

The Invasive Seaweed *Asparagopsis Taxiformis* Erodes the Primary Productivity and Biodiversity of Native Algal Forests in the Mediterranean Sea

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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 *Ericaria brachycarpa* to the invasive *Asparagopsis taxiformis* habitat at 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 *E. brachycarpa* and *A. taxiformis*. Results showed that the biomass of primary producers is reduced by 90% in the *A. taxiformis* invaded habitat compared to the *E. brachycarpa* 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 *E. brachycarpa* to the invasive *A. taxiformis*. Seaweed biomass was the structural attribute better explaining the variation of epifaunal abundance, species richness and diversity. Overall, our results suggest that the shift from *E. brachycarpa* to *A. taxiformis* habitat would drastically erode the biomass of primary producers and the associated biodiversity. We hypothesize that a complete shift from native to invasive seaweeds can ultimately lead to bottom-up effects in rocky shore habitats, with negative consequences for the ecosystem structure, functioning and the services provided.

Introduction

Invasive species are globally recognized among the main drivers of habitat shift in

Invasive species are globally recognized among the main drivers of habitat shift in both terrestrial and marine ecosystems (Gallardo et al., 2016; Mačić et al., 2018). In marine environments, decades of human activities related to global aquatic trade have enabled the dispersion of invasive species among distant geographic areas worldwide (Bax et al., 2003; Williams and Smith, 2007; Molnar et al., 2008; Servello et al., 2019). In addition, the rise in seawater temperature caused by global warming have allowed non-native species to cross environmental and geographical barriers facilitating their expansion and in turn eroding indigenous resistance (Occhipinti-Ambrogi and Galil, 2010; Lo Brutto et al., 2019). Concerns over ecological and social-economic consequences have led researches to investigate the effects of invasive species on many marine ecosystems around the world.

Seaweeds are a significant component of marine non-native and invasive species (227 taxa globally), with some of them being responsible of drastic habitat shifts (Williams and Smith, 2007). Studies have highlighted how invasive seaweeds can negatively impact the recipient habitats by reducing biomass of primary producers, biodiversity and nutrient flows, compromising ecosystems functioning (Boudouresque et al., 2005; Streftaris and Zenetos, 2006; Thomsen et al., 2014; Maggi et al., 2015; Ramsay-Newton et al., 2017; Geburzi and McCarthy, 2018). Interestingly, the effects of non-native seaweeds seem to change depending on the complexity of the recipient habitat (Thomsen et al., 2014). In less structured habitats

(e.g. soft bottoms) the introduction of non-native seaweeds enhances structural complexity that may favor the increase of biodiversity and food web length (Dijkstra et al., 2017). Conversely, the introduction in well-structured habitats (e.g. seagrass meadows, algal canopies) may alter the diversity and functioning, depending on the structural features of the recipient habitat (Engelen et al., 2013; Veiga et al., 2014, 2018). It is interesting to observe that the same invasive species can determine opposite effects. For example, Veiga et al. (2018) found that the invasive *Sargassum muticum* (Yendo) Fensholt hosted a low diverse epifaunal assemblage compared to the native *Sargassum flavifolium* Kützinger. These results were in contrast with previous studies which suggested only weak to no impact of *S. muticum* on native faunal diversity (Wernberg et al., 2004; Buschbaum et al., 2006; Gestoso et al., 2010; Engelen et al., 2013; Veiga et al., 2014; Rubal et al., 2018).

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, 2018; Maggi et al., 2015; Dijkstra et al., 2017; 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). As mentioned before, studies comparing the epifaunal diversity between invasive and native seaweeds revealed that, when invasive species are structurally less complex than the 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 to the 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 structural features. However, other studies have shown that native and invasive seaweeds with similar morphologies can host either similar (Suárez-Jiménez et al., 2017) or different epifaunal diversity (Navarro-Barranco et al., 2019). Overall, these contrasting evidences suggest that apart from seaweed morphology, other factors can be involved in structuring the associated assemblages.

In the last decades, the Mediterranean basin has witnessed the increase in the number of non-native and invasive seaweeds with consequent modification of biodiversity and ecosystem functioning of coastal areas (Ribera Siguan, 2002; Streftaris et al., 2005; Streftaris and Zenetos, 2006; Piazzzi and Balata, 2009; Musco et al., 2014; Bulleri et al., 2016; Corriero et al., 2016; Giangrande et al., 2020). In particular, *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon is listed among the 100 worst invasive species of this basin (Streftaris and Zenetos, 2006). The earliest reports of its presence in the Mediterranean Sea date back to 1798–1801 in Alexandria (Egypt) as a result of trading operations and the opening of the Suez Canal (Verlaque et al., 2015). It was first recorded along the Italian coast on the western shore of Sicily, close to the city of Trapani, in May 2000 (Barone et al., 2003). While *A. taxiformis* has been suspected to produce harmful effects on native habitats (Barone et al., 2003), as far as we know, only one

to this species to that of the native *Halopteris scoparia* (Linnaeus) Sauvageau (Navarro-Barranco et al., 2018). The results of this last research indicate that *A. taxiformis* hosted less diverse epifaunal assemblages compared to the native algae (Navarro-Barranco et al., 2018).

Along the Italian coast, gametophytes of *A. taxiformis* can colonize coastal areas dominated by habitat-forming seaweeds, mainly belonging to the genus *Cystoseira* - recently divided into three genera *Cystoseira*, *Gongolaria* and *Ericaria* and hereafter referred as to *Cystoseira sensu lato* to include all the three genera (Orellana et al., 2019; Molinari Nova and Gury, 2020). *Cystoseira sensu lato* species are important ecological engineers, greatly increasing the habitat surface, complexity and productivity in coastal ecosystems from the infra-littoral zone to the upper circalittoral zone. (Giaccone et al., 1994; Bulleri et al., 2002; Falace and Bressan, 2006; Ballesteros et al., 2009; Mancuso et al., 2021). By creating shelter, *Cystoseira sensu lato* species improve the biodiversity of their related assemblages, leading to the development of well-structured food webs (Schiel and Foster, 2006; Cheminée et al., 2013; Mineur et al., 2015; Mancuso et al., 2021). According to the European Water Framework Directive (2000/60), they are also considered indicators of good water and environment quality (European Commission, 2000).

