeding apparatus able to use the same type  
178 of resource (Steneck and Watling, 1982; Chemello et al., 1997; Arruda et al., 2003; Rueda et al.,  
179 2009). Analysis of the trophic structure provides information about the dominant energy pathways  
180 in a habitat. Moreover, the trophic structure can be related, to some degree, to the physical  
181 characteristics of the alga, because algae with high structural complexity can provide a high number  
182 of micro-habitats increasing the availability of food for different molluscs (Chemello et al., 1997).  
183 The following trophic guilds were assigned according to Rueda et al. (2009): carnivores (C),  
184 feeding on other mobile organisms; scavengers (SC), feeding on remains of dead organisms;  
185 ectoparasites or carnivores on sessile prey (E), feeding on much larger organisms on which they  
186 live during their adult stage; filter feeders (F), capturing the seston particles with their gills and/or  
187 with mucous strings; microalgal grazers (MG), feeding on microalgae (e.g. diatoms) that cover the  
188 branches of *E. brachycarpa*; macroalgae grazers (AG), feeding on macroalgae; deposit feeders  
189 (D), feeding on organic particles contained in the sediment trapped by seaweeds.

190

### 191 2.3. Algal substrate attributes

192 For each thallus of *E. brachycarpa* and *A. taxiformis* collected, we measured four substrate  
193 attributes (thallus volume, canopy volume, interstitial volume, and biomass), to explore their  
194 relationships with the diversity of the molluscan assemblage. Thallus volume (*TV*) was measured as  
195 the variation of volume, in ml, after the immersion of a thallus into a graduate cylinder filled with  
196 seawater. Canopy volume (*CV*: the volume, in ml, created by the overall dimension of a  
197 thallus submerged in seawater) and the interstitial volume (*IV*: the volume, in ml, of water among  
198 the fronds of the alga) were estimated according to Hacker and Steneck (1990). The Canopy

199 volume was defined as the volume of a theoretical cylinder ( $CV = \pi \times r^2 \times h$ ), where  $\pi = 3.14$ ,  
200  $h$  is the length of thallus from the base to the apical portion of the frond, including epiphytes, and  $r$   
201 is the radius calculated as the average of the radius of the thallus measured with a ruler ( $\pm 1$  mm)  
202 at the apical, median and basal parts.

203 The interstitial volume ( $IV$ ) was obtained by subtracting the thallus volume ( $TV$ ), and the axis  
204 volume ( $caV$ , estimate as the volume of cylinder obtained measuring the height and the radius of the  
205 perennial axis) to the canopy volume  $CV$  ( $IV = (CV - TV) - caV$ ).

206 Finally, the biomass of macroalgae was calculated as dry weight ( $DW$ , gr) drying them at  $60^\circ\text{C}$   
207 for 48 h (Stein-Taylor et al., 1985). Biomass was also used as a proxy of the primary production of  
208 each habitat.

#### 210 2.4. Data analysis

211 The total abundance (N), the Frequency (F%; the percentage of samples in which a particular  
212 species occurred) and the Dominance index (D%; the percentage of the rate between the percentage  
213 of individuals of a particular species and the total number of individuals within the sample) was  
214 calculated for each molluscan species identified (Magurran, 1988). The molluscan assemblage was  
215 characterized according to the total abundance of individuals (N), the total number of species (S),  
216 Shannon-Wiener diversity ( $H'$ ) and Pielou's Evenness (J). The hierarchical structure of the  
217 taxonomic classifications of the molluscan assemblage of both *E. brachycarpa* and *A. taxiformis*  
218 was visualized using the "heat\_tree" function in the "Metacoder" R- package (Foster et al., 2017).

219 A two-way analysis of variance (ANOVA) was used to test differences in the malacofauna  
220 indexes (N, S,  $H'$ , J) between habitats (fixed and orthogonal with 2 levels: *E. brachycarpa* and *A.*  
221 *taxiformis*) and area (random and nested within habitat with 2 levels: area 1 and area 2). Cochran's  
222 test was used to check for the homogeneity of variances (Underwood 1997). Tukey's HSD  
223 procedure was used to separate means (at  $\alpha = 0.05$ ) following significant effects in the ANOVAs  
224 (Underwood, 1996). Moreover, we used the non-parametric Chao1 and Chao2 methods (Chao,

225 1987; Cowdell and Coddington, 1994) to estimate the true species richness in the two habitats and  
226 compared them with the accumulation curve of the number of taxa observed. Chao1 is an  
227 abundance-based estimator whereas Chao2 is based on species presence/absence. The Chao2  
228 method avoids possible confounding effects of larger abundances of species in certain samples. It  
229 rests on the hypothesis that non-observed taxa are rare species, and considers that a species is rare  
230 when the taxon occurs at only 2 samples. The advantage of Chao1 and Chao2 indexes is that the  
231 estimated diversity of samples can be compared, even when the true diversity of the whole  
232 population is not known.

233 SIMPER analysis (Clarke, 1993) was performed to identify those taxa that contributed to the  
234 dissimilarity of the molluscan assemblage between habitats ( $\delta_i\%$ ). The ratio  $\delta_i/SD_{(\delta_i)}$  was used to  
235 quantify the consistency of the contribution of a particular taxon to the average dissimilarity in the  
236 comparison between habitats. A cut-off value of 70% was used to exclude low contributions.

237 Differences on malacofauna community structure (which takes into account species identity and  
238 relative abundance) and composition (presence/absence, which only takes into account species  
239 identity) between habitats and areas were assessed by performing a multivariate Permutational  
240 Analyses of Variance (PERMANOVA). The analyses were based on a zero-adjusted Bray-Curtis  
241 distance matrix of square-root transformed relative abundances (structure) or on Jaccard distances  
242 (species presence/absence data) with 9999 permutations. Non-metric Multidimensional Scaling  
243 (nMDS) plots was generated to visualize the variation of malacofauna community structure (based  
244 on a Bray-Curtis distance matrix) and composition (based on the Jaccard distance matrix).

245 For each trophic guild identified we calculated abundance and tested differences between  
246 habitats and areas by two-way ANOVAs according to the design described before.

247 Differences in each of the substrate attributes (CV, IV, TV, DW) between habitats and area  
248 were analysed by ANOVAs according to the two-way design described before. Cochran's test was  
249 used to check for the homogeneity of variances (Underwood, 1996).

250 Linear regression (LM) analysis was used to test which substrate attributes explained better the  
251 variation of the abundance (N), species richness (S), Shannon-Wiener diversity (H') and Pielou's  
252 Evenness (J) of the molluscan assemblage. Moreover, the distance-based redundancy analysis  
253 (dbRDA, Legendre and Anderson, 1999) was used to explore the relationship between substrate  
254 attributes and the multivariate structure of molluscan assemblage. Because dbRDA is sensitive to  
255 multicollinearity (i.e. a high correlation between environmental variables), draftsman plots were  
256 done to check skewness or detect strong correlations between substrate attributes. A  $\log(x + 1)$   
257 transformation was applied to thallus volume (TV) and biomass (DW) to correct right-skewness.  
258 Due to the high correlation between canopy volume (CV) and interstitial volume (IV) we removed  
259 CV from the subsequent analyses. Then, substrate attributes were normalized using a z-score  
260 transformation because of their different measurement scales. Finally, forward selection  
261 was used to retain the substrate attributes that significantly explained the variation of the  
262 multivariate structure of the molluscan assemblage.

263 Statistical analyses were performed in R software 3.5.1 (R Core Team, 2018). See the “*Data*  
264 *availability and reproducible research*” section for further details.

