Article

The Effects of Non-Indigenous Macrophytes on Native Biodiversity: Case Studies from Sicily

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Abstract: Biological invasions are widely recognized as a major threat to native biodiversity, ecosystem functioning and services. Non-indigenous species (NIS) may in time become invasive (invasive alien species (IAS)), determining significant environmental, socioeconomic and human health impacts such as biodiversity loss and ecosystem service degradation. The Mediterranean islands, particularly Sicily and the circum-Sicilian islands (northwestern Mediterranean Sea), which are important hotspots of biodiversity, are notably vulnerable to anthropogenic pressures such as biological invasions. Therefore, monitoring NIS distribution as well as understanding their effects on native biodiversity is critical in these areas for planning effective conservation strategies. Here, we report four different case studies from Sicily that highlight how NIS may affect native biodiversity and habitats. The first three case studies were carried out within Marine Protected Areas (MPAs) and highlight (1) the ability of *Caulerpa cylindracea* to promote the establishment of other NIS, including biofouling worms belonging to the genus *Branchiomma*; (2) how the shift in habitat from the native *Ericaria brachycarpa* to the invasive *Asparagopsis taxiformis* may drastically erode the primary producer biomass and associated biodiversity; and (2) that the presence of *Lophocladia lallemandii* can affect the molluscan assemblage inhabiting the canopy-forming *Gongolaria montagnei*. The fourth case study, performed along the northwestern coast of Sicily, shows how *Halophila stipulacea* can affect the growth of the co-occurring native seagrass *Cymodocea nodosa*. Overall, these case studies demonstrate various ways in which NIS can interact with native biodiversity and habitats. Furthermore, they emphasize that MPAs are ineffective at preventing the introduction and spread of NIS.

Keywords: invasive species; species interaction; seagrasses; macroalgae; Mediterranean Sea; islands

1. Introduction

Biological invasions are globally recognized as a major driver of global change, threatening biodiversity and natural ecosystem functioning [1,2]. In marine environments, the phenomenon has been accelerated in recent decades by globalization, which has favored the dispersion of invasive species among distant geographic areas worldwide [3–6]. In addition, global warming has allowed non-indigenous species (NIS) to cross environmental and geographical barriers, facilitating their expansion and in turn eroding indigenous resistance [7,8]. Concerns over ecological and socioeconomic consequences have led researchers to investigate the effects of invasive species on many marine ecosystems around the world.

The Mediterranean Sea is particularly vulnerable to NIS introduction [9,10], and in recent decades, there has been a rapid increase (estimated at eight species per year for the whole Mediterranean basin) in NIS, with an expansion of tropical and sub-tropical species aided by warming of the Mediterranean waters [11]. NIS introduction could be mainly attributed to the following factors: the Suez Canal, shipping vectors and the aquarium trade [10].

Macrophytes (i.e., algae and seagrasses (Figure 1)) are a significant component of marine NIS, with some of them being responsible for drastic habitat shifts [4,12]. Studies have highlighted how invasive seaweeds and seagrasses can negatively impact the recipient habitats by reducing the biomass of primary producers, biodiversity and nutrient flows and compromising ecosystem functioning [9,13–18].
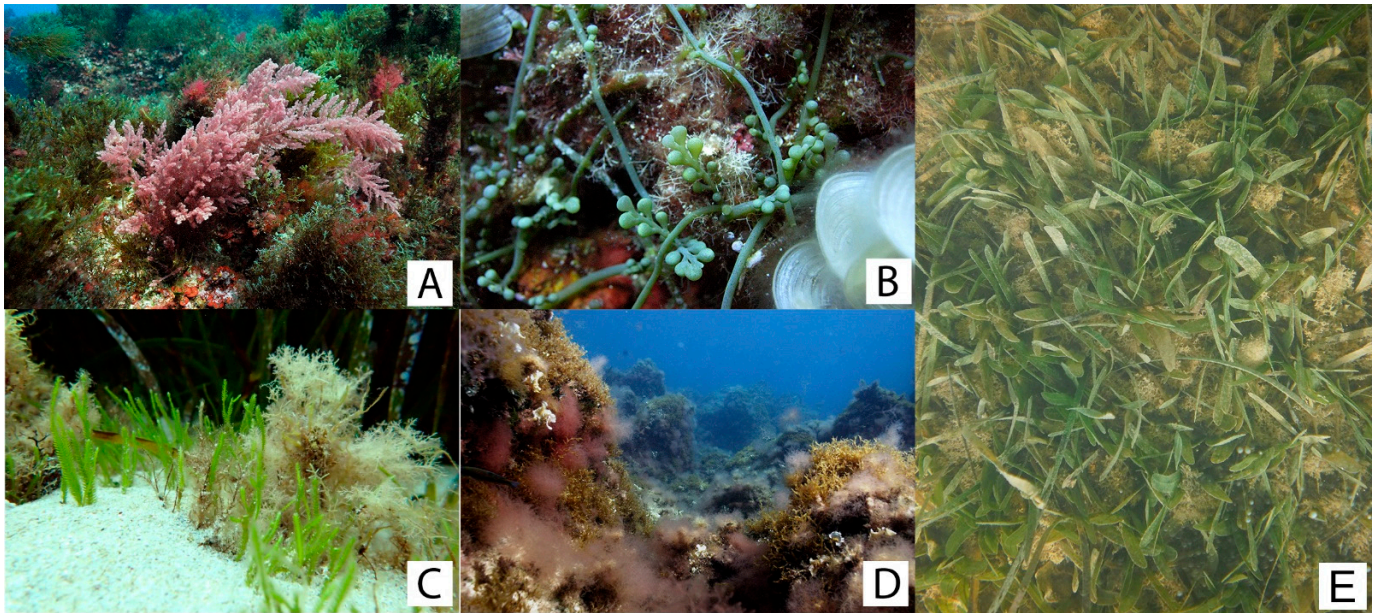