Decline or loss of *Cystoseira sensu lato* populations have been recorded from several rocky coasts, especially close to urban areas as a result of anthropogenic impacts and climate-change (Benedetti-Cecchi et al., 2001; Thibaut et al., 2005; Arevalo et al., 2007; Mangialajo et al., 2008; Strain et al., 2014; Mineur et al., 2015; Mancuso et al., 2018; Blanfuné et al., 2019). The introduction of invasive algae may further threaten these fragile habitats by leading their shift towards less diverse and less organised systems (Navarro-Barranco et al., 2018).

In this study, we evaluated the consequences of the habitat shift from the native *Ericaria brachycarpa* (J.Agardh) Orellana & Sansón to the invasive *A. taxiformis* analyzing the epifaunal community associated with three plausible alternative states of the transition between native to invasive seaweeds habitats. In particular, we characterized and compared the biomass and the diversity (richness, evenness, structure and composition) of the epifauna associated with the fronds of homogenous and mixed stands of *E. brachycarpa* and *A. taxiformis*. Moreover, we explored the variation of the epifaunal diversity in relation to the structural features of the two algae (dry weight, thallus volume, canopy volume and interstitial volume).

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Materials And Methods

Study area and algal species characteristics

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

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

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

Asparagopsis taxiformis is a red alga (Bonnemaisoniales) common in the tropics and subtropics across the globe. The species experiences a heteromorphic life cycle, with an erect gametophyte alternating with a filamentous sporophyte known to as *Falkenbergia hillebrandii* (Bornet) Falkenberg (Andreakis et al., 2004; Ní Chualáin et al., 2004). The gametophytes are characterized by sparsely branched, creeping stolons and erect shoots from which several side branches grow in all directions. The latter ramifies over and over again giving the thallus a plumose appearance. At the study area, *A. taxiformis* develops in the upper sublittoral zone of the rocky substrate or as epiphyte of other algal species. The gametophytes are present during all seasons with a maximum occurrence in spring (Barone et al., 2013).

Samples were collected by scuba diving at a depth of 5–7 m. For each site (hereafter referred as habitat), two areas (5 x 5 m) were haphazardly selected. For each area, 10 thalli of *E. brachycarpa* from homogenous stands (100% algal coverage), 10 thalli of *E. brachycarpa* from mixed stands and 10 gametophytes of *A. taxiformis* from homogenous stands (100% algal coverage) were collected (n = 20 per habitat). Underwater, each thallus and the associated epifauna were enveloped with a plastic bag, then the alga was detached from the substrate and the plastic bag was immediately closed to prevent the escape of vagile fauna. After collection, each sample was carefully drained from seawater in order to prevent escape of small epifauna and stored at -20°C until laboratory analysis. In the laboratory, each thallus of *E. brachycarpa* and gametophytes of *A. taxiformis* were transferred into buckets filled with tap water and shaken vigorously, allowing the associated fauna to detach from the algae. Then, the water was sieved through a 1 mm mesh. After sorting, molluscs, amphipods and annelids were stored in 70% seawater ethanol solution and subsequently counted and identified to species, or nearest possible taxonomic level. Taxonomy and nomenclature were updated according to the World Register of Marine Species database (T Horton et al., 2021).

Seaweeds structural attributes

For each thallus of *E. brachycarpa* and gametophyte of *A. taxiformis* collected, we measured 4 structural features (thallus volume, canopy volume, interstitial volume, and biomass), to explore their relationships with the diversity indices calculated for the epifaunal assemblages. Thallus volume (measured as the variation of volume, in ml, after the immersion of a thallus into a graduate cylinder filled with seawater); canopy volume (the volume, in ml, created by the overall dimension of a thallus submerged in seawater) and interstitial volume (the volume, in ml, of water among the fronds of the alga) were estimated according to Hacker and Steneck (1990). The canopy volume was defined as the volume of a theoretical cylinder ($CV = \pi \times r^2 \times h$), where $\pi = 3.14$, h is the length of thallus from the base to the apical portion of the frond, including epiphytes, and r is the radius calculated as averaged measure of the radius of the thallus measured with a ruler (+/- 1 mm) at the apical, median and basal parts. The interstitial volume (IV) was obtained by subtracting the thallus volume (TV), and the axis volume (caV , estimate as the volume of cylinder obtained measuring the height and the radius of the perennial axis) from the canopy volume $CV(IV = (CV - TV) - caV)$.

Finally, the biomass of the macroalgae was calculated as dry weight (DW , gr) after drying in stove at 60°C for 48 h (Stein-Taylor et al., 1985). Biomass was used as a proxy of primary production of each habitat.

Data analysis

For each epifaunal species, we calculated total abundance (N), Frequency (F%; the percentage of samples in which a particular species is present) and Dominance index (D%; the percentage of the rate between the percentage of individuals of a particular species and the total number of individuals within the sample) (Magurran, 1988). The epifaunal assemblages of each habitat were characterized according to total abundance of individuals (N), total number of species (S), Shannon-Wiener diversity index (H') and

Pielou's Evenness index (J). A two-way analysis of variance (ANOVA) was used to test differences in the epifaunal indices (N, S, H', J) between habitats (fixed and orthogonal with 3 levels: *E. brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*) and area (random and nested within habitat with 2 levels: area 1 and area 2). Cochran's test was used to check for the homogeneity of variances (Underwood 1997). Tukey's HSD procedure was used to separate means (at $\alpha = 0.05$) following significant effects in the ANOVAs (Underwood, 1996). The hierarchical structure of the taxonomic classifications of the epifaunal assemblages of *E. brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis* was visualized using the "heat_tree" function in the "Metacoder" R- package (Foster et al., 2017).