265

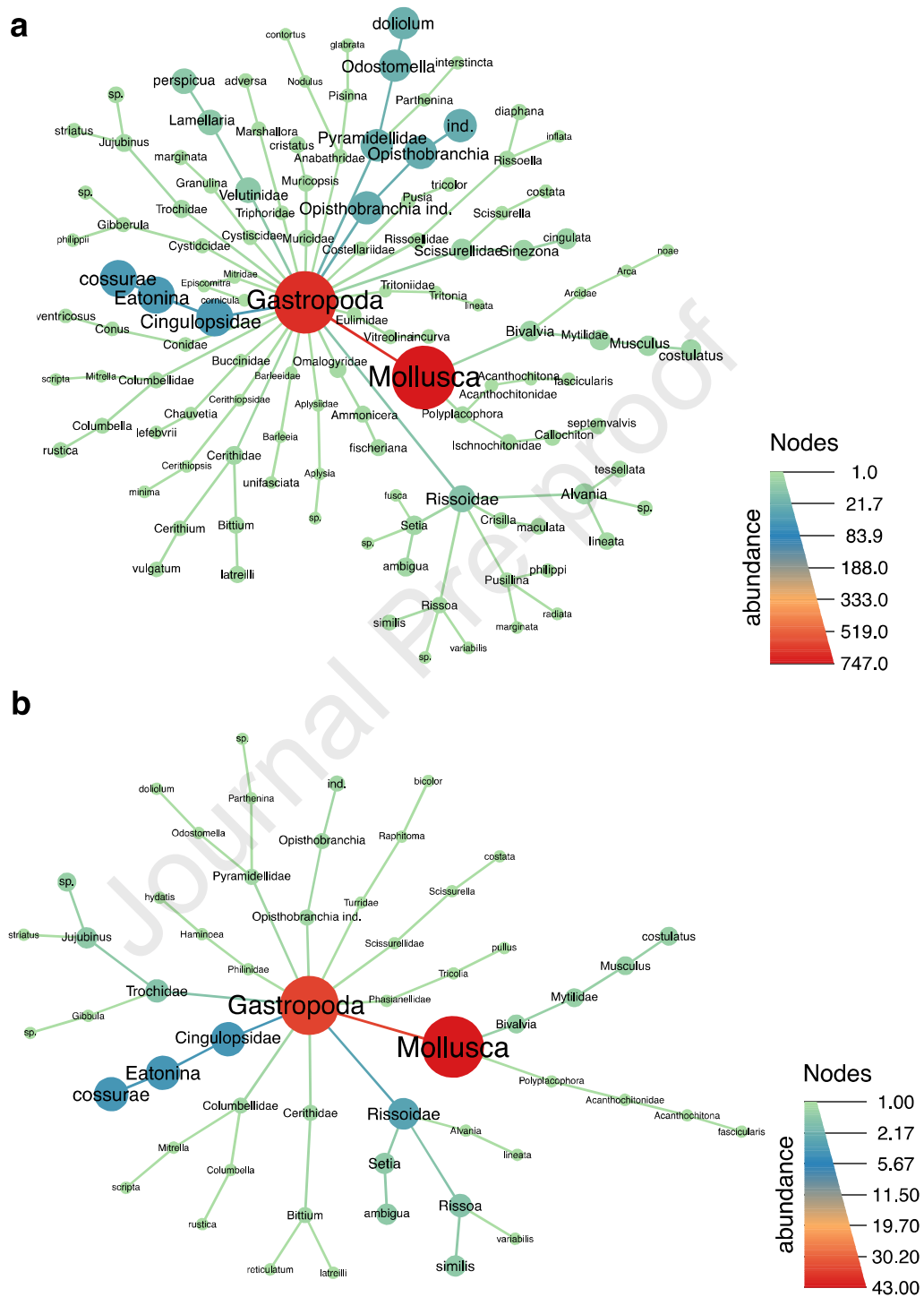
### 266 **3 Results**

#### 267 3.1 Molluscs

268 A total of 790 individuals belonging to 55 taxa made up the molluscan assemblage. Of  
269 these, 34 taxa were unique of the native *E. brachycarpa* and 6 of the invasive *A. taxiformis*, while  
270 15 taxa were shared between habitats (Fig. 2, Table S1-S2). Gastropods were the most represented  
271 class (92.7%), followed by Bivalvia (3.6%) and Polyplacophora (3.6%). The molluscs belonged to  
272 35 different families, of which Rissoidae displayed the highest number of species (35%) followed  
273 by Buccinidae, Pyramidellidae and Trochidae at 7% (Fig. S1, Table S1-S2). At the species level,  
274 *Eatonina cossurae* (Calcara, 1841) was the most dominant taxa on both *E. brachycarpa* and *A.*  
275 *taxiformis* with 25% and 28% respectively (Table S1-S2).

276

277



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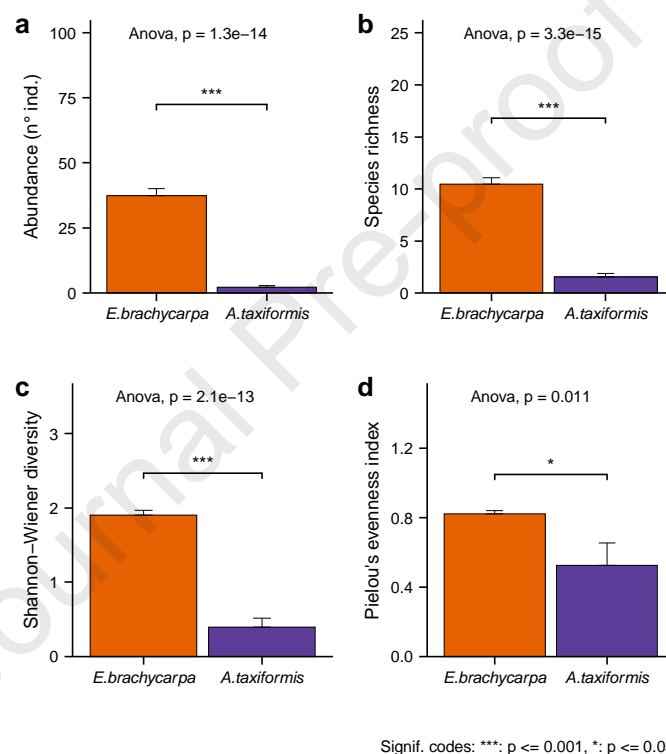
279 **Fig. 2. Differences in the molluscan assemblage between native (a) and invasive (b) seaweeds.**280 Heat trees showing the total abundances of taxa classified at the lower taxonomic level on *E.*

281 *brachycarpa* (a) and *A. taxiformis* (b). Node sizes and colors are related to the total abundance  
 282 (number of individuals) of taxa.

283

284 Abundance (N), species richness (S), Shannon-Wiener diversity (H') and Pielou's evenness  
 285 (J) differed significantly between habitats with values that were higher in *E. brachycarpa* compared  
 286 to *A. taxiformis* (Fig. 3, Table S3).

287



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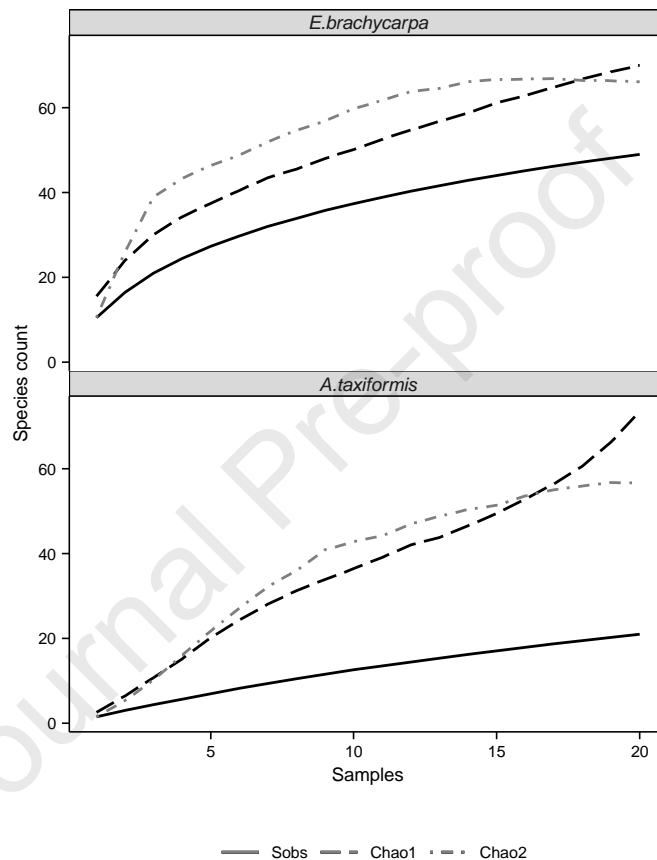
289 **Fig. 3. Comparison of alpha diversity indexes between native and invasive seaweeds.**  
 290 Abundance (a), species richness (b), Shannon-Wiener diversity (c), and Pielou's evenness index (d)  
 291 of the molluscan assemblage associated with *E. brachycarpa* and *A. taxiformis*. Bar plots show  
 292 mean +/- 1 standard error (n = 20). See Table S3 material for more details.