Figure 1. Invasive species found within the MPA of Capo Gallo-Isola delle Femmine: (**A**) *Asparagopsis taxiformis*; (**B**) *Caulerpa cylindracea*; (**C**) *Caulerpa taxifolia* var. *distichophylla*; (**D**) *Lophocladia lallemandii*; and (**E**) *Halophila stipulacea*.

Non-indigenous seaweeds have been shown to have different effects on native habitats and, in some cases, seem to depend on the complexity of the recipient habitat [16].

The introduction of non-native seaweeds into less structured ecosystems (e.g., soft bottoms) increases structural complexity, which may promote an increase in biodiversity and food web length [19]. In contrast, their introduction in well-structured habitats (e.g., seagrass meadows and algal canopies) may affect diversity and function [20–23]. Interestingly, opposite effects have been highlighted for the same NIS. Research discovered that the invasive *Sargassum muticum* (Yendo) Fensholt had a less diverse epifaunal assemblage than the native *Sargassum flavifolium* Kützing [21]. Conversely, other researchers had observed little or no effect from *S. muticum* on native faunal diversity [20,22,24–27]. Another interesting case is that of the invasive seaweed *Caulerpa cylindracea* Sonder (native to southwestern Australia), which can change environmental conditions by increasing sediment accumulation, promoting the development of algal turfs [28], compacting layers of sediment up to 15 cm thick and altering the hydrodynamics near the seabed [29], as well as influencing the quantity and biochemical composition of sedimentary organic matter (OM) [30].

Non-indigenous seagrasses have also been proven to cause the loss or decline of native habitats. Because of their high ecophysiological adaptability, non-indigenous seagrasses can contribute to the direct decline of indigenous species by out-competing native species in shared areas and recovering more quickly than native seagrasses after the disturbance [31,32]. For example, *Halophila stipulacea* (Forsskål) Ascherson, a small seagrass native to the Red Sea, Persian Gulf and Indian Ocean, is able to modify its morphology and physiology in response to changes in environmental conditions, such as temperature, light and hydrodynamics [33–35]. Understanding how NIS interact with native habitats and how indigenous ecosystems adapt to the introduction of an intruder is critical for evaluating the long-term effects of NIS on natural environments.

The aim of this paper is to highlight the effects of the interaction between NIS and native species, providing four case studies from Sicily (northwestern Mediterranean Sea; Figure 2). The first three study cases involve the effects of the NIS *C. cylindracea*, *Asparagopsis taxiformis* (Delile) Trevisan, a tropical-to-warm temperate species considered a pre-Lessepsian immigrant or native in the eastern Mediterranean Sea [36], and *Lophocladia lallemandii* (Montagne) F.Schmitz, which is native to the Red Sea, on native habitats within the Marine Protected Areas (MPAs) of the Egadi Islands and Capo Gallo-Isola delle Femmine, while the fourth case involves the effects of the non-indigenous seagrass *H. stipulacea* on the native *Cymodocea nodosa* (Ucria) Ascherson.
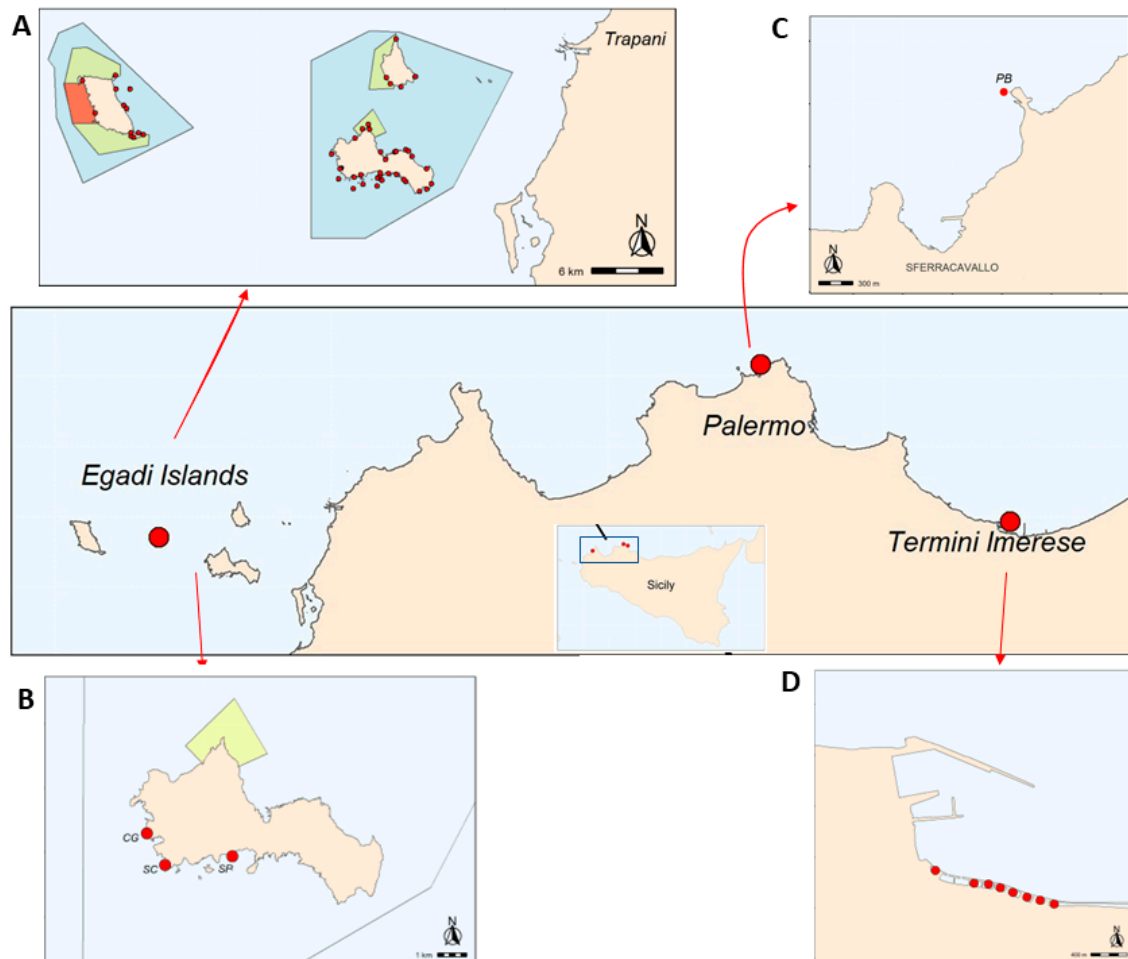