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

Differences in the epifaunal community structure (which takes into account species identity and relative abundance) and composition (presence/absence, which only takes into account species identity) among habitats and areas were assessed by Permutational Multivariate Analysis of Variance (PERMANOVA). The analyses were based on a Bray-Curtis distance matrix of square-root transformed epifaunal abundances (structure) and on Jaccard distances matrix of presence/absence data (composition) using 9999 permutations. A principal coordinate analysis (PCoA) plot was generated to visualize the variation of the epifaunal community structure (based on a Bray-Curtis distance matrix) and composition (based on Jaccard distance matrix).

Differences in each of the structural attributes (*CV*, *IV*, *TV*, *DW*) among habitats and areas were analyzed by two-way ANOVAs according to the above mentioned design. Cochran's test was used to check for the homogeneity of variances (Underwood, 1996).

Linear regression (LM) analysis was used to test which algal structural attributes explained better the variation of total abundance (N), species richness (S), Shannon-Wiener diversity (H') and Pielou's Evenness (J) of the epifaunal assemblages. In addition, a distance-based redundancy analysis (dbRDA, Legendre and Anderson, 1999) was used to investigate the relationship between structural attributes and the epifaunal multivariate structure. Since dbRDA is susceptible to multicollinearity (i.e. high correlation between environmental variables), draftsman plots were used to verify skewness or identify clear correlations between structural attributes. A $\log(x + 1)$ transformation was used to correct right-skewness of thallus volume (*TV*) and biomass (*DW*). Moreover, due to the high correlation between canopy volume (*CV*) and interstitial volume (*IV*) we removed *CV* from the subsequent analyses. Then, the structural attributes were normalised using a z-score transformation due to their varying measurement scales. Finally, forward selection was used to identify the structural properties that mostly contributed to the heterogeneity in the multivariate structure of the epifaunal assemblages.

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

Results

Epifauna

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

Total abundance (**N**) and 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'**) was similar between *E. brachycarpa* and *E. brachycarpa* in mixed stands, and significantly higher compared to *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).

PERMANOVA showed that the structure and composition of the epifaunal assemblages differed significantly among habitats (Table S4). PERMDISP analysis revealed a high dispersion of samples within habitats, especially for *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. 4). Notwithstanding this high dispersion, the epifaunal assemblages of the three habitats were clearly separated as showed by the PCoA ordination plot (Fig. 4). The proportion of variance explained by the first two axes was 62.8% for structure and 45.6% for composition. The first axis accounted for the larger part of the variance (structure = 49.5% and composition = 36.1%) and highlighted a shift, in both structure and composition, from *E. brachycarpa* to *A. taxiformis*, with *E. brachycarpa* in mixed stands placed between the two homogeneous stands of native and invasive seaweeds (Fig. 4). The second axis explained lower variation (structure = 13.3% and composition = 9.5%) and separated *E. brachycarpa* and *A. taxiformis* from *E. brachycarpa* in mixed stands (Fig. 4).

SIMPER analysis revealed that 28 taxa contributed 70% to the dissimilarity between *E. brachycarpa* and *A. taxiformis*; 37 taxa contributed 70% to the dissimilarity between *E. brachycarpa* and *E. brachycarpa* in mixed stands; 12 taxa contributed 70% to the dissimilarity between *A. taxiformis* and *E. brachycarpa* in mixed stands.

brachycarpa (Table S5). Most of the species contributing to the dissimilarities belonged to amphipods. The polychaete *Amphiglena mediterranea* (Leydig, 1851) was the species mostly contributing to the differences observed between both *E. brachycarpa* and *A. taxiformis* and between *E. brachycarpa* and *E. brachycarpa* in mixed stands contributing respectively to 8% and 6% of the observed differences. The amphipod *Apherusa alacris* Krapp-Schickel, 1969 was the species mostly contributing to the differences (7%) between *E. brachycarpa* in mixed stands and *A. taxiformis*. In addition, gastropod *Obtusella macilenta* (Monterosato, 1880) was the species that contributed consistently (higher $\delta_i/SD(\delta_i)$ values) to the difference between *E. brachycarpa* and *A. taxiformis* (Table S5), while the amphipod *Stenothoe monoculoides* (Montagu, 1813) and the gastropod *Eatonina cossurae* (Calcara, 1841) were the species that contributed consistently to the differences between *E. brachycarpa* in mixed stands and *E. brachycarpa*, and between *E. brachycarpa* in mixed stands and *A. taxiformis* (Table S5). The polychaete *S. prolifera* was among the first 5 species contributing to the differences between each couple of habitats (Table S5).

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

Seaweeds structural attributes and relationships with the epifaunal assemblages.

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

Linear regression analysis revealed that biomass (DW) was the attribute that explained better the variation of abundance ($R^2_N = 0.51$), species richness ($R^2_S = 0.61$) and Shannon-Wiener diversity ($R^2_{H'} = 0.54$) of the epifaunal assemblages (Table S8). The variance explained by algal biomass increased if we considered a quadratic relationship between those variables (Fig. 6). Otherwise, canopy volume (CV) interstitial volume (IV) and thallus volume (TV) explained less variation (although highly significant $p < 0.001$) of the epifaunal attributes (R -squared < 0.5 , Table S8). The analysis conducted separately on the three dominant epifaunal groups (molluscs, annelids and amphipods) revealed similar results, albeit with some differences. In fact, the variation of abundance, species richness and diversity explained by algal biomass decreased in both annelids ($R^2_N = 0.35$, $R^2_S = 0.51$, $R^2_{H'} = 0.49$) and amphipods ($R^2_N = 0.23$, $R^2_S = 0.43$, $R^2_{H'} = 0.31$) although resulting the most related explanatory variable for both groups, while molluscs revealed patterns of variation similar to the whole assemblage ($R^2_N = 0.5$, $R^2_S = 0.53$, $R^2_{H'} = 0.48$) (Table S8). Moreover, annelids showed a weaker and not significant relationship with the canopy and interstitial volumes in respect to amphipods and molluscs (Table S8).

Biomass (DW) was also the structural attribute selected for constrained db-RDA, explaining 24.7% of the variation of the structure of the epifaunal assemblages (Table S9). The first two axes of the dbRDA plot explained the 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).