293

294 Species accumulation curves estimated by the non-parametric Chao1 and Chao2 indexes  
 295 showed a similar pattern but with higher values compared to the observed richness on both *E.*  
 296 *brachycarpa* and *A. taxiformis*. Chao1 index reached a maximum value of 70 species for the native



297 seaweed and 73.5 species for the invasive (Fig. 4). However, Chao2 (that minimizes the effects of  
 298 larger abundances of species in certain samples) showed a lower maximum value compared to  
 299 Chao1 with 66 species for the native seaweed and 56.6 species for the invasive (Fig. 4). These  
 300 values were respectively 35% and 170% higher compared to the observed richness.  
 301

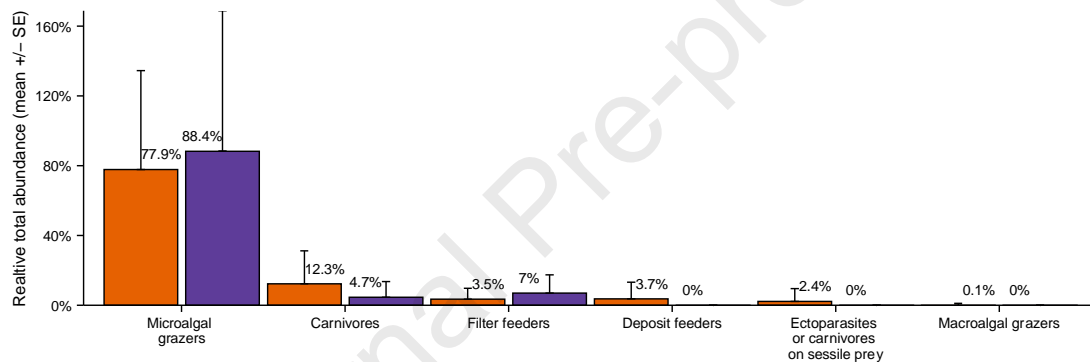


302  
 303 **Fig. 4. Observed and estimated species richness.** Species accumulation curves based on the  
 304 Chao1 (long dashed lines) and Chao2 (dot-dashed lines) estimators and for the observed taxonomic  
 305 richness (solid lines) for *E. brachycarpa* and *A. taxiformis*.

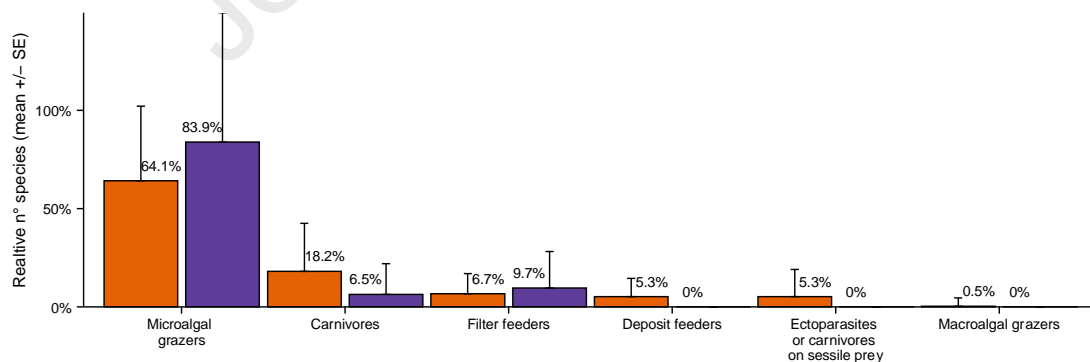
306  
 307 The number of feeding guilds differed between native and invasive seaweeds (Fig. 5).  
 308 Molluscs on *E. brachycarpa* were classified into 6 trophic guilds (MG, C, FF, D, E and AG), while  
 309 on *A. taxiformis* only 3 trophic guilds (MG, C and FF) were identified. Microalgal grazers (mainly  
 310 Rissoidae) was the most represented group on both native (27 spp.) and invasive (18 spp.)

311 seaweeds (Fig. 5, Table S1). Carnivores and filter feeders were also present of both *E. brachycarpa*  
 312 (C = 12 spp., FF = 2 spp.) and *A. taxiformis* (C = 2 spp., FF = 1 spp.) (Fig. 5, Table S1). Moreover,  
 313 on *E. brachycarpa* we found six taxa of ectoparasites or carnivores on sessile prey (E; *Marshallora*  
 314 *adversa* (Montagu, 1803), *Parthenina sp.* (Bucquoy, Dautzenberg & Dollfus, 1883), *Vitreolina*  
 315 *incurva* (Bucquoy, Dautzenberg & Dollfus, 1883), *Parthenina interstincta* (J. Adams, 1797),  
 316 *Odostomella doliolum* (Philippi, 1844) and *Cerithiopsis minima* (Brusina, 1865)), one deposit  
 317 feeders (D; *Sinezona cingulata* (O.G. Costa, 1861)) and one macroalgae grazers (AG; *Aplysia sp.*)  
 318 (Fig. 5, Table S1).

a



b



319

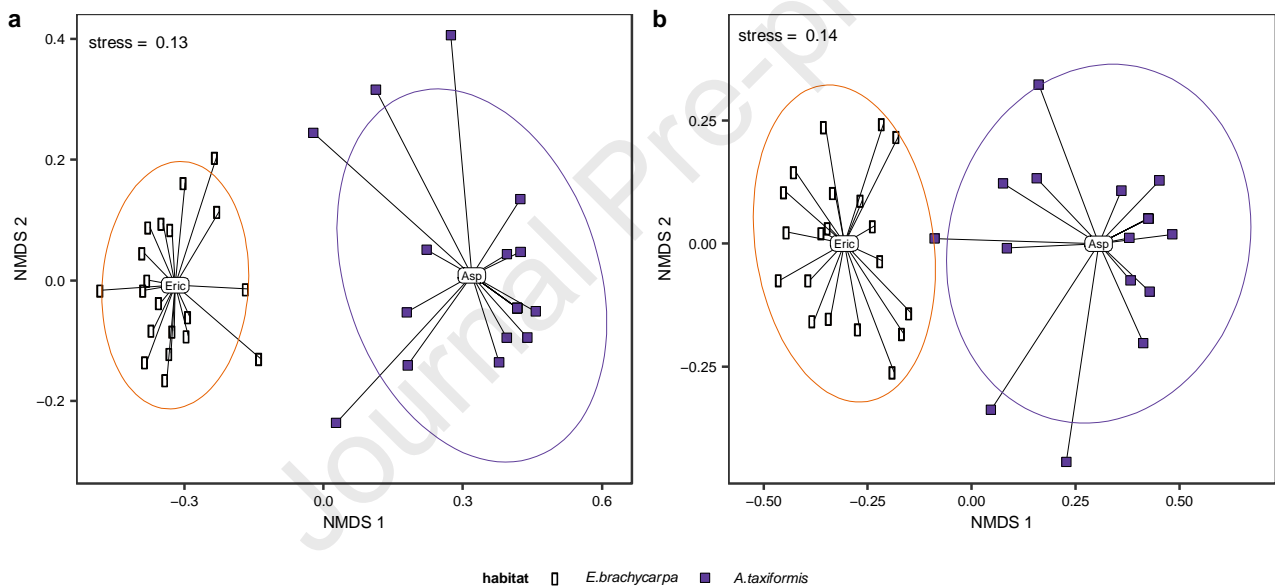
320 **Fig. 5. Variation of the trophic guilds between native and invasive seaweeds.** Bar plots show  
 321 relative percentage (mean +/- 1 standard error, n = 20) based on total abundance (a) and number of  
 322 species (b) of each trophic group on both *E. brachycarpa* and *A. taxiformis*. MG = microalgal

323 grazers, C = carnivores, SC = scavengers, E = ectoparasites or carnivores on sessile prey, F = filter  
 324 feeders, AG = macroalgae grazers, D = deposit feeders.