Figure 2. Study areas (red dots) of the four case studies summarized in this work. (**A**) Sites (red dots) of the first case study placed along the rocky shore of the Egadi Islands MPA. The red, green and blue areas denote no-take, general and limited protection zones, respectively. (**B**) Sites (red dots) of the second case study placed along the rocky shore of Favignana Island (the Egadi Islands MPA), where SC = Scoglio Corrente, SP = Scoglio Palumbo and CG = Cala Grande. The green and blue areas denote general and limited protection zones, respectively. (**C**) Sampling site (red dot) of the third case study placed at the rocky shore of the Capo Gallo-Isola delle Femmine MPA, Palermo, Sicily, Italy, where *PB* = Punta Barcarello. (**D**) Sites (red dots) of the fourth case study placed at the shallow water basins close to the harbor of Termini Imerese.

2. Materials and Methods

Case 1. The distribution and effects of *Caulerpa cylindracea* within an MPA environment

This case study reports the data on the distribution and cover percentage of *C. cylindracea* and its colonization strategies around the coasts of the three main islands within the Egadi Islands MPA (Figure 2A [37–39]). The data were gathered within the citizen

science project "*Caulerpa cylindracea*—Egadi Islands" between 2014 and 2016. The project, addressed to a different group of volunteers, aimed to collect data on the occurrence of *C. cylindracea* within the MPA. The collected data consisted of the site, date, typology of substrate and coverage percentage (within a 20 × 20 cm quadrat), including photos. Only data validated by the scientific team of the project were gathered. The Egadi Islands MPA (Aegadian archipelago) is located approximately 7–9 km off the northwest coat of Sicily (Trapani, Sicily, Italy). The MPA was instituted in 1991 and has an extension of about 54 hectares. It surrounds the Egadi archipelago, including the islands of Favignana (37°56′00″ N, 12°19′00″ E), Levanzo (38°00′00″ N, 12°20′00″ E) and Marettimo 37°58′00″ N, 12°03′00″ E).

Case 2. The effects of *Asparagopsis taxiformis* on native habitats and the associated biodiversity

This case study reports the effects of the invasive *A. taxiformis* on native habitats characterized by the presence of the foundation seaweed *Ericaria brachycarpa* (J.Agardh) Molinari & Guiry, particularly for the associated epifauna [23]. The study was carried out at three sites (Scoglio Corrente (37°55′2.0778″ N, 12°17′6.0432″ E), Cala Grande (37°55′35.385″ N, 12°16′39.514″ E) and Scoglio Palumbo (37°55′10.4226″ N, 12°18′41.097″ E)) located at the southwestern shallow rocky shore of Favignana Island (Sicily, Italy) within the Egadi Islands MPA (Figure 1B). The three sites were characterized by the simultaneous presence of three conditions that represent three possible alternative states of the transition from native to invasive seaweeds (Scoglio Corrente, with stands of 100% coverage of *E. brachycarpa*, Cala Grande, in a transition state where *E. brachycarpa* and *A. taxiformis* form mixed stands (~50% of each alga), and Scoglio Palumbo, a situation where *A. taxiformis* has completely supplanted the native species). At each site, 10 thalli of the target seaweeds were sampled from two haphazardly selected areas (5 × 5 m). The thalli were collected at a depth of about 6 m and 50 cm apart to avoid spatial autocorrelation among the samples. Underwater, the thalli with associated epifauna were collected, enveloping them into a plastic bag and detaching the alga from the substrate. After collection, seawater was drained from each sample and stored at −20 °C until laboratory analysis. In the laboratory, the associated fauna with each thallus of *E. brachycarpa* and *A. taxiformis* were detached, washing the algae with seawater above a sieve with a 1 mm mesh. After sorting, the mollusks, amphipods and annelids were stored in a 70% seawater ethanol solution and subsequently counted and identified as species or the nearest possible taxonomic level. The taxonomy and nomenclature were updated according to the World Register of Marine Species database [40]. The epifaunal assemblages of each habitat condition were characterized according to the total abundance of individuals (N), total number of species (S), Shannon–Wiener diversity index (H′) and Pielou's Evenness index (J). Two-way analysis of variance (ANOVA) was used to test for differences in the epifaunal indices (N, S, H′ and J) between habitats (fixed with three levels: *E. brachycarpa, E. brachycarpa* in mixed stands and *A. taxiformis*) and areas (random and nested within a habitat with two levels: area 1 and area 2). Cochran's test was used to check for the homogeneity of variances [41]. Tukey's HSD procedure was used to separate the means (at α = 0.05) following significant effects in the ANOVA [41]. SIMPER analysis [42] 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.

