

Article

# An Alien Invader is the Cause of Homogenization in the Recipient Ecosystem: A Simulation-Like Approach

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**Abstract:** Biotic homogenization is an expected effect of biological invasions. Invasive alien species typically show great adaptability to a wide range of environmental conditions and may expand into different habitats, thus reducing the dissimilarity among the recipient communities. We tested this assumption by analyzing a comprehensive database (78 species × 229 samples) collected between 2012 and 2017 in the marine protected area of Portofino (NW Italy), where *Caulerpa cylindracea*, one of the worst invaders in the Mediterranean Sea, exhibits high substratum cover at depths between 1 m and 45 m in 14 different communities (identified according to the European Nature Information System EUNIS for habitat classification). Five samples for each of the eight depth zones (i.e., 5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 35 m, and 40 m) were randomly re-sampled from the comprehensive database to produce a dataset of 67 species × 40 samples. Then, a second dataset of 66 species × 40 samples was simulated by excluding *Caulerpa cylindracea*. Both re-sampled datasets underwent multivariate analysis. In the presence of *C. cylindracea*, the overall similarity among samples was higher, thus indicating homogenization of the rocky reef communities of Portofino Marine Protected Area. Continued monitoring activity is needed to understand and assess the pattern and extent of *C. cylindracea*'s inclusion in the recipient ecosystems.

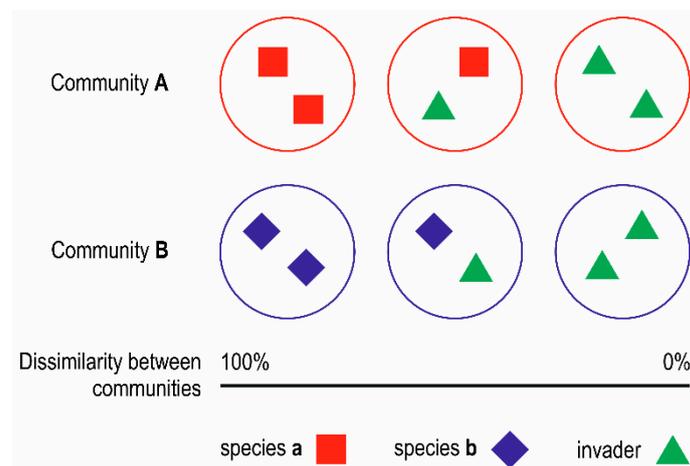
**Keywords:** rocky reefs; biotic homogenization; *Caulerpa cylindracea*; EUNIS habitats; marine protected area; Mediterranean Sea

## 1. Introduction

Biological invasions, i.e., the successful establishment and spread of species outside their native range [1,2], are a major component of global change [3–5]; they reshuffle the planet's biota and represent a distinctive mark of the Anthropocene [6,7]. Biological invasions have been dubbed “biological pollution” [8,9] that causes biodiversity loss and alters the composition of communities and ecosystem functioning [10,11], thus compromising ecosystem services [12]. In terrestrial habitats, biological invasions have been the concern of biogeographers and ecologists for decades [13,14], whereas in marine environments they have remained less known until recently [15,16]. Today, meta-analysis and reviews are available that highlight the impact of marine invasions [12,17–19]. Studies in the Mediterranean Sea indicate that biological invasions represent a serious ecological and economical menace leading to fishery and tourism impairment [20].

In terrestrial environments, invasive alien species have been considered important agents of biotic homogenization at different spatial scales [21–23]. In the present paper, biotic homogenization means the process that diminishes floral and faunal differences among previously distinct communities within a specific region [24,25]. The rationale beyond the idea that biological invasions may cause

homogenization in the recipient biota is simple—invasive species typically show great adaptability to a wide range of environmental conditions and may thus enter different habitats, often becoming dominant [26,27]. If an abundant invader replaces or simply adds to the native species that used to characterize the recipient communities, then the dissimilarity among communities is expectedly reduced (Figure 1). This rather simplistic scheme just aims at illustrating the rationale of our study, while more complete schemes illustrating the many ways invaders can impact recipient communities can be found in review papers [24,28,29].