325

326 PERMANOVA analysis showed that the structure and composition of the molluscan  
 327 assemblage differed significantly between the two habitats (Fig. 6, Table S4). PERMDISP analysis  
 328 was not significant (structure:  $F = 0.187$ ,  $p = 0.67$ , composition:  $F = 0.349$ ,  $p = 0.56$ ), indicating that  
 329 the dispersion of samples did not provide a significant contribution to the differences detected by  
 330 PERMANOVA (Fig. 6).

331



332

333 **Fig. 6. Structure (a) and composition (b) of the molluscan assemblage associated with *E.***  
 334 ***brachycarpa* and *A. taxiformis*.** Non-metric Multidimensional Scaling (nMDS) based on zero-  
 335 adjusted Bray–Curtis measure of square-root transformed molluscan abundances (structure) or  
 336 Jaccard measure (composition). Circles show the 90 % confidence of interval for each seaweed.

337

338 When we looked at the taxa that contributed to the differences between native and invasive  
 339 seaweeds, SIMPER analysis revealed that 6 taxa (*Eatonina cossurae* (Calcara, 1841), *Rissoella*  
 340 *inflata* (Alder, 1848), *Rissoella diaphana* (Monterosato, 1880), *Lamellaria perspicua* (Linnaeus,

341 1758), *Sinezona cingulata* (O.G. Costa, 1861) and *Setia ambigua* (Brugnone, 1873)) contributed to  
 342 70% of the dissimilarity between *E. brachycarpa* and *A. taxiformis* (average dissimilarity 96%),  
 343 with their average abundance was larger in *E. brachycarpa* compared to *A. taxiformis*. *E. cossuriae*  
 344 contributed alone to the 23% of the differences between native and invasive habitats, while *R.*  
 345 *inflata* was the species that contributed consistently (higher  $\delta_i/SD(\delta_i)$  value) to that differences  
 346 (Table 1).

347

348 **Table 1. Taxa contributing to 70% of the dissimilarity between native and invasive**  
 349 **seaweeds.** Results of SIMPER analysis showing the average abundances, consistency ( $\delta_i/SD(\delta_i)$ )  
 350 and cumulative contributions (cum\_ $\delta_i\%$ ).

Species	Average abundance		$\delta_i/SD(\delta_i)$	cum. $\delta_i\%$
	<i>E. brachycarpa</i>	<i>A. taxiformis</i>		
<i>Eatonina cossuriae</i>	9.30	0.60	1.89	23
<i>Rissoella inflata</i>	6.70	0.10	2.08	41
<i>Rissoella diaphana</i>	6.15	0.05	0.82	55
<i>Lamellaria perspicua</i>	2.95	0.00	0.99	63
<i>Sinezona cingulata</i>	1.40	0.00	0.78	67
<i>Setia ambigua</i>	0.90	0.20	0.67	71

351

352

353 3.2 Seaweeds substrate attributes and relationships with the molluscan assemblage

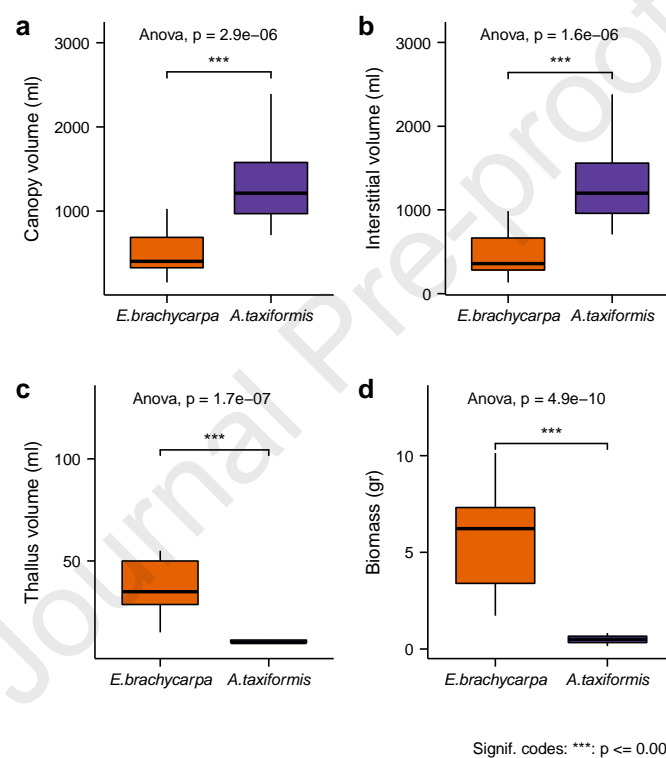
354 Canopy volume (CV) and interstitial volume (IV) were significantly higher in the invasive *A.*  
 355 *taxiformis* compared to the native *E. brachycarpa* (Fig. 7 a-b, Table S5). However, biomass (DW)  
 356 and thallus volume (TV) were significantly higher in the native habitat compared to the invasive  
 357 (Fig. 7 c-d, Table S5).

358 Linear regression analysis revealed that the biomass (DW) was the substrate attribute that better  
 359 explained (R-squared > 0.5) the variation of the abundance and species richness of the molluscan  
 360 assemblage (Table 2). Otherwise, canopy volume (CV) interstitial volume (IV) and thallus volume

361 (TV) explained less variation of the molluscan assemblage ( $R$ -squared  $< 0.5$ ), although highly  
 362 significant ( $p < 0.001$ , Table 2).

363 Biomass (DW) was also the substrate attribute selected for constrained db-RDA, explaining  
 364 24.7% of the variation of the structure of the molluscan assemblage (Table S6). The first two axes  
 365 of the dbRDA plot explained the 32.2% of the total variance of the multivariate structure of the  
 366 molluscan assemblage, with 29.2% for axis 1 and 3% for axis 2 (Fig. 8).

367



368

369 **Fig. 7. Differences in the substrate attributes between native and invasive seaweeds.** Canopy  
 370 volume (CV), Interstitial volume (IV), thallus volume (TV) and biomass (expressed as dry weight,  
 371 DW) of the molluscan assemblage associated with *E. brachycarpa* and *A. taxiformis*. Boxplots  
 372 show extreme and lower whisker (vertical black line), lower and upper quartile (box), and median  
 373 (horizontal black line). Grey dots are raw data ( $n = 20$ ). For more details see Table S5.

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382 **Table 2. Relationship between substrate attributes and molluscan diversity.** Results of the  
 383 linear regression analysis (LM) between each substrate attributes and the abundance (**N**), species  
 384 richness (**S**), Shannon-Wiener diversity (**H'**) and Pielou's Evenness (**J**) of the molluscs associated  
 385 with *E. brachycarpa* and *A. taxiformis*. R-squared values major than 50% are in bold.