Case 3. The effect of *Lophocladia lallemandii* on the mollusks associated with *Gongolaria montagnei*

This study case reports the effects of *L. lallemandii* on the molluscan assemblage associated with the brown canopy-forming seaweed *Gongolaria montagnei* [43]. Samples were collected at a depth of 6 m on the shallow rocky shore within the "Capo Gallo-Isola delle Femmine" MPA, Palermo (Sicily, Italy) in August 2011 (Figure 2C).

The site is mainly exposed to the northwest, with rocky carbonates providing substrates for dense stands of *G. montagnei* [43]. At this site, thalli of *G. montagnei* were collected with (*n* = 5) and without (*n* = 5) *L. lallemandii*, which can be found attached to the apical

part of *G. montagnei*. Thalli were collected with their associated fauna by an airlift sampler supplied with a 500 μm nylon mesh bag [43]. The seaweed was gently scraped out of the substrate using a hammer and chisel and sucked up by the airlift, and then the mesh bag was immediately closed. In the laboratory, each thallus of *G. montagnei* was rinsed under tap water, and the associated fauna was sieved through a 1 mm mesh. Mollusks were separated from the other fauna and stored in a solution of 70% ethanol and seawater. Living mollusks were sorted out with a stereomicroscope and determined to the lowest possible taxonomic level. They were subsequently counted and listed according to the updated taxonomy and nomenclature of the World Register of Marine Species database (see http://www.marinespecies.org, accessed on 10 January 2023).

Differences in the epifaunal community structure between *G. montagnei* with and without *L. lallemandii* 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 using 9999 permutations. A principal coordinate analysis (PCoA) plot was generated to visualize the variation in the epifaunal community structure (based on a Bray–Curtis distance matrix). SIMPER analysis [42] was performed to identify those taxa that contributed to the dissimilarity of the epifaunal assemblages between *G. montagnei* with and without *L. lallemandii* ($\delta i\%$). 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.

Case 4. Does *Halophila stipulacea* inhibit the growth of native seagrasses?

This case study reports the effects of the presence of *H. stipulacea* on the growth of the native seagrass *C. nodosa* [44–46]. The study was carried out from August 2010 to August 2011 at shallow water basins close to the harbor of Termini Imerese (Figure 2D; 37°59′ N, 13°42′ E; northwestern Sicily, Italy in the southern Mediterranean Sea). The basins are connected to the sea via a central opening and present comparable environmental characteristics, with sandy bottoms and depths ranging from 0.8 to 2.5 m, a consistent salinity of 38 ppt and temperatures ranging from 25 °C in summer to 13 °C in winter. These basins host populations of *H. stipulacea* and *C. nodosa* and can be used as experimental units to investigate the interaction between the two seagrasses. The experiment was carried out at eight basins (hereafter referred as sites), with four sites characterized by the presence of monospecific populations of *C. nodosa* (natural conditions) and four sites characterized by the co-occurrence of *C. nodosa* and *H. stipulacea* (impacted conditions). The shoot density (number of shoots/m^2) of *C. nodosa* and *H. stipulacea* was estimated using three randomly quadrats (20 × 20 cm) at each site. Sampling was carried out four times (T_1 = August, T_2 = October, T_3 = January and T_4 = April).

For each site, the average shoot density ($n = 3$) of *C. nodosa* and *H. stipulacea* was calculated. Moreover, for *H. stipulacea*, the average length and width ($n = 30$) of the leaves were calculated. One-way ANOVA was used to assess if there were significant differences in the density of *C. nodosa* between the controlled and impacted sites across seasons.

3. Results

Case 1. The project (2014–2016) highlighted that *C. cylindracea* was widespread within the MPA (through approximately 160 sightings), and anchorage activities seemed to have encouraged its spread. The alga was present between 0 and 40 m deep, mainly on rocky substrates covered by sediment (65%), followed by rocky (31%) and sandy (4%) substrates (Figure 3). It was also recorded in valuable habitats, being more evident in the vermetid reef and the *Cystoseira s. l.* communities than in the coralligenous habitat. Moreover, most of the time, *C. cylindracea* was found with a coverage percentage higher than 20%. In particular, Favignana was the only island where *C. cylindracea* was found at all three types of substrates, while in Levanzo and Marettimo, the seaweed was found only on rocky substrates covered by sediment. Observations in the field also revealed that *C. cylindracea* has the ability to expand its range by using stolons to create bridges with new areas