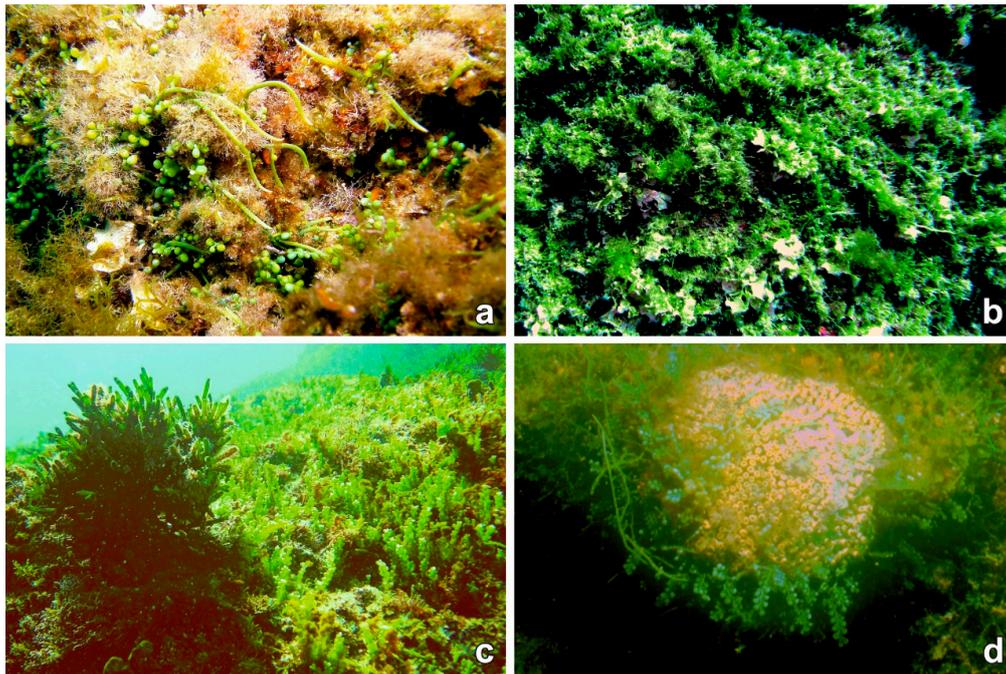
**Figure 1.** A schematic representation of how an invader may cause biotic homogenization in the recipient communities. Community A is characterized by its exclusive species a, and community B is characterized by its exclusive species b; the two communities are evidently highly dissimilar. If an invasive species enters both communities to flank or even replace the exclusive species, then the two communities become more similar, and hence homogenized.

We tested the assumption above by analyzing the change that may be observed in the zonation of communities along a sharp ecological gradient (i.e., depth) in the presence or absence of an alien invader. We used a comprehensive database collected in the marine protected area of Portofino (NW Italy), where *Caulerpa cylindracea*—one of the worst invaders in the Mediterranean Sea [30,31]—has become abundant in recent years [32]. After a descriptive analysis of the comprehensive database, we generated two distinct datasets to go through multivariate analysis: the first contained observed data, and the second was a “simulated” one where *C. cylindracea* was excluded from the dataset, under the hypothesis that the latter dataset will exhibit greater dissimilarity than the former one. We used the term “simulated” to make it clear that we did not perform a real, physical removal experiment in the field. Our procedure ties in with the so-called “inclusion versus exclusion” approach, which has been said to be not only relevant to invasion biology, but to any field where the component of interest is an integrated part of the response [18,33].

## 2. Materials and Methods

### 2.1. The Invader

*Caulerpa cylindracea* Sonder, formerly considered a variety of *Caulerpa racemosa* (Sonder) Verlaque, Huisman, and Boudouresque, but presently recognized as an independent species [34,35], is a green alga with a cylindrical stolon bearing erect fronds up to 20 cm high, with bunches of vesicular branchlets or ramuli (Figure 2a). *C. cylindracea* is of southwest Australian origin, but in recent decades has expanded its range to many subtropical areas of the Pacific and Atlantic oceans [36].



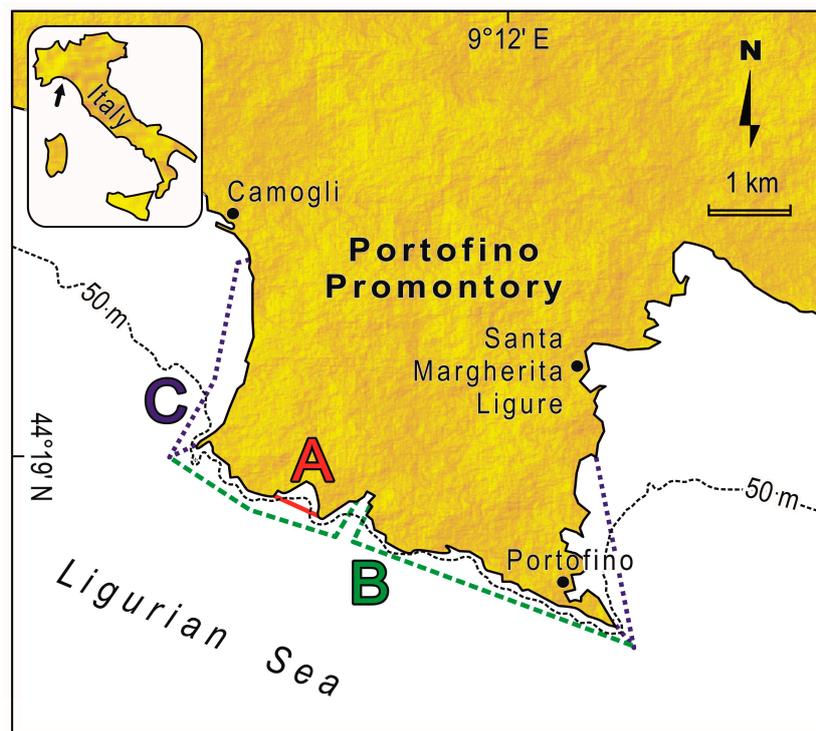
**Figure 2.** *Caulerpa cylindracea* Sonder: (a) Typical aspect with creeping and jutting stolons and clavate branchlets; (b) exhibiting high cover (22%) amid infralittoral algae in shallow water; (c) invading the *Codium vermilara* association (EUNIS A3.231); (d) overgrowing a partially bleached colony of the zooxanthellate coral *Cladocora caespitosa* (EUNIS A3.238).