	<b>N</b>		<b>S</b>		<b>H'</b>		<b>J</b>	
<b>Structural features</b>								
CV	0.38	***	0.33	***	0.34	***	0.08	ns
IV	0.4	***	0.35	***	0.35	***	0.08	ns
TV	0.37	***	0.44	***	0.4	***	0.1	ns
DW	<b>0.66</b>	***	<b>0.56</b>	***	0.46	***	0.1	ns

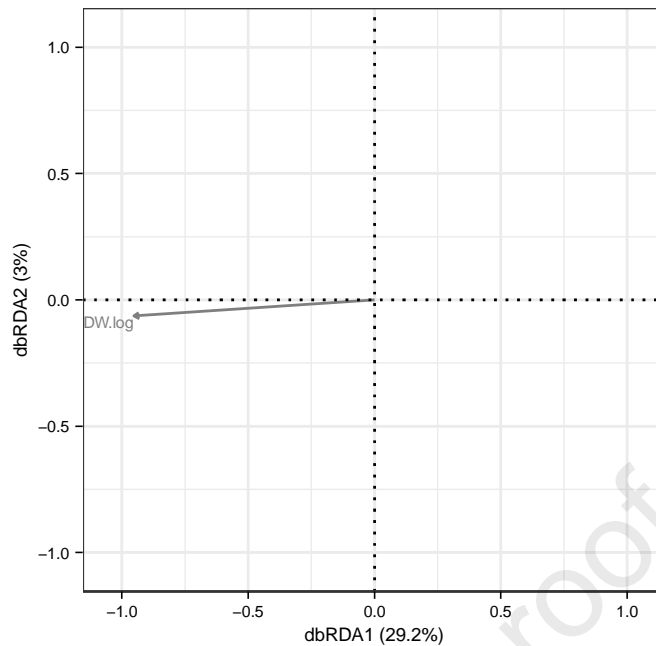
Note:

CV = Canopy volume, IV = Interstitial volume, TV = Thallus volume, DW = Biomass  
 Signif. codes: \*\*\* p < 0.001, ns p > 0.5

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390 **Fig. 8. Relationship between substrate attributes and the multivariate structure of native and**  
 391 **invasive seaweeds.** Distance-based redundancy (dbRDA) plot illustrating the substrate attribute  
 392 better explained the multivariate structure of the *E. brachycarpa* and *A. taxiformis*. DW.log =  
 393 seaweeds biomass (log + 1).

394

#### 395 4 Discussion

396 Invasive seaweeds threaten the biodiversity and socio-economics values of marine ecosystems  
 397 around the world. Currently, sea warming caused by climate change as well as human activities are  
 398 increasingly facilitating the introduction and of new invasive species increasing concerns about this  
 399 phenomenon. The Mediterranean basin provides a good example of biological invasion hosting  
 400 some of the worst invasive seaweeds able to modify normal ecosystem functioning. Although the  
 401 majority of studies have focused on the interactions (e.g. space competition) between invasive and  
 402 native species, the effects of invasive seaweeds on native fauna still deserve more attention.  
 403 Knowing how invasive seaweeds change the biodiversity of the recipient habitats can allow us to  
 404 predict bottom-up impacts of non-native macroalgae on higher trophic levels.

405 In this study, we investigated the effects of the invasive *A. taxiformis* by comparing the  
406 abundance, diversity and multivariate structure of its molluscs assemblages with those associated  
407 with the native canopy-forming *E. brachycarpa*. Our results pointed out that the invasive *A.*  
408 *taxiformis* hosted a lower diverse and less trophic structured molluscan assemblage compared to the  
409 native *E. brachycarpa*. This result is in accordance with other studies which found that invasive  
410 seaweeds exhibit a lower diverse associated fauna compared to native seaweeds (Navarro-Barranco  
411 et al., 2018; Veiga et al., 2018). In particular, we found that *A. taxiformis* hosted almost six times  
412 lower diverse molluscan assemblage compared to *E. brachycarpa*, with Gastropoda representing the  
413 dominant class and Rissoidae the main family. It is important to note, however, that although *A.*  
414 *taxiformis* hosted a less diverse molluscan assemblage, the dominant species (*Eatonina*  
415 *cossurae*) was the same as that in the native seaweed. Species of the genus *Eatonina*, where present,  
416 are largely distributed between shallow seaweeds (Rubio and Rodriguez Babio, 1995). This, led us  
417 to hypothesize that *E. cossurae* does not perceived differences (e.g. substrate) between native and  
418 invasive seaweeds, but that probably the uniform distribution of this mollusc on the two algae  
419 depends on other factors (e.g. environmental conditions).

420 Contrary to *A. taxiformis*, the native *E. brachycarpa* hosted a diverse molluscan assemblage.  
421 Gastropoda was the dominant class, followed by Bivalvia and Polyplacophora, being represented at  
422 the family level mainly by Rissoidae. These results are consistent with what observed in other  
423 studies, where *Cystoseira sensu lato* supported rich and diverse molluscan assemblage (Milazzo et  
424 al., 2000; Chemello and Milazzo, 2002; Pitacco et al., 2014; Chiarore et al., 2017, 2019; Lolas et  
425 al., 2018; Piazzzi et al., 2018; Bitlis, 2019; Mancuso et al., 2021). At the species level, most of the  
426 taxa were equal to those found in other species of *Cystoseira sensu lato* (Chemello and Milazzo,  
427 2002; Pitacco et al., 2014; Chiarore et al., 2017, 2019; Lolas et al., 2018; Piazzzi et al., 2018; Bitlis,  
428 2019; Mancuso et al., 2021), confirming the key role of these seaweeds in supporting rich and  
429 diverse molluscan assemblage.



430 Moreover, *A. taxiformis* showed a less-structured molluscan community compared to *E.*  
431 *brachycarpa*, as evidenced by the lack of some trophic guilds. The trophic guilds of *A. taxiformis*  
432 were represented by microalgae grazers, carnivores, and only one species of filter feeders.  
433 Conversely, consistent with other studies (Pitacco et al., 2014; Chiarore et al., 2017, 2019; Lolas et  
434 al., 2018; Mancuso et al., 2021) the molluscan assemblage inhabiting *E. brachycarpa* was well-  
435 structured being represented by six trophic guilds (microalgal grazers, carnivores, filter feeders,  
436 ectoparasites or carnivores on sessile prey, deposit feeders, and macroalgae grazers). Microalgal  
437 grazers was the main group on both native and invasive species. Taxa belonging to this group feed  
438 mainly on diatom film, small microalgae, crustose algae, articulated calcareous algae and  
439 filamentous algae that grow on the surface of seaweeds (Steneck and Watling, 1982). The  
440 differences in trophic structure between *E. brachycarpa* and *A. taxiformis* could be related to  
441 variation in the micro-habitats provided by native and invasive algae, which are in some extent  
442 related to the structural complexity of the algae. Thalli of *E. brachycarpa* are more strength and  
443 complex compared to *A. taxiformis*, providing a larger number of micro-habitats able to retain  
444 sediment with organic matter and promote the growth of a large number of epiphytes, sponges and  
445 sessile invertebrates (Chemello et al., 1997; Frascchetti et al., 2002; Mačić and Svirčev, 2014),  
446 increasing food supply for grazers and carnivores (e.g. *Lamellaria perspicua*, *Granulina marginata*  
447 and *Cerithiopsis minima* that were exclusive of *E. brachycarpa*). Other studies have suggested a  
448 main role of epiphytes in shaping the fauna associated with native and invasive seaweeds (Viejo,  
449 1999; Wikström and Kautsky, 2004). For example, authors have been suggested that the amount of  
450 epiphytes could explain the higher species richness found in the invasive *S. muticum* compared to  
451 native seaweeds (Viejo, 1999; Cacabelos et al., 2010). In our study, we observed that *A. taxiformis*  
452 had null or fewer epiphytes compared to *E. brachycarpa* (data not formalized). Since most of the  
453 epifauna species were microalgal grazers (that rely on microalgae for obtaining their food) we think  
454 that differences in epiphytes abundances between *A. taxiformis* and *E. brachycarpa* can be another  
455 factor that can explain the variation of the epifauna observed. We hypothesize that *A. taxiformis* can

456 provide less habitat complexity supporting less amount of epiphytes, and reducing suitable  
457 resources for many free-living epifauna species, finally generating a less structured associated  
458 molluscan assemblage compared to the native *E. brachycarpa*.