(Figure 4). Furthermore, of particular relevance is the ability of *C. cylindracea* to entrap sediment among the stolons that favor the settlement of invasive sabellids belonging to the genus *Branchiomma* (McIntosh, 1885). *Caulerpa cylindracea* was most abundant in areas with low biodiversity (low presence of surrounding macroalgal species). Finally, it was observed that the fronds of *C. cylindracea* were smaller on the rocky substrate compared with the sandy one.
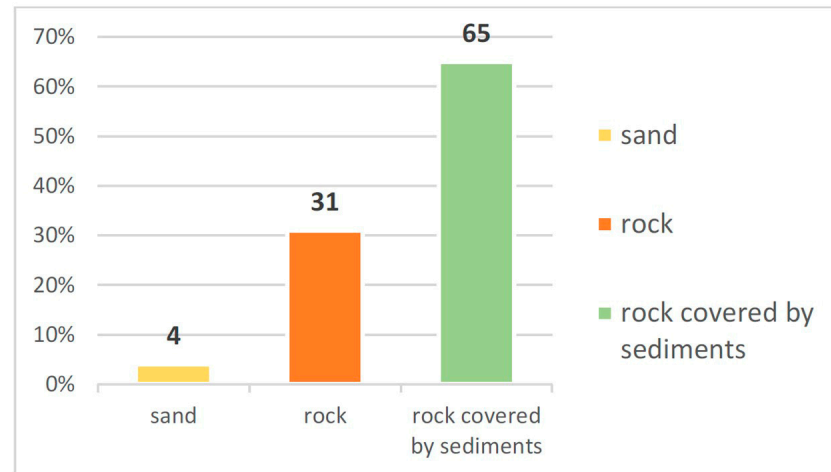

Figure 3. Percentage of records of *C. cylindracea* in the different types of substrates.

Figure 4. Bridges created by the stolons of *C. cylindracea* (photo by Paolo Balistreri).

Case 2. In total, 5676 epifaunal individuals from 199 taxa (74 mollusks, 50 amphipods and 75 annelids) were identified. 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 (Figure 5). The total abundance and rarefied species richness changed significantly among habitats, with values greater in *E. brachycarpa* compared with *E. brachycarpa* in the mixed stands and *A. taxiformis* (Figure 5).
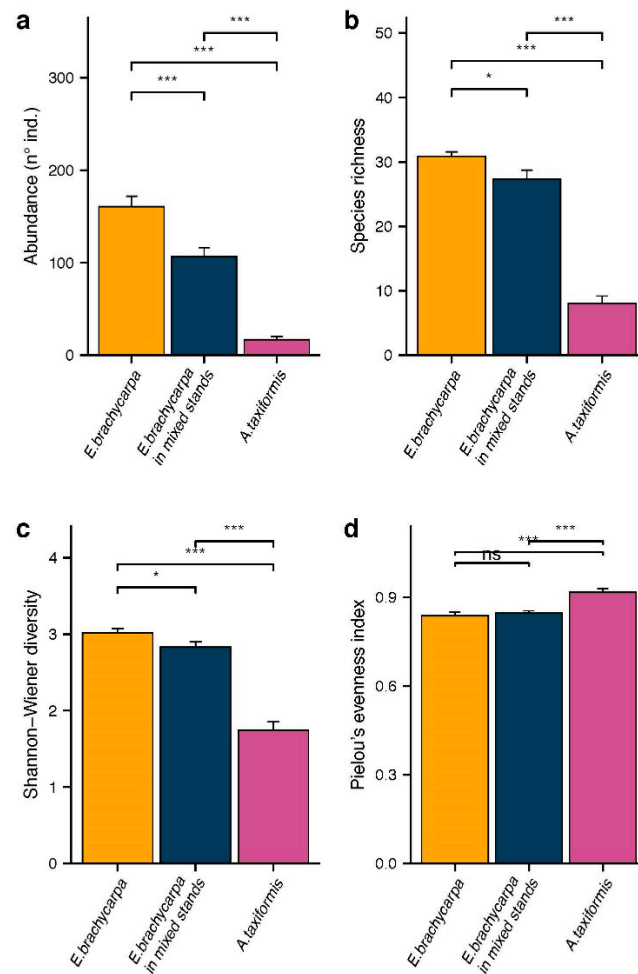
Figure 5. Comparison of the alpha diversity indices among habitats. Abundance, rarefied species richness, Shannon–Wiener diversity and Pielou's evenness index of the epifaunal assemblage associated with *E. brachycarpa, E. brachycarpa* in mixed stands and *A. taxiformis*. Bar plots show mean +/− 1 standard error (*n* = 20). Significant codes: *** $p \leq 0.001$, * $p \leq 0.05$ and $p > 0.05$.

The Shannon–Wiener diversity varied significantly across habitats, with *E. brachycarpa* and *E. brachycarpa* in mixed stands exhibiting closer and higher values than *A. taxiformis*. Pielou's evenness was higher in *A. taxiformis* than in the other two habitats, which had equivalent values (Figure 5). The structure of the epifaunal assemblages differed significantly among the habitats, and the PCoA plot clearly distinguished the epifaunal assemblages of the three habitats (Figure 6). The first two axes explained 63% of the variance, with the first axis accounting for the majority of the variance (49.5%), highlighting a shift from *E. brachycarpa* to *A. taxiformis* with *E. brachycarpa* in mixed stands placed between the two homogenous stands of the native and invasive seaweeds (Figure 6). Only 13.3% of the variance was explained by the second axis, which distinguished *E. brachycarpa* and *A. taxiformis* from *E. brachycarpa* in the mixed stands (Figure 6).