Discussion

The biodiversity and the socio-economic value of marine ecosystems are threatened by biological invasions around the world (Bax et al., 2003; Molnar et al., 2008). Understanding how invasive seaweeds modify the functioning of recipient ecosystems may allow to better understand large scale effects on native rocky shore habitats. Here we investigated the effects of the invasive *A. taxiformis* on the native *E. brachycarpa* by comparing the epifaunal assemblage associated with to three alternative states of the transition between native and invasive seaweeds, homogenous and mixed stands of the two seaweeds. Our results showed that *A. taxiformis* can determine drastic shift in the epifaunal assemblages associated with the native *E. brachycarpa*, leading to the reduction of abundance, number of species and diversity. In particular, *A. taxiformis* hosted almost 6 times less epifaunal individuals compared to *E. brachycarpa* in mixed stands, and 10 folds less individuals compared to homogenous stands of *E. brachycarpa*. Also, the number of epifaunal species was more than 4 folds lower in the invasive compared to the native habitat, while diversity (Shannon-Wiener) reduced by a half. These results confirm the negative role played by invasive seaweeds in invaded habitats (Maggi et al., 2015), with invasive seaweeds exhibiting in general a less diverse epifaunal component compared to native seaweeds (Guerra-García et al., 2012; Janiak and Whitlatch, 2012; Navarro-Barranco et al., 2018; Veiga et al., 2018).

We found that variation in diversity and multivariate structure of the epifaunal assemblages was related to changes in algal structural features. In particular, biomass was the variable better explaining the variation of abundance, number of species and the multivariate structure of the epifaunal assemblages. The role of the macroalgal complexity in shaping the associated biota has been highlighted in several studies, with complex algae hosting larger abundance and diversity of epifauna than simpler ones (Chemello and Milazzo, 2002; Pitacco et al., 2014; Veiga et al., 2014, 2018; Lolas et al., 2018; Bitlis, 2019; Chiarore et al., 2019; Poursanidis et al., 2019; Mancuso, 2020). In general, studies highlighted that invasive seaweeds host lower (Guerra-García et al., 2012; Navarro-Barranco et al., 2018; Rubal et al., 2018; Veiga et al., 2018) or higher (Veiga et al., 2014) epifaunal abundance, species richness and diversity, depending on whether their structural complexity is respectively lower or higher compared to the native seaweeds. Navarro-Barranco et al. (2018) showed that *A. taxiformis* had low fractal complexity and hosted an impoverished faunal assemblage compared to the native seaweeds. Guerra-García et al., (2012) found that *A. armata* had low algal volume and showed lower abundance, species richness and diversity of associated isopods fauna compared to the native *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders. Moreover, lower dry weight and fractal dimension in the invasive *S. muticum* compared to native seaweeds have shown to play a major role in shaping the associated faunal assemblages (Veiga et al., 2014, 2018). Likewise other studies (Janiak and Whitlatch, 2012; Veiga et al., 2018) quantity of habitat (biomass) was the best

predictor variable explaining variation in terms of abundance, species richness as well as multivariate structure of the associated epifauna.

Interestingly, our results highlight that *A. taxiformis* affected each component (molluscs, annelids and amphipods) of the epifaunal assemblages in the same way. This is in contrast with other studies that showed different responses among epifaunal components associated to invasive seaweeds (Schmidt and Scheibling, 2006; Gestoso et al., 2010; Guerra-García et al., 2012; Bedini et al., 2014; Veiga et al., 2018; Navarro-Barranco et al., 2019). For example, species richness, Shannon diversity and total abundance of isopods were significantly lower in *A. armata* compared to native algae (Guerra-García et al., 2012). Bedini et al. (2014) found that the invasive *Lophocladia lallemandii* (Montagne) F. Schmitz hosted a higher abundance of amphipods, isopods and polychaetes, while native habitats harbored a greater abundance of molluscs and decapods. Bivalves associated to the invasive *S. muticum* were more abundant compared to native seaweeds, which in contrast hosted more gastropods (Veiga et al., 2018), and Gestoso et al. (2010) found that isopods and amphipods were more abundant in *S. muticum* than in native seaweeds. Moreover, the invasive *Codium fragile* subsp. *fragile* (Suringar) Hariot supported higher densities of nematodes, bivalves and specialist herbivores compared to fronds of the native kelp, that in contrast supported greater densities of gastropods and asteroids (Schmidt and Scheibling, 2006). Other authors revealed that differences among invasive and native seaweeds in single components of epifaunal assemblages changed depending on the site and the identity of the algal species (Navarro-Barranco et al., 2019). The fact that in our study, the *A. taxiformis* habitat showed lower abundance, species richness and diversity values for all the epifaunal organisms, regardless of the groups investigated, led us to hypothesize that a potential shift from the native (i.e. *E. brachycarpa*) to the invasive (i.e. *A. taxiformis*) habitat could cause large negative cascade effects within the benthic ecosystem.

Although differences in the epifaunal assemblages among native and invasive seaweeds have been already largely explored, our results also suggest that the presence of *A. taxiformis* affects the epifaunal assemblages associated to *E. brachycarpa* in mixed stands. This result could be explained by other attributes that differed between native and invasive seaweeds, such as the amount of epiphytes and/or the presence of chemical defenses, that have been related to the ability of seaweeds to shape their associated fauna (Hay et al., 1987; Viejo, 1999; Paul et al., 2006; Cacabelos et al., 2010; Máximo et al., 2018; Gache et al., 2019). Invasive seaweeds can release secondary metabolites (e.g. halogenated compounds) able to act as deterrents against epiphytes and herbivores (Paul et al., 2006; Cacabelos et al., 2010; Vega Fernández et al., 2019). Secondary metabolites released by *A. taxiformis* can affect the survival of fish in the post-larval stages, eventually leading to alteration of the grazing pressure on the surrounding habitat (Máximo et al., 2018; Gache et al., 2019). Other studies suggest that invasive seaweeds can alter the trophic web by changing the composition of epiphytes which reduces suitable habitat for many epifaunal species (Viejo, 1999; Wikström and Kautsky, 2004). Several authors suggested that the amount of epiphytes could explain the higher species richness found in the invasive *S. muticum* compared to native seaweeds (Viejo, 1999; Cacabelos et al., 2010). In our study, *A. taxiformis* had no or Loading [MathJax]/jax/output/CommonHTML/fonts/TeX/fontdata.js al observation). As epifauna is mostly

represented by microalgae grazers, we can hypothesize that differences in the abundance of epiphytes between *A. taxiformis* and *E. brachycarpa* could contribute to the variation in epifaunal assemblages observed in this study. It is therefore arguable that further studies analyzing the direct and indirect role of epiphyte abundance and secondary metabolites released by *A. taxiformis* in structuring its associated epifauna would allow to better clarify the effects of this seaweed on the recipient habitats.