459 Differences in the molluscan assemblage diversity and multivariate structure were related to the  
460 variation of substrate attributes of the algae. According to other studies, biomass was the variable  
461 that better explained the variation of the abundance, the number of species and the multivariate  
462 structure of the molluscan assemblage (Janiak and Whitlatch, 2012; Veiga et al., 2018). The role of  
463 the algal substrate attributes in shaping their associated biota has been highlighted in many studies  
464 (Chemello and Milazzo, 2002; Pitacco et al., 2014; Veiga et al., 2014, 2018; Lolas et al., 2018;  
465 Bitlis, 2019; Chiarore et al., 2019; Poursanidis et al., 2019; Mancuso et al., 2021). Previous studies  
466 highlighted that invasive seaweeds host either low (Guerra-García et al., 2012; Navarro-Barranco et  
467 al., 2018; Rubal et al., 2018; Veiga et al., 2018) or high (Veiga et al., 2014) abundance, species  
468 richness and diversity compared to native macroalgae, with this depending on their structural  
469 complexity being respectively low or higher with respect to native seaweeds. For example,  
470 Navarro-Barranco et al. (2018) showed that *A. taxiformis* had low fractal complexity and hosted an  
471 impoverished faunal assemblage compared to the native seaweeds. Other authors found that the  
472 congeneric *A. armata* had low algal volume and showed lower abundance, species richness and  
473 diversity of its associated fauna compared to the native *Corallina elongata* (Guerra-García et al.,  
474 2012). Moreover, dry weight and fractal dimension were lower in the invasive *Sargassum*  
475 *muticum* (Yendo) Fesholt compared to native seaweeds, and have shown to play a main role in  
476 shaping the faunal assemblage associated with macroalgae (Veiga et al., 2014, 2018). According to  
477 other studies (Janiak and Whitlatch, 2012; Veiga et al., 2014; Rubal et al., 2018), our results  
478 indicated that habitat size (as biomass) was the best predictor explaining variation in abundance and  
479 richness as well as the multivariate structure of molluscs.

480 Apart from structural complexity, other indirect factors such as the presence of chemical  
481 defences can potentially explain the differences of molluscan assemblage between invasive and

482 native seaweeds. Secondary metabolites released by algae have been related to the ability of habitat-  
483 forming seaweeds to shape their associated fauna (Hay et al., 1987; Viejo, 1999; Paul et al., 2006;  
484 Cacabelos et al., 2010; Máximo et al., 2018; Gache et al., 2019). For example, secondary  
485 metabolites released by *A. taxiformis* have been responsible for the survival of fish in the post-larval  
486 stages, eventually lead to an alteration of the grazing pressure on coral reefs (Gache et al., 2019).  
487 Although our study lacks information about metabolites released by *A. taxiformis* and their possible  
488 consequences on the molluscan assemblage. We think that further studies could focus on the effects  
489 of metabolites released by *A. taxiformis* in shaping its associated molluscs, especially on the  
490 molluscan juvenile stages which may results more vulnerable. This would allow to better clarify  
491 how invasive seaweeds shape their associated molluscs.

492 In summary, our study provides evidence that the invasive *A. taxiformis* threaten the biodiversity  
493 in coastal areas, reducing the diversity of the molluscan assemblage in native stands of the habitat-  
494 forming *E. brachycarpa*. This suggests that a habitat shift from native towards invasive seaweeds  
495 could have strong negative effects decreasing local biodiversity, which may have negative impacts  
496 on the higher trophic levels (Martin et al., 1992; Heck et al., 2003), potentially triggering bottom-up  
497 effects in rocky shores habitats. Moreover, the low biomass provided from the invasive species also  
498 suggests that a large habitat shift towards invasive *A. taxiformis* would reduce the overall primary  
499 productivity of coastal areas.

500 The process of biological invasion in the marine environment is difficult to contrast because of  
501 the high environmental connectivity and dispersion capacity of species. Possible solutions have  
502 been proposed, including the eradication of small invasive populations where feasible (Secord,  
503 2003).

504 However, since the impacts of invasive species on resident diversity are highly invader- and  
505 species-specific, due the complex pathways through which bottom-up effects can take place (Maggi  
506 et al., 2015), we think that assessing the effects caused by invasive seaweeds should be posed as the  
507 first step before taking any action (Olenin et al., 2011).

508

509 **Data availability and reproducible research**

510 The repository with all the data and the scripts used to reproduce the research in this paper is

511 available at <http://dx.doi.org/10.17632/xs4t3ddgsz.1> (Mancuso, 2021)