Case 3. PERMANOVA analysis showed that the structure of the molluscan assemblage differed significantly between *G. montagnei* with and without *L. lallemandii* (Figure 7 and Table 1). When we looked at the taxa that contributed to the differences between *G. montagnei* with and without *L. lallemandii*, SIMPER analysis revealed that six taxa (*Barleeia unifasciata* (Montagu, 1803), *Alvania hirta* (Monterosato, 1884), *Alvania lineata* (Risso, 1826), *Rissoa variabilis* (Megerle von Mühlfeld, 1824), *Columbella rustica* (Linnaeus, 1758) and *Rissoa guerinii* (Récluz, 1843)) contributed to 70% of the dissimilarity between *G. montagnei* with and without *L. lallemandii*. *Barleeia unifasciata* contributed solely and consistently (higher

δi/SD(δi) value) to 39% of the observed differences, being more abundant in *G. montagnei* with *L. lallemandii* (Table 2).
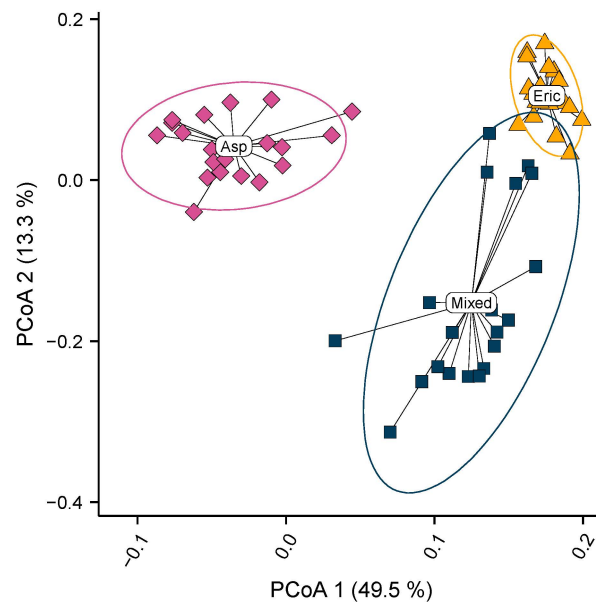

Figure 6. Structure of the epifaunal assemblages associated with *A. taxiformis* (Asp), *E. brachycarpa* (Eric) and mixed stands of *A. taxiformis* and *E. brachycarpa* (mixed)**.** Principal coordinate analysis plot (PCoA) based on a Bray–Curtis distance matrix of square root-transformed relative abundances. The circles show the 90% confidence interval for each seaweed.
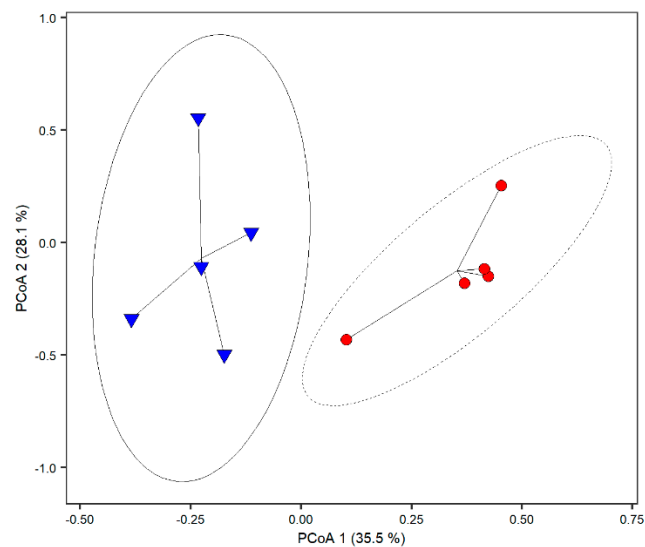

Figure 7. Structure of the molluscan assemblage of *G. montagnei* with (red dots) and without (blue dots) *L. lallemandii*. Principal coordinate analysis plot (PCoA) based on a Bray–Curtis distance matrix of square root-transformed relative abundances. The circles show the 90% confidence interval.

Case 4. Under natural conditions (no presence of *H. stipulacea*), the density of *C. nodosa* showed a mean value of 1200 ± 291 shoots/m^2. Moreover, where the invasive seagrass was absent, the density of *C. nodosa* shoots changed across seasons, with higher values in summer (1616 ± 87 shoots/m^2) and lower values in winter (1029 ± 38 shoots/m^2). Conversely, in impacted conditions (with *H. stipulacea*), the density of *C. nodosa* was conspicuously lower compared with that in natural conditions, with an overall average shoot density of 566 ± 96 shoots/m^2 and lower seasonal variation, having higher values in spring (715 ± 11 shoots/m^2) and comparable densities during the other seasons (Figure 8).

Table 1. PERMANOVA results for the structure of the molluscan assemblage associated with *G. montagnei* in the presence or absence of *L. lallemandii*. Significant code: ** $p < 0.01$.

Source of Variation				
	df	MS	Model-F	
Presence or absence *L. lallemandii*	1	0.871	3.802	**
Residuals	8	0.229		
Total	9			

Table 2. Taxa contributing to 70% of the dissimilarity between *G. montagnei* with and without *L. lallemandii*. Results of SIMPER analysis show the average abundances, consistency (δi/SD(δi)) and cumulative contributions (cum_δi%).