Moreover, as suggested by other authors (Navarro-Barranco et al., 2019), landscape features could be another key aspect explaining the effect of *A. taxiformis* on *E. brachycarpa* associated assemblages in mixed stands. In fact, the presence of invasive seaweeds may contribute to the fragmentation of native habitats, reducing the patch size of native seaweeds, and at the same time increasing their isolation (Roberts and Poore, 2006; Lanham et al., 2015). It has been observed that the reduction of patch size of *Cystoseira sensu lato* habitats reduces the diversity of associated faunal assemblages (Mancuso et al., 2021). Thus, we can hypothesize that the presence of *A. taxiformis* in mixed stands can act as a physical barrier for the dispersal of vagile fauna, reducing connectivity at small scale and ultimately eroding the diversity of native habitats (Lanham et al., 2015).

In summary, our study suggests that shifting from native to invasive habitats may pose serious threat to biodiversity in coastal areas (Martin et al., 1992; Heck et al., 2003), potentially leading to bottom-up effects in rocky shore ecosystems. In addition, the low biomass supplied by the herein studied invasive species suggests that the shift from native canopy-forming algae to the invasive *A. taxiformis* habitat would also drastically reduce the biomass of primary producers of affected coastal areas. Predicting the ecological effects of invasive seaweeds is one of the main goals in the study of biological invasions. Previous research have highlighted a context-dependent effects of invasive seaweeds, with larger impact caused by invasive species exerting a different functional role compared to the native habitat forming species (Ricciardi and Atkinson, 2004; Ricciardi et al., 2013; Navarro-Barranco et al., 2019). Our results not only remark the negative effect of *A. taxiformis* of *E. brachycarpa* habitats, but also suggest that invasive species are able to affect native habitats in a transitional phase (mixed stands) of the habitat shift, facilitating fragmentation and isolation. Further studies, aimed to understand the effects of the habitat shift from native to invasive seaweeds should include multiple transitional phases (different percentage coverage), as well as the analysis of changes in the trophic structure of the associated epifaunal assemblages.

Declarations

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Conflicts of interest/Competing interests

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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.

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

Code availability: All the R scripts used to reproduce the research in this paper are available at <http://dx.doi.org/10.17632/h3r8ygnjfd.1>[2]

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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Figures

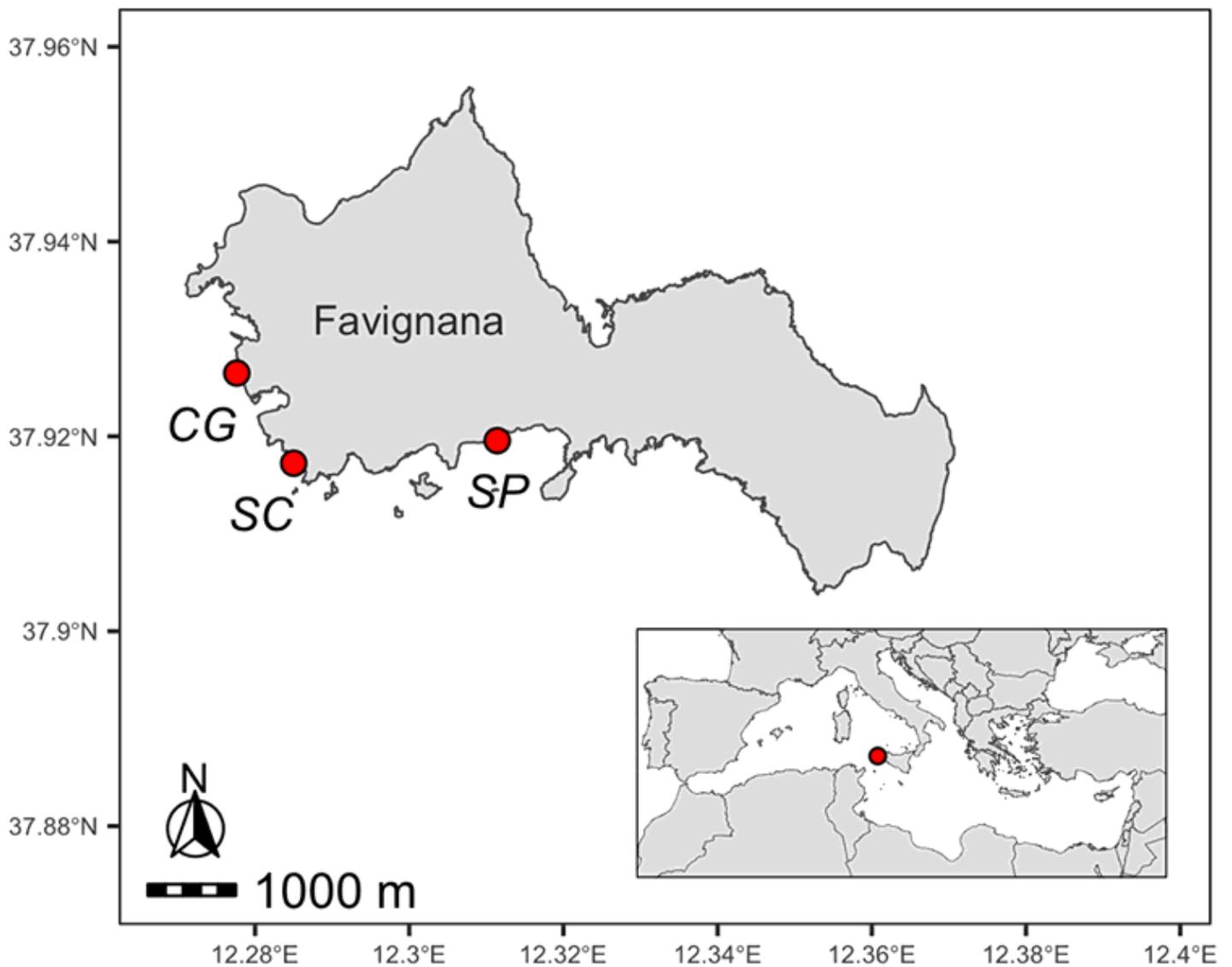


Figure 1

Location of the three study sites (red dots) along the rocky-shore of Favignana Island (MPA), Trapani, Sicily, Italy. SC = Scoglio Corrente, SP = Scoglio Palumbo, CG = Cala Grande. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