512

513 **Author Contributions**

514 Conceptualization, C.R., M.M. and D.R.; Methodology, C.R. and M.M.; Investigation, D.R.;

515 Formal Analysis, M.F.P.; Data curation, M.F.P.; Writing – Original Draft Preparation, M.F.P.;

516 Writing – Review &amp; Editing, M.F.P., M.M., C.R.; Visualization, M.F.P.; Validation, M.F.P.;

517 Supervision, C.R.; Project Administration, C.R.; Funding Acquisition, C.R.; Resources, C.R.

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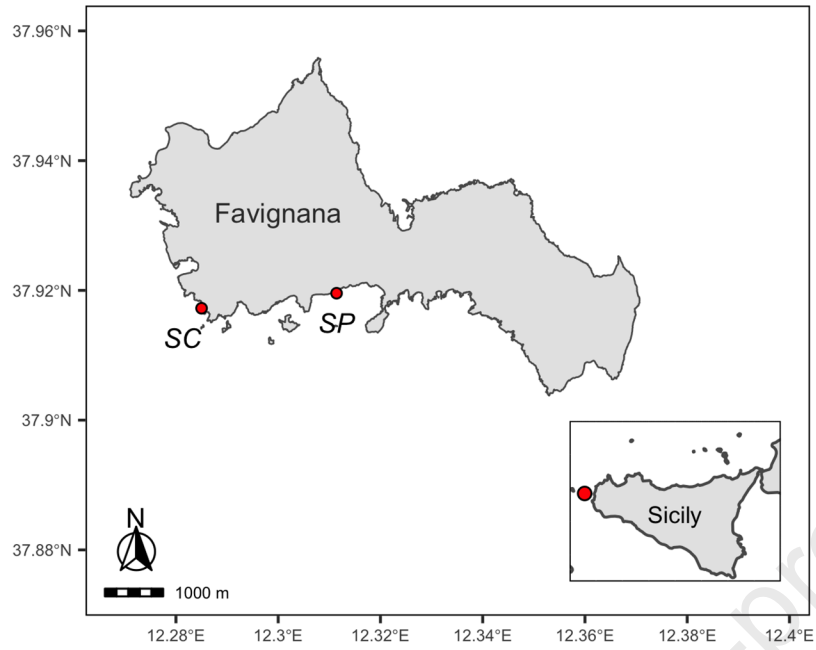
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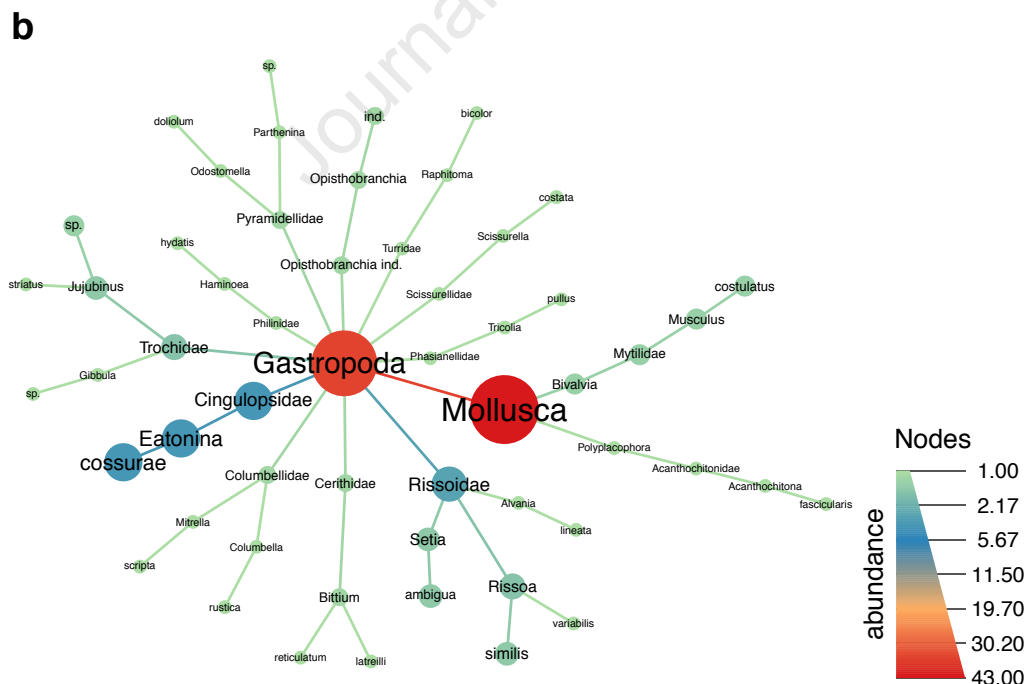
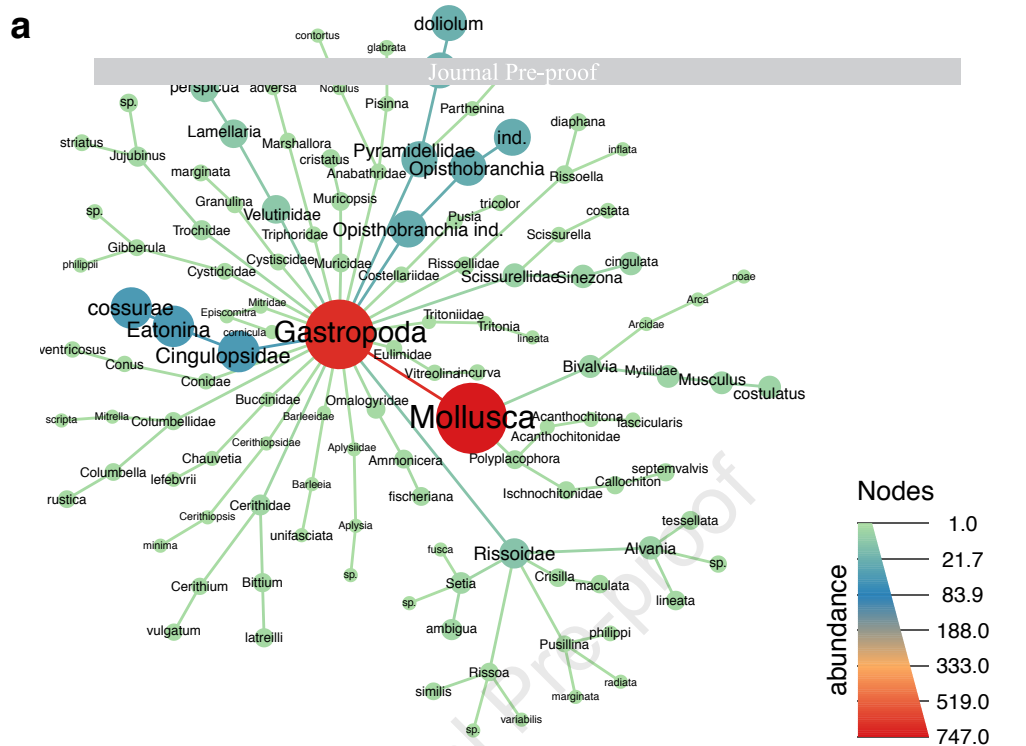
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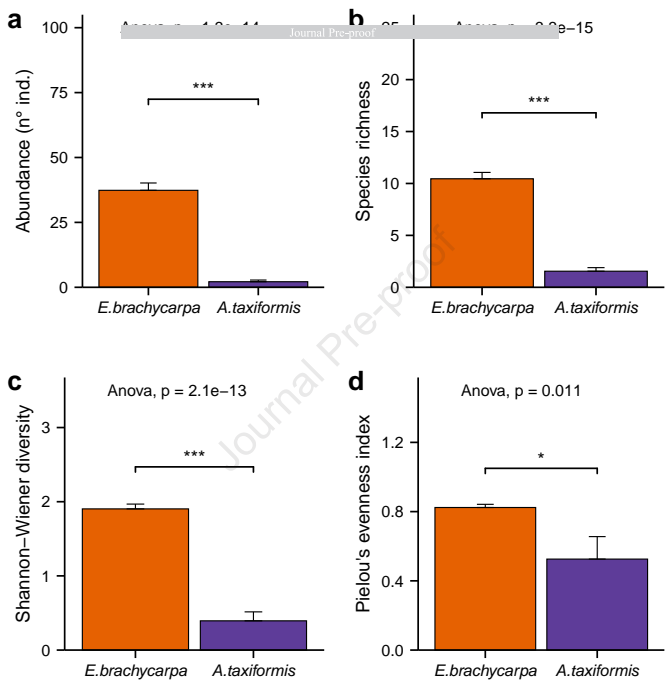
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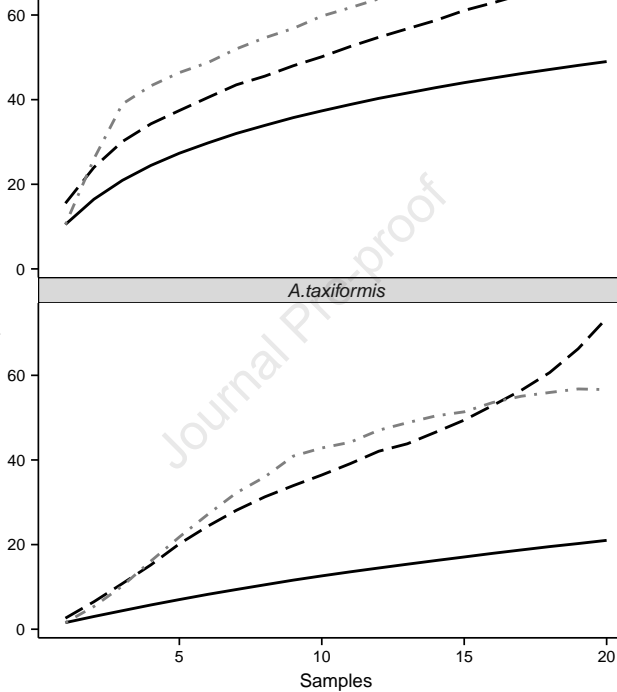