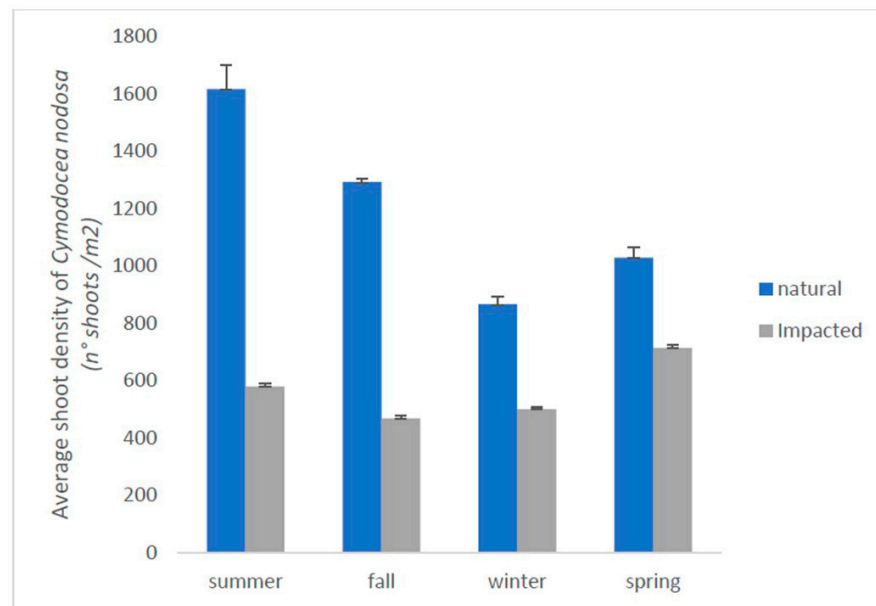|	Average Abundance			
Species	With *L. lallemandii*	Without *L. lallemandii*	δi/SD(δi)	Cum_δi%
Barleeia unifasciata	5.8	0.0	2.46	0.29
Alvania hirta	2.6	0.0	0.68	0.39
Alvania lineata	1.4	1.0	1.28	0.47
Rissoa variabilis	0.6	1.2	1.11	0.54
Columbella rustica	1.4	1.2	1.20	0.60
Rissoa guerinii	1.0	0.8	1.04	0.66

Figure 8. Comparison of impact vs. control sampling sites of *Cymodocea nodosa* shoot density. Bars show mean + SD.

4. Discussion

Non-indigenous species are one of the major threats to the Mediterranean Sea. The four study cases reported here confirm the negative role of NIS in native habitats, that MPAs are not immune from NIS invasions and protection does not hinder the introduction and spreading of NIS [47]. Overall, the four case studies also highlight the ability of NIS to colonize different types of substrates (sandy, rocky and mixed), to modify the sedimentation rates of natural habitats and to inhibit the growth of native species by competing for space, likely due to their high ecophysiological adaptability compared with native species.

Moreover, shifting from native to NIS decreases biodiversity as well as reducing the biomass of primary producers, with relevant effects on coastal primary production.

Case 1. *Caulerpa cylindracea*, which is widespread in northwestern Sicily [37], was also well established within the Egadi Islands MPA, especially around Favignana, where it was found in different habitats and types of substrates [38,47]. The ability to cover different types of substrates is related to the high rates of elongation of stolons that, during the maximal growth period, are able to grow up to 2 cm per day, allowing rapid colonization of the substratum [48]. Vegetative fragments can easily re-establish with variable performance depending on the season, and several days of detachment have no effect on their ability to establish themselves [49]. Furthermore, this species reproduces through specialized propagules and probably sexually [50]. It was also observed that *C. cylindracea* stolons can build bridges to reach new areas of anchorage, with the strength of the anchorage guaranteed by a large number of rhizoids.

According to [29], it was observed that *C. cylindracea* is also capable of trapping sediments among its stolons, which has a negative impact on native macroalgal assemblages [51] and facilitates the settlement of invasive sabellid polychaetes belonging to the genus *Branchiomma* [52], confirming the role of invasive species in setting the stage for the subsequent invasion of a trophic specialist that takes advantage of niche opportunities [53]. The frond length of *C. cylindracea* and the substrate type were also found to be related, with longer fronds growing on sandy substrates. It was hypothesized that because higher coverage values were observed in areas where boat anchorage is permitted (mainly sandy substrates), the anchorage activities, which are mostly carried out by pleasure boats, may also favor the spread of *C. cylindracea.*

The high presence of *C. cylindracea* in the Egadi Islands MPA confirms that although MPAs are a useful management tool for the protection of biodiversity, they are still vulnerable to NIS invasion [54]. The expansion of NIS by recreational vessels contributes to MPA invasion risk, as they are popular tourist destinations [55]. It can be assumed that the frequent and heavy maritime traffic between Sicily and the Egadi Islands MPA, particularly Favignana, may have facilitated the arrival of non-indigenous taxa commonly found in fouling communities.

Case 2. This case concerns *A. taxiformis*, a species present in northwestern Sicily since 2000 and widespread within the Egadi Islands MPA (see [56]). We showed that NIS are able to cause a loss of biodiversity in native habitats. We showed differences in the abundance and diversity of the epifaunal assemblages between three alternative states of the transition from native *E. brachycarpa* to invasive *A. taxiformis.* In particular, the NIS *A. taxiformis* hosted almost 6 times fewer epifaunal individuals compared with *E. brachycarpa* in mixed stands, and 10 times fewer individuals compared with the homogenous stands of *E. brachycarpa*. Moreover, the biodiversity of the associated epifauna was reduced by half in the invasive habitat compared with the native ones. These data confirm that generally invasive seaweeds exhibit a less diverse epifaunal component compared with native seaweeds [14,21,57–59].