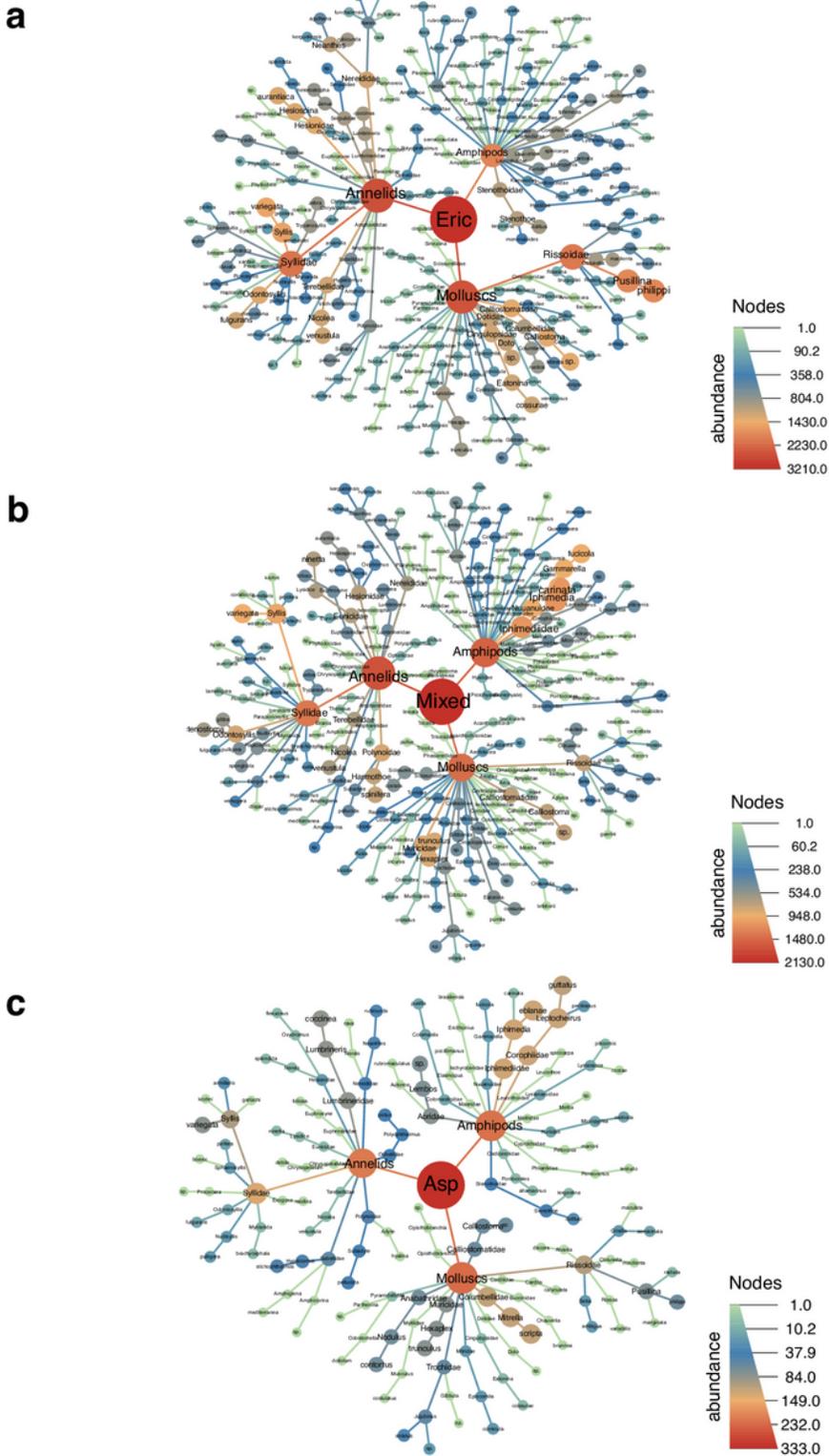


Figure 2

Differences in the epifaunal assemblages among habitats. Heat trees showing 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).