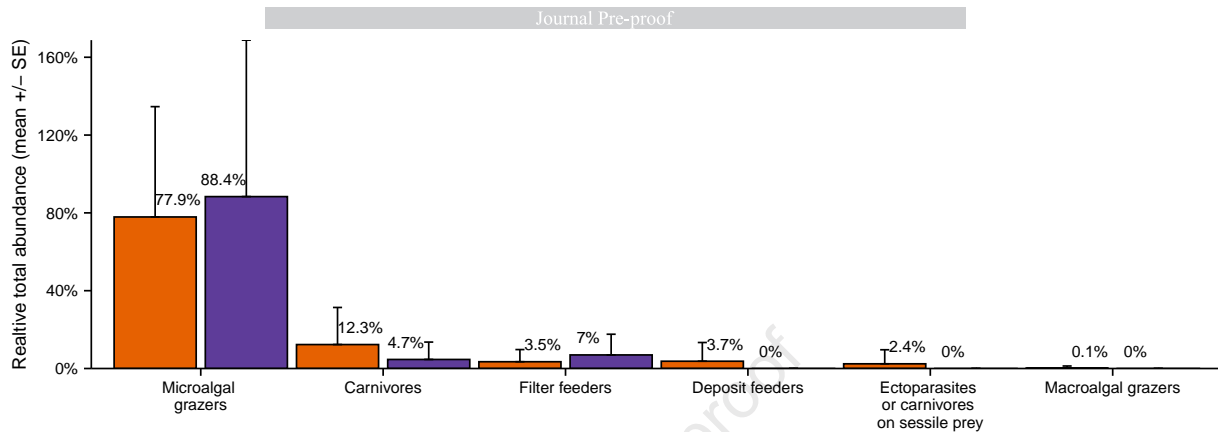
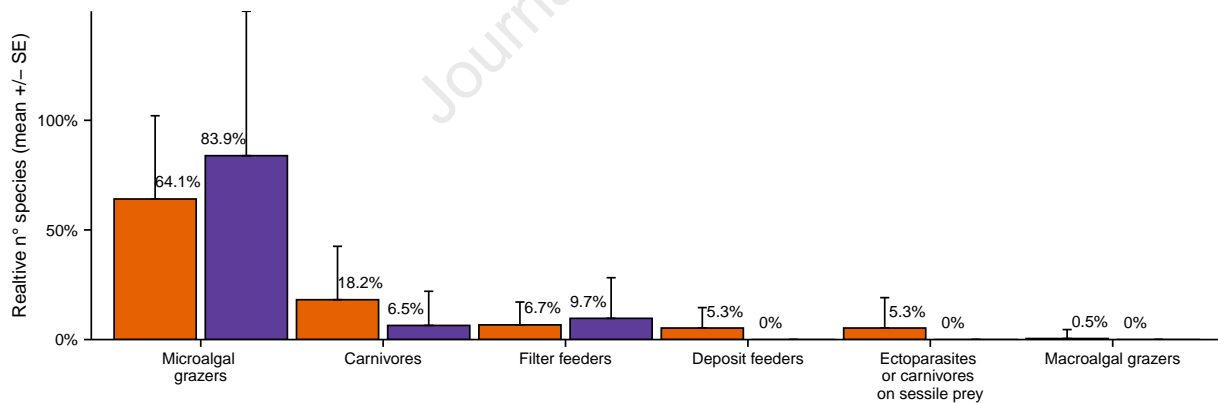
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Species count

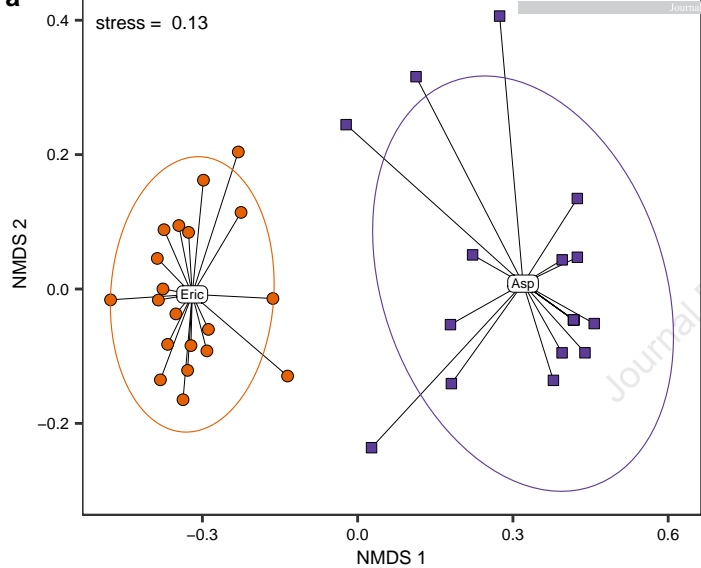


*A. taxiformis*

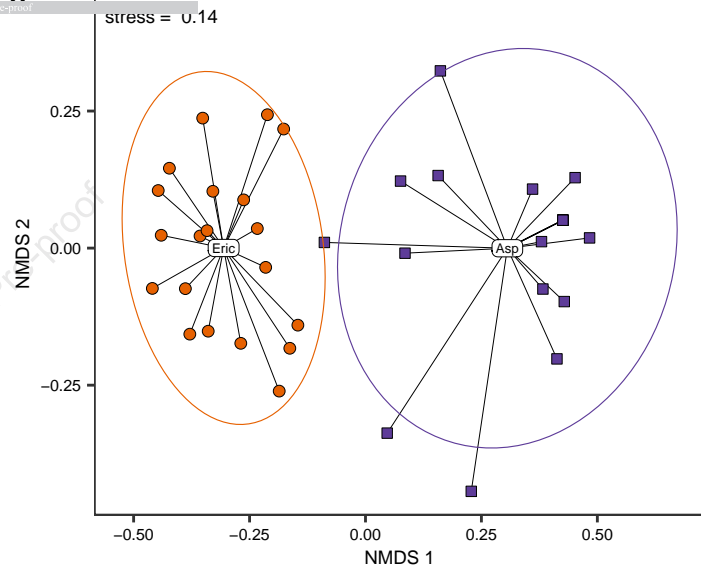
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**a****b**

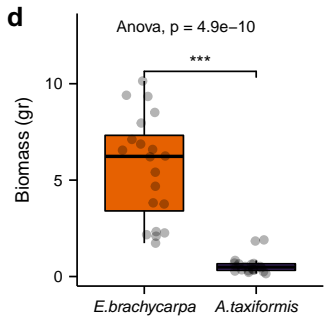
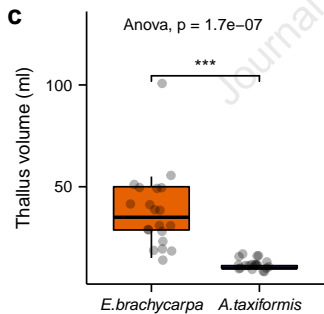
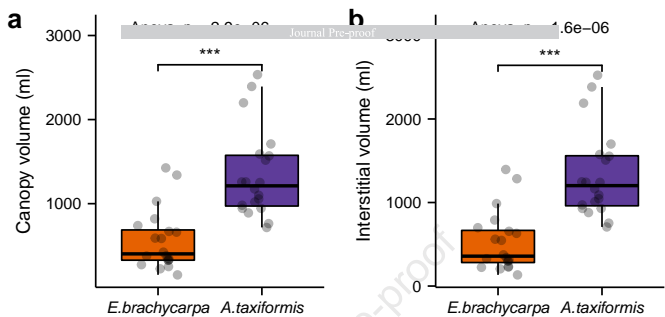
*E. brachycarpa*
 *A. taxiformis*

**a****b**

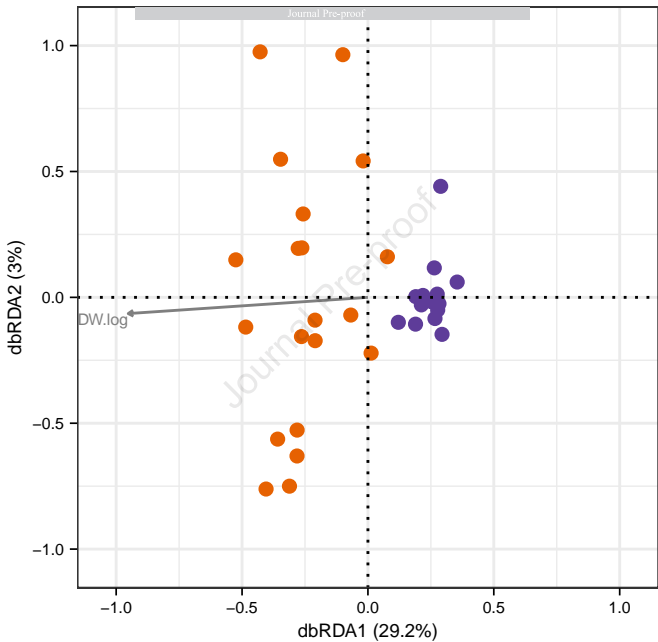
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habitat ● *E.brachycarpa* ■ *A.taxiformis*



Signif. codes: \*\*\*:  $p <= 0.001$



**Highlights:**

- *A. taxiformis* hosted lower diverse molluscan assemblage compared to *E. brachycarpa*
- Molluscan abundance and diversity changed with variation in algal biomass
- *A. taxiformis* undermine the biodiversity and the services provided by *E. brachycarpa*



**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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