In the Mediterranean Sea, *C. cylindracea* was observed for the first time in 1990 [37]. Since then, the species has exhibited an impressive and apparently restless spread across the whole basin [38–40], locally covering the substratum to 100% [41]. The rapid spread of this invader has few equivalents among introduced marine macrophytes [42], and ship traffic has been blamed as the main vector [43,44]. *C. cylindracea* has a high adaptability to physical and biotic factors [45], is resistant to grazing because of the production of toxic metabolites [46], and may colonize virtually all types of substrata, in either sheltered or exposed areas, at depths ranging from the intertidal zone down to 90 m depth [47–52] in disturbed or pristine habitats [53–55]. *C. cylindracea* is able to out-compete native algae [56] and seagrass [57], which contrasts with studies dealing with other species of *Caulerpa* [58].

## 2.2. Study Area

Field data for this study came from the marine seabed around the Portofino promontory (Figure 3), an impressive 6-km wide rocky headland in the Ligurian Sea (NW Mediterranean). The headland runs out toward the sea for about 5 km, and the southern front exhibits high vertical or sub-vertical cliffs that continue underwater to about 50 m depth, while the eastern and western sides are comparatively shallower. The heterogeneous features of the Portofino promontory allow for the coexistence in a limited area of numerous species and of varied benthic communities and underwater seascapes [59]. *Caulerpa cylindracea* was first recorded in the area in 1996 [60,61].

In 1999, the Portofino marine protected area (MPA) was established around the promontory, and was organized into three zones subject to different levels of protection: the A zone (“no entry, no take”), limited to a small cove; the B zone (general reserve), covering the southern front of the promontory; the C zone (partial reserve), along the eastern and western sides of the headland (Figure 3). The MPA of Portofino is included in the European Natura 2000 Network as a Site of Community Importance (SCI IT1332674: Fondali Monte di Portofino), and since 2005 has been a Specially Protected Area of Mediterranean Interest (SPAMI) according to the decision of the UNEP-RAC/SPA (the Regional Activity Centre for Specially Protected Areas of the United Nations Environment Programme) office [62].



**Figure 3.** Geographic situation of the study area: the Portofino promontory in northwest Italy (see arrow in the inset). Capital letters denote the three zones of the marine protected area of Portofino subject to different levels of protection: the A zone is the “no entry, no take” area; the B zone is the general reserve; the C zone is the partial reserve. The three municipalities of the Portofino Promontory are also indicated.

### 2.3. Data Sources and Management

Data on the benthic communities of Portofino reefs were collected between 2012 and 2017 by scuba diving between 1 m and 45 m depth in summer months. Cover data of *Caulerpa cylindracea* and other conspicuous sessile species were obtained using 1 m<sup>2</sup> visual quadrats [63].

The resulting comprehensive database of 78 species × 229 samples (Table S1) was used to explore the patterns of abundance and distribution of *Caulerpa cylindracea* in Portofino MPA and its diffusion within the benthic communities existing there. The latter have been identified and named according to the habitat classification of the European Nature Information System EUNIS ([www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification](http://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification)). One-way analysis of variance (ANOVA) was used to assess differences where applicable; in the resulting tables, SS is the sum of squares, df is the degrees of freedom,  $s^2$  is the variance (mean square) and  $F$  is the ratio between the variance between groups and the variance within groups.

