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Exploring the Structure of Seaweed Assemblages Under the Pressure of Non-Indigenous Species (NIS) in the Transitional Water System Mar Piccolo of Taranto (Mediterranean Sea, Southern Italy)

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Highlights

What are the main findings?

- The basin shows a heterogeneous response to NIS expansion, driven by local environmental filtering.
- Diverse native canopies act as biological barriers limiting NIS dominance and preventing replacement.
- NIS integrate into spatial frameworks without erasing site-specific biological signatures.

What are the implications of the main findings?

- Monitoring must move beyond species lists to biomass-based evenness for better health assessment.
- Preserving diverse native canopies is critical to buffering against NIS spatial dominance.
- Local abiotic factors provide a predictable landscape for managing future biological invasions.

Abstract

This study characterizes macroalgal assemblage structure in the transitional water system Mar Piccolo of Taranto (