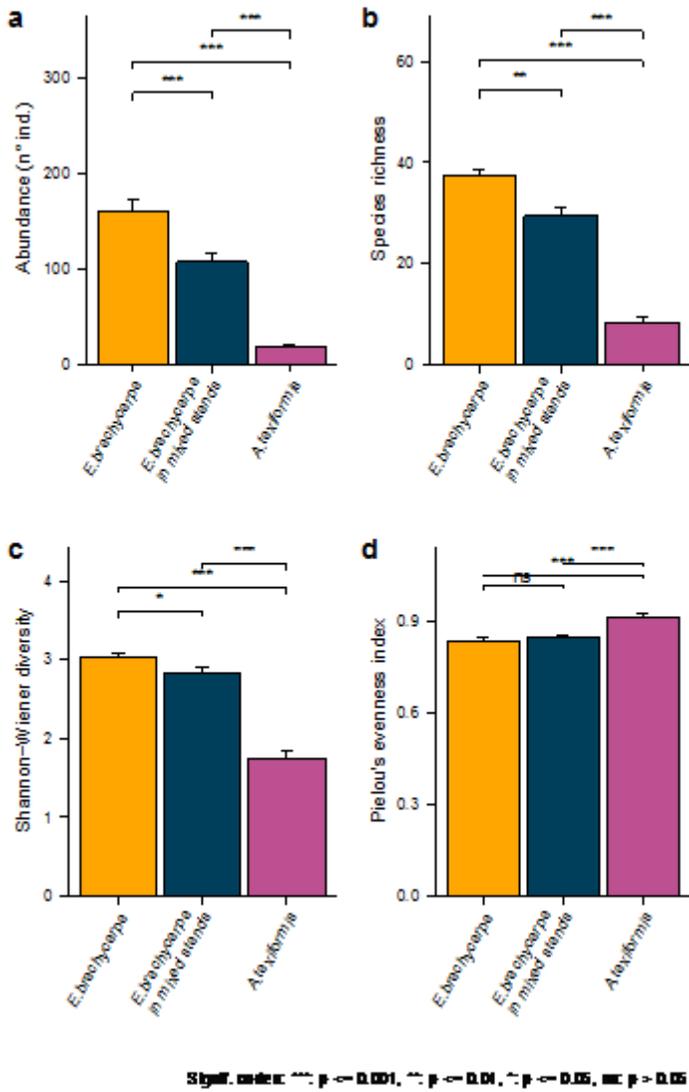


Figure 3

Comparison of the alpha diversity indices among habitats. Abundance (a), species richness (b), Shannon-Wiener diversity (c), and Pielou's evenness index (d) of the epifaunal assemblage associated with *E. brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*. Bar plots show mean +/- 1 standard error (n = 20). See Table S3 for further details.

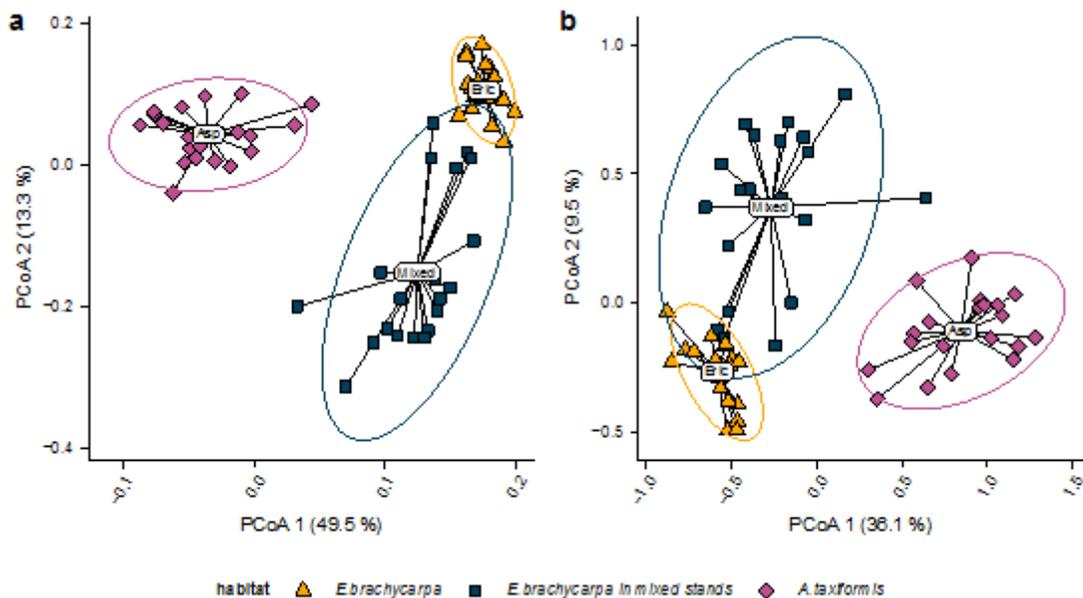


Figure 4

Structure (a) and composition (b) of the epifaunal assemblages associated with the three habitats. Principal coordinate analysis plot (PCoA) based on a Bray-Curtis distance matrix of square-root transformed relative abundances (structure) or on Jaccard distances matrix of presence/absence data (composition). Circles show the 90 % confidence of interval for each seaweed.

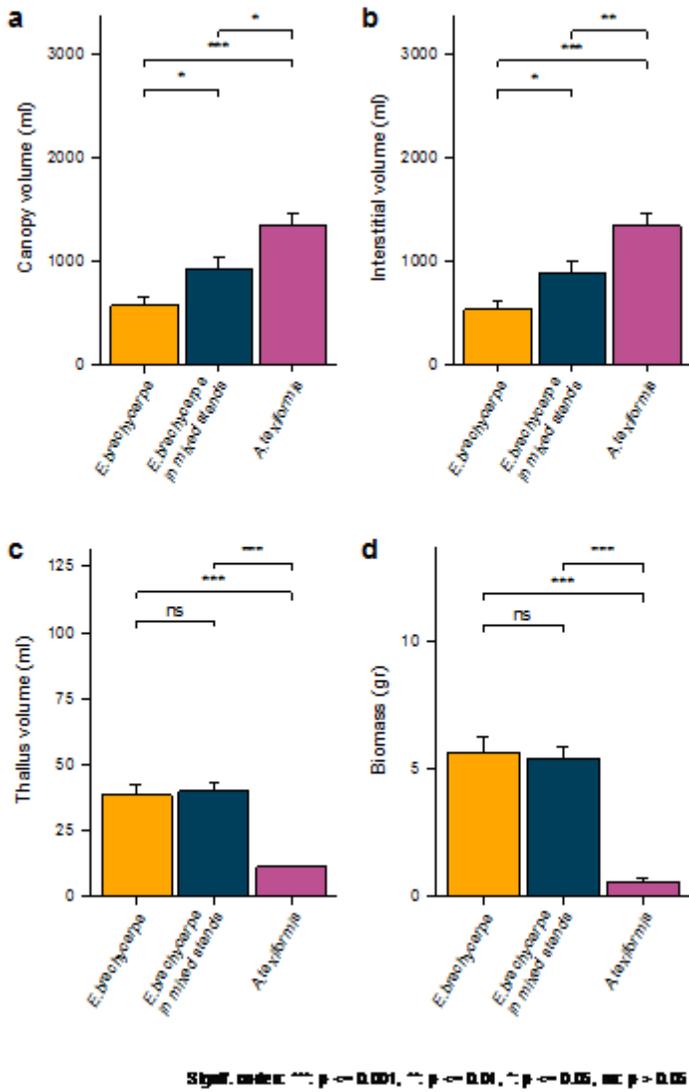


Figure 5

Differences in the structural attributes among habitats. Canopy volume (CV), Interstitial volume (IV), thallus volume (TV) and biomass (expressed as dry weight, DW) of the epifaunal assemblages associated with *E. brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*. Boxplots show extreme and lower whisker (vertical black line), lower and upper quartile (box), and median (horizontal black line). Grey dots are raw data ($n = 20$). See Table S7 for further details.