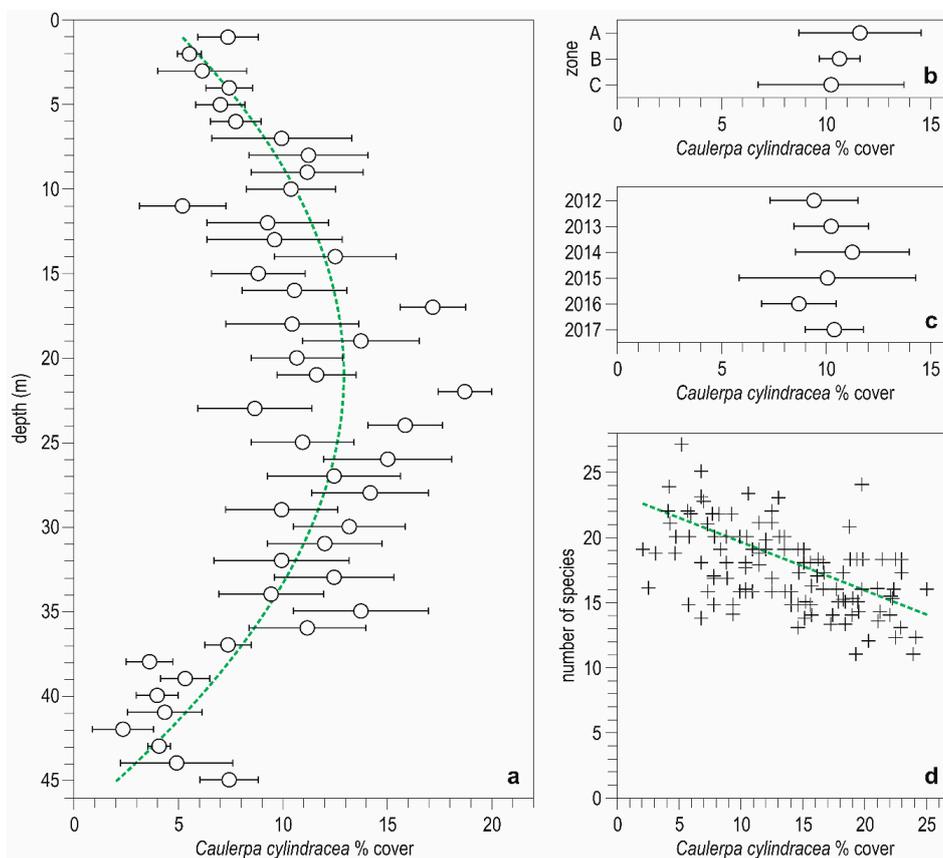
Then, to test the assumption that *C. cylindracea* may cause biotic homogenization in the recipient ecosystem, we analyzed the change in the zonation of communities along a sharp ecological gradient, i.e., depth. To reduce noise and to have a balanced design, 5 quadrats for each of 8 depth zones (5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 35 m, and 40 m) were randomly re-sampled (in the statistical sense) from the comprehensive database to produce a first dataset of 67 species × 40 samples (Table S2). A second dataset of 66 species × 40 samples was simulated by excluding *C. cylindracea*. Both the first (“observed”) and the second (“simulated”) datasets underwent principal component analysis (PCA) using the free software PaSt [64]. Significance of the axes was evaluated by 9999 row-wise bootstrap replicates, and 95% bootstrapped confidence intervals were given for the eigenvalues [65]. The eigenvalues expected under a random model (broken stick) were also computed, with lower eigenvalues possibly representing non-significant components [66]. The geometry of the resulting ordination models has been interpreted according to Fresi and Gambi [67]. Prior to the analyses, cover

values were arcsine $\sqrt{(x/100)}$  transformed [68]. As the two datasets are not independent of each other, we did not attempt to statistically test the differences between the two ordination models. We drew the convex hulls, i.e., the smallest convex polygons enclosing the sample points, in both scatter plots to visualize and compare graphically the respective multivariate dispersions. In addition, for each dataset we computed the average dissimilarity (1—Bray-Curtis coefficient), the standard deviation, and the coefficient of variation among samples, with lower values of these indices being indicative of reduced  $\beta$ -diversity, and hence homogenization [69].

### 3. Results

#### 3.1. Descriptive Analysis

Based on the comprehensive database of 78 species  $\times$  229 samples, *Caulerpa cylindracea* proved abundant on the rocky reefs of the marine protected area of Portofino (Figure 2b), exhibiting considerable substratum cover (up to 25%) at all depths investigated (1 m to 45 m), with the highest values especially around 20 m (Figure 4a). No other species in Portofino exhibited similar abundance and ubiquity.