These data also suggest that the presence of *A. taxiformis* affects the epifaunal assemblages associated with *E. brachycarpa* in mixed stands. We believe that landscape feature modification caused by NIS can explain this result [60]. The presence of non-indigenous seaweeds may contribute to the fragmentation of native habitats, reducing the patch size of native seaweeds and at the same time increasing their isolation [61,62]. It has been observed that the reduction in patch size of *Cystoseira s. l.* habitats reduces the diversity of the associated faunal assemblages [43]. Thus, it can be hypothesized that the presence of *A. taxiformis* in mixed stands can act as a physical barrier to the dispersal of vagile fauna, reducing connectivity on a small scale and ultimately eroding the diversity of native habitats [62]. Another explanation for the low diversity of epifauna associated with *E. brachycarpa* in mixed stands is the ability of epifauna to disperse through different seaweeds [63]. Then, mixed stands may facilitate the movement of epifauna, which would benefit from a greater variety of resources (e.g., food or protection) than those found in *E. brachycarpa*- or *A. taxiformis*-dominated stands. This study, however, cannot address the effects of epifauna

movement among seaweeds on the observed results, and more studies are necessary to understand the possible role of mobile epifaunal assemblage movement patterns in mixed stands of *E. brachycarpa*.

Overall, this case study suggests that shifting from native to invasive habitats may pose a serious threat to biodiversity in coastal areas [64,65], potentially leading to bottom-up effects in rocky shore ecosystems. In addition, the low biomass supplied by the invasive species herein studied suggests that the shift from native canopy-forming algae to the invasive *A. taxiformis* habitat would also drastically reduce the biomass of primary producers in affected coastal areas.

Case 3. This case study confirms what was already observed in the second case study. In fact, the presence of *L. lallemandii*, recorded in northwestern Sicily since 2001 (see [56]), affects the structure of the molluscan assemblage, inhabiting the habitat-forming *G. montagnei*. In particular, we observed that the presence of *L. lallemandii* increases the abundance of the gastropods *B. unifasciata* and *A. hirta*. *Lophocladia lallemandii* tends to form large bushes, which can greatly increase the surface on which mollusks can live. We hypothesize that the big surface provided by *L. lallemandii* can act as a trap, facilitating the recruiting of *B. unifasciata*. Then, the bigger surface of the NIS can facilitate retaining those mollusks characterized by a foot with low adhesiveness, such as *B. unifasciata* and *A. hirta* [66,67].

Case 4. We showed that NIS are also able to interact with native species, inhibiting their growth. In fact, the presence of *H. stipulacea* contrasted the growth of *C. nodosa*, also inhibiting the natural temporal variation observed when *C. nodosa* grows in the absence of NIS. The co-occurrence of these two seagrasses was already observed in the Mediterranean Sea by different authors but without highlighting the clear negative effects of this NIS on the native seagrass, except, for instance, along the Tunisian coasts [66], possibly due to the small shoot size of this NIS compared with those of larger native species [68]. Conversely, in other cases, *H. stipulacea* was observed to be able to compete for space with native species by displacing local seagrass and altering the native benthic community [13,69].

Furthermore, in this study, no flowers or fruits were observed for *C. nodosa*. This observation might be linked to a negative effect of *H. stipulacea* on *C. nodosa* growth. It can be hypothesized that the dense multi-layered mat formed by *H. stipulacea* rhizomes and sediment pushes down the *C. nodosa* rhizomes in a layer with oxygen depletion [70]. The behavior of *H. stipulacea* seems comparable to that of invasive *Caulerpa* species, being able to negatively affect seagrass growth through the modification and deterioration of sediments [51].

Halophila stipulacea, recorded in northwestern Sicily since 2000 (see [71]), is becoming more and more common around the whole Mediterranean area, but it has never shown any clear or regular invasive behavior [72], and its occurrence is relatively limited in some areas. However, *H. stipulacea* shows the potential for long-distance dispersal [73] and possesses some features that could make it a potential threat to native seagrasses, also facilitating the introduction or persistence of other alien species [53].

5. Conclusions

Predicting the ecological effects of invasive seaweeds is one of the main goals in the study of biological invasions. Here, we reported that NIS are able to easily colonize different types of native substrates, decrease the biodiversity of native habitats and undermine native species through space competition. In all cases analyzed, we observed that NIS seem to colonize areas where human pressure is markedly present, supporting the idea that anthropogenic pressures facilitate the spreading of NIS populations [74]. Previous research has highlighted the context-dependent effects of invasive seaweeds, with larger impacts caused by invasive species exerting a different functional role compared with native habitat-forming species [60,75,76]. The reported data not only show the negative effect of NIS on native assemblages but also suggest that NIS are able to affect native habitats in a transitional phase (mixed stands) of the habitat shift, facilitating fragmentation and

isolation. Further studies aimed at understanding 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.

The role of MPAs in preventing the arrival of NIS appears to be ineffective, bringing into question their fundamental role in the conservation of native marine biodiversity.

Management planning that invests in understanding connectivity and vector processes (human behaviors) is more likely to derive effective policies to stem the flow of NIS under both current and future conditions. Biosecurity measures, such as vessel biofouling restrictions within MPAs and MPA-specific programs for NIS prevention, monitoring and mitigation, are particularly needed.

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