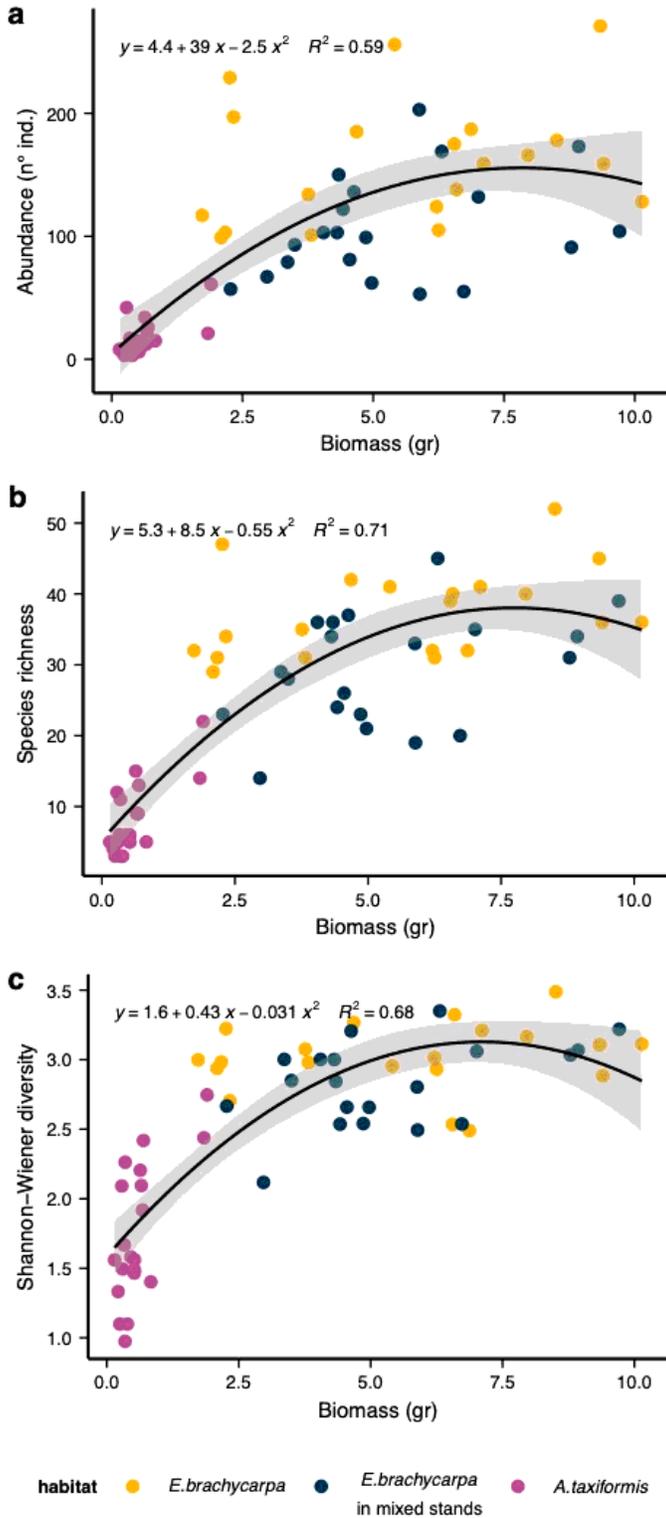


Figure 6

Relationship between seaweeds structural attributes and epifaunal diversity. Results of the linear regression analysis (LM) between the algal biomass (expressed as dry weight, DW) and the abundance (N), species richness (S), Shannon-Wiener diversity (H) of the epifaunal assemblages.

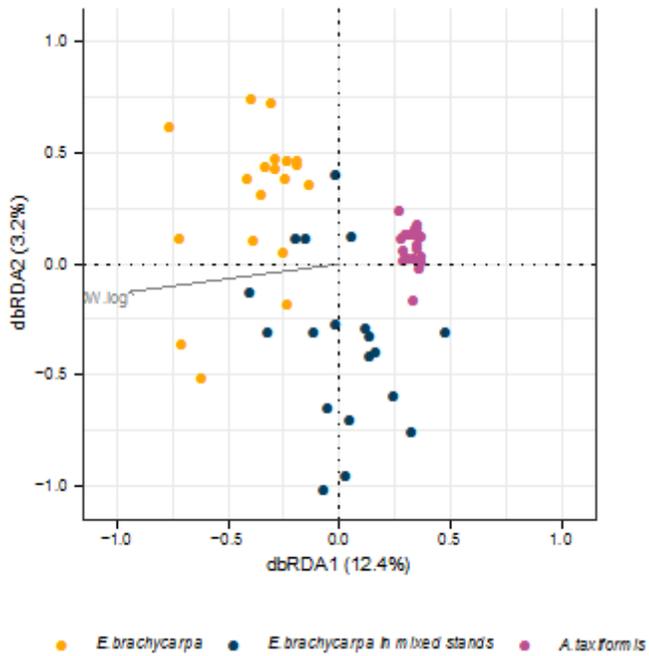


Figure 7

Relationship between structural attributes and the multivariate structure of the epifaunal assemblages associated to the three habitats. Distance-based redundancy (dbRDA) plot illustrating the structural attribute better explaining the multivariate structure of the three habitats. DW.log = seaweeds biomass (log + 1).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [DraftshiftE.brachy.A.taxisupp.docx](#)