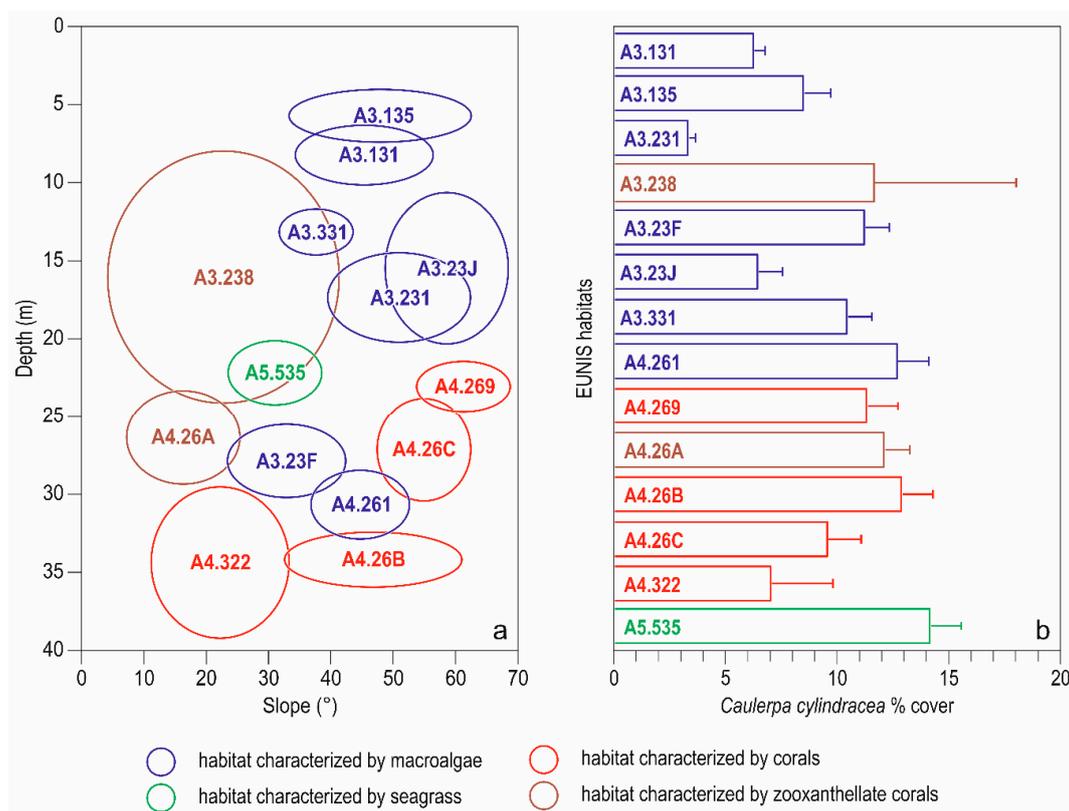


**Figure 4.** Occurrence of *Caulerpa cylindracea* in the marine protected area of Portofino (from the comprehensive database of 78 species  $\times$  229 samples): (a) Depth distribution of the species cover (circles identify the mean depth, error bars are standard errors) between 1 m and 45 m; the binomial curve (dashed line) represents the best fit of mean data (cover =  $0.0196 \cdot \text{depth}^2 + 0.8313 \cdot \text{depth} + 4.1168$ ,  $R^2 = 0.5003$ ,  $n = 229$ ,  $p < 0.01$ ); (b) mean ( $\pm$  standard error) cover in the three protection zones (A = “no-entry no-take” area, B = general reserve, C = partial reserve); (c) change in yearly mean ( $\pm$  standard error) cover in the Portofino MPA between 2012 and 2017; (d) linear regression (dashed line) between *C. cylindracea* cover and species richness (number of species =  $-0.3653 \cdot \text{cover} + 23.111$ ,  $R^2 = 0.3309$ ,  $n = 229$ ,  $p < 0.01$ ).

There was no difference in the occurrence of *C. cylindracea* among areas with varying degree of protection (Figure 4b), nor among the years 2012 to 2017 (Figure 4c), as indicated by the large overlap among error bars. Notwithstanding high variability, a significant negative relationship was found between the cover of *C. cylindracea* and the total number of species (Figure 4d).

A total of 14 EUNIS habitats have been recognized in the rocky reefs of Portofino MPA between 1 m and 45 m depth. Seven of them were characterized by macroalgae (*Lithophyllum incrustans*, *Ellisolandia elongata*, *Codium vermilara*, *Dictyopterus polypodioides*, *Flabellia petiolata* and *Peyssonnelia squamaria*, *Halopteris scoparia*, *Cystoseira zosteroides*), four by gorgonian or soft corals (*Eunicella cavolini*, *Paramuricea clavata*, *Parazoanthus axinellae*, *Leptogorgia sarmentosa*), two by zooxanthellate corals (*Cladocora caespitosa*, *Eunicella singularis*), and one by the seagrass *Posidonia oceanica* (Table 1).

These 14 habitats were zoned chiefly according to depth and substratum slope (Figure 5a). *C. cylindracea* was found in all of them, although with different cover values (Table 2)—the most invaded habitats were the *Posidonia oceanica* beds, the *Paramuricea clavata* facies, and the *Cystoseira zosteroides* association, while the least invaded were the *Codium vermilara* association, the encrusting algae (*Lithophyllum incrustans*) and sea urchins facies, and the *Flabellia petiolata*-*Peyssonnelia squamaria* association (Figure 5b). Even in the least invaded habitats, however, *C. cylindracea* could occasionally be very abundant (Figure 2c). In the case of zooxanthellate corals, *C. cylindracea* invasion occurred especially after coral colonies had bleached because of summer warming events (Figure 2d).



**Figure 5.** EUNIS habitats in Portofino MPA and incidence of *Caulerpa cylindracea* (from the comprehensive database of 78 species  $\times$  229 samples): (a) Depth and slope preferences of the 14 EUNIS habitats identified on the rocky reefs of Portofino. See Table 1 for habitat codes and extended names. Codes are centered on mean values, while ellipses depict the 95% confidence region (the two axes of the ellipses represent confidence limits for depth and slope, respectively); (b) mean % cover of *C. cylindracea* in the 14 EUNIS habitats (error bars represent 1 standard error). For the number of samples belonging to each EUNIS habitat see Table 1 (column *n*).

**Table 1.** EUNIS habitats recognized in the rocky reefs of Portofino MPA between 1 m and 45 m depth. Here, *n* is the number of samples belonging to a specific EUNIS habitat. Where necessary (e.g., nomenclatural updates), extended names have been emended with respect to the original ones.

Code	Extended Name	<i>n</i>
HABITATS CHARACTERIZED BY MACROALGAE		
A3.131	Facies with encrusting algae ( <i>Lithophyllum incrustans</i> ) and sea urchins	23
A3.135	Association with <i>Ellisolandia elongata</i>	17
A3.231	Association with <i>Codium vermilara</i>	5
A3.23F	Association with <i>Dictyopteris polypodioides</i>	43
A3.23J	Association with <i>Flabellia petiolata</i> and <i>Peyssonnelia squamaria</i>	17
A3.331	Association with <i>Halopteris scoparia</i>	109
A4.261	Association with <i>Cystoseira zosteroides</i>	32
HABITATS CHARACTERIZED BY SEAGRASS		
A5.535	<i>Posidonia oceanica</i> beds	31
HABITATS CHARACTERIZED BY ZOOXANTHELLATE CORALS		
A3.238	Facies with <i>Cladocora caespitosa</i>	16
A4.26A	Facies with <i>Eunicella singularis</i>	43
HABITATS CHARACTERIZED BY CORALS		
A4.269	Facies with <i>Eunicella cavolini</i>	82
A4.26B	Facies with <i>Paramuricea clavata</i>	29
A4.26C	Facies with <i>Parazoanthus axinellae</i>	26
A4.322	Facies with <i>Leptogorgia sarmentosa</i>	9

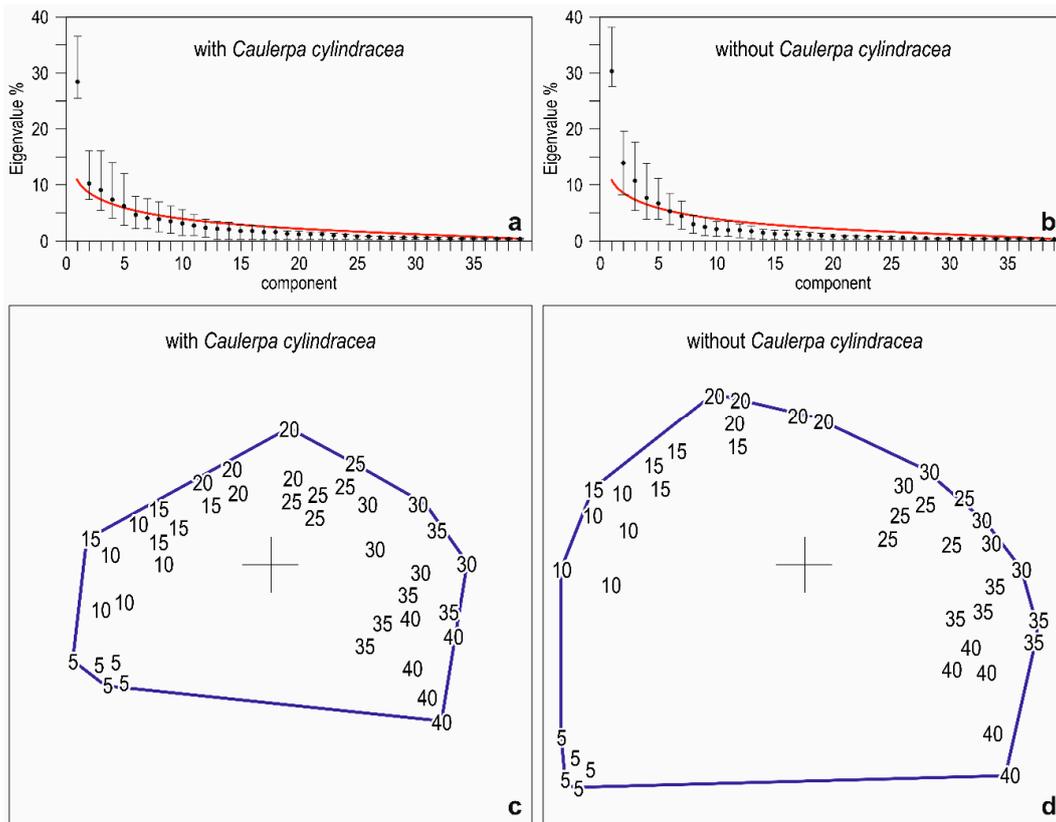
**Table 2.** Results of one-way analysis of variance on *Caulerpa cylindracea* cover data in the 14 EUNIS habitats recognized in the marine protected area of Portofino.

Source of Variation	SS	df	<i>s</i> <sup>2</sup>	<i>F</i> <sub>13,468</sub>	<i>p</i>
Among habitats	2077.91	13	159.84	2.45	0.003
Within habitats	30478.26	468	65.12		
Total	32556.17	481			

### 3.2. Simulation-Like Approach

As for the re-sampled datasets, PCA on the “observed” dataset of 67 species × 40 samples gave one highly significant component (Figure 6a), represented by the first (horizontal) axis in the resulting ordination model (Figure 6c). Sample points were ordered along a horse-shoe cloud, with shallow (5 m) samples on the left and deep (40 m) samples on the right, and with the remaining samples being regularly spaced among them. This geometry of the ordination model is known to indicate the existence of a major gradient, essentially expressed along the first axis. In this case, the gradient was obviously depth, with scores along the first axis being significantly correlated with depth ( $R^2 = 0.913$ ,  $n = 40$ ,  $p < 0.001$ ). Consistently, differences among depth scores were highly significant (Table 3).

Also the PCA on the “simulated” dataset of 66 species × 40 samples gave one highly significant component (Figure 6b) and a horse-shoe ordination model (Figure 6d). Even in this case, the first axis was highly correlated with depth ( $R^2 = 0.954$ ,  $n = 40$ ,  $p < 0.001$ ), and differences among depth scores were again highly significant (Table 3). However, the sample points were not as regularly spaced as in the case of the “observed” dataset (Figure 7a), but rather formed three groups separated by obvious gaps: 5 m depth, 10 m to 20 m depth, and 25 m to 40 m depth (Figure 7b). The difference among these three groups was highly significant (Table 4). The convex hull of the “simulated” dataset was visibly wider—and thus multivariate dispersion was larger—than that of the “observed” dataset (Figure 6c,d). Consistently, average dissimilarity, standard deviation, and coefficient of variation among samples were greater in the absence of *C. cylindracea* than in its presence (Table 5).



**Figure 6.** Results of principal component analysis on the “observed” dataset (67 species × 40 samples) (a,c) and on the “simulated” dataset (66 species × 40 samples) (b,d). Panels (a,b) illustrate the percentage of the total variance explained by each axis (component), with 95% bootstrapped confidence intervals (error bars); the red curves represent the eigenvalues expected under a broken-stick random model. Sample points in (c,d) are indicated by their depth (in m), while the convex hulls visualize the multivariate dispersion of the points, with axes being always drawn at the same scale.

**Table 3.** Results of one-way analysis of variance on the first axis scores of depth-points in PCA plots for both the “observed” and the “simulated” datasets.

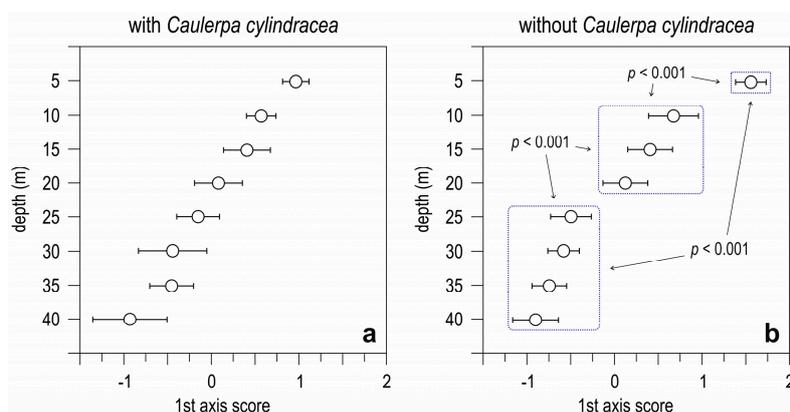
Source of Variation	SS	df	s <sup>2</sup>	F <sub>7,32</sub>	p
<b>“Observed” Dataset</b>					
Among depths	3.73	7	0.53	83.4	9.96 × 10 <sup>-19</sup>
Within depths	0.20	32	0.01		
Total	3.93	39			
<b>“Simulated” Dataset</b>					
Among depths	6.42	7	0.92	111.1	1.29 × 10 <sup>-20</sup>
Within depths	0.26	32	0.01		
Total	6.68	39			

**Table 4.** Results of one-way analysis of variance on PCA first axis scores among the three depth groups recognized in the case of the “simulated” dataset.

Source of Variation	SS	df	s <sup>2</sup>	F <sub>2,37</sub>	p
Among depth groups	23.2559	2	11.6279	225.6	1.87 × 10 <sup>-21</sup>
Within depth groups	1.9068	37	0.0515351		
Total	25.1627	39			

**Table 5.** Values of the average dissimilarity (1—Bray-Curtis coefficient), standard deviation, and coefficient of variation among samples in the “observed” and in the “simulated” datasets.

Indices	“Observed” Dataset	“Simulated” Dataset
Average dissimilarity	0.51	0.61
Standard deviation	0.16	0.19
Coefficient of variation	0.32	0.49



**Figure 7.** Relationship between PCA first axis scores and sample depth for both the “observed” (a) and the “simulated” datasets (b). In both graphs, circles represent mean scores and error bars are the 95% confidence limits. In the “observed” dataset no discontinuity is apparent, while in the “simulated” dataset three groups can be distinguished (dotted line rectangles). All differences in first axis scores for the three groups are highly significant (Tukey’s pairwise comparisons).

#### 4. Discussion

*Caulerpa cylindracea* was abundant in the rocky reefs of Portofino, as illustrated by field data. Relative abundance (here expressed as % cover) is a recommended index to gauge the invasion level of an alien species [70]. With an average cover of about 10% (with peaks to 25%), *C. cylindracea* can be defined a strong invader [54]; nevertheless, its impact to the recipient communities has been shown significant already with low cover [71].

*C. cylindracea* spread through the whole Marine Protected Area, including the “no entry, no take” zone. MPAs are mostly designed to manage fisheries [72], and may even help restore ecosystems through enhanced top-down control [73], but cannot prevent the introduction of alien species [74,75]. In Portofino, constancy of *C. cylindracea* cover values for six years (2012 to 2017) suggests that it has reached the so-called phase of persistence—the last of the four phases identified in the process of naturalization of introduced species [76,77].

As already observed in other Mediterranean sites [41], *C. cylindracea* showed a wide depth range at Portofino, with a preference for about 20 m depth, and invaded all the communities existing there, although with different intensities. Our study is the first to make a direct comparison of the quantitative incidence (in term of % cover) in as many as 14 communities (defined following EUNIS habitat classification). Notwithstanding significant differences of *C. cylindracea* cover among the 14 individual habitats, no clear pattern (aside from depth) was discernible according to the nature of the habitats, with macroalgal associations, seagrass beds, coral facies, and zooxanthellate coral facies all being colonized by *C. cylindracea*. It has been recognized that the impacts of invasive species are often context-dependent, both on land [78,79] and in the sea [29], and may depend on the idiosyncrasy of the eco-evolutionary history of the recipient communities [80]. The relationship between species richness and the invasions of alien species may be either positive or negative, mostly depending on scale [81]. At Portofino, increased cover values of *C. cylindracea* were associated with reduced species richness,

as reported in many studies [82,83]. It has been shown that reduced species richness can in turn further accelerate invasion [81].

The depth gradient in the presence of *C. cylindracea* showed no discontinuity, suggesting that the benthic communities replaced each other gradually. On the contrary, when *C. cylindracea* was excluded from the analysis three sharply distinguished situations were recognizable, separated by discontinuities that correspond well with known ecological thresholds in light intensity and water movement [84]. Such a result indicates that the high environmental adaptability of *C. cylindracea* [40] overcomes the severity of the ecological gradients that typically dictate the depth zonation of native communities in the infralittoral and circalittoral zones in Mediterranean rocky reefs [84]. This effect and other indicators and indices (multivariate dispersion, average dissimilarity, standard deviation, and coefficient of variation) consistently point to the homogenization caused by *C. cylindracea* invasion.

The problem of homogenization in terrestrial ecosystems is better known than in marine ecosystems, which affects our ability to make ecological assessments of change [85]. We used a simulation-like approach to evidence that *C. cylindracea* is cause of homogenization in the recipient ecosystem. In particular, the depth gradient was better defined, with a greater multivariate dispersion, when the invader was excluded from the analysis. Multivariate dispersion is considered a measure of  $\beta$  diversity [86], i.e., the variability in species composition among communities within an area. Consistently, it has been demonstrated experimentally that *C. cylindracea* depresses  $\beta$  diversity in invaded ecosystems [87].

Apparently *C. cylindracea* did not replace any native species, most of them having already disappeared or got rarer due to climatic and local human impacts during the 1980–90s ecosystem shift at Portofino reefs [32]. Thus, *C. cylindracea* acted more as a “passenger”, i.e., a passive opportunist taking advantage of environmental change, than a “driver”, i.e., a genuine actor of ecosystem degradation [88]. There is presently a debate about whether invasive species act as passengers or drivers of global change [89,90]. Removal experiments led to the conclusion that *C. cylindracea* acted as a passenger at the beginning of the invasion to become a driver once established [91]. As drivers, invasive species exert an impact on Mediterranean marine ecosystems that may exceed that of sea water warming [92]. The analysis of many correlative and experimental studies led to the conclusion that the invasion by *C. cylindracea* is one of the most threatening in the Mediterranean Sea [93].

## 5. Conclusions

This study assessed the abundance and widespread occurrence of *Caulerpa cylindracea* in Portofino across depth zones and EUNIS habitats. EUNIS, the European Nature Information System, was created to provide European administrators and scientists with a common frame for conservation [94]. Future studies on *C. cylindracea* should refer to the invaded EUNIS habitats in order to establish their vulnerability ranking and to search for common approaches to the management of biological invasions. Further evidence of the role that invasive species may play in the biotic homogenization of the recipient ecosystem is also needed.

Two recent European Union Directives, the Marine Strategy and the Biodiversity Strategy, stressed the importance of collecting information on trends in abundance, temporal occurrence, and spatial distribution of invasive species [40,95]. Beside experimental studies, continued monitoring activity carried out with a macroecological approach [96] similar to the one undertaken in the present paper is needed to understand and assess the pattern and extent of *C. cylindracea* insertion in the recipient ecosystems.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/11/9/146/s1>. Table S1: Comprehensive database. Table S2: Re-sampled dataset.

**Author Contributions:** Conceptualization, C.M. and C.N.B.; Methodology, M.M., G.G., P.V., C.P.; Software, P.V., C.P. and C.N.B.; Validation, P.V. and C.P.; Formal Analysis, P.V., C.P. and C.N.B.; Investigation, M.M., G.G., and C.N.B.; Resources, C.M. and C.N.B.; Data Curation, C.M., M.M., G.G. and C.N.B.; Writing – Original Draft

Preparation, C.M., M.M., P.V., C.P. and C.N.B.; Writing – Review & Editing, C.M. and C.N.B.; Visualization, C.M. and C.N.B.; Supervision, C.M. and C.N.B.; Project Administration, C.M.; Funding Acquisition, C.M.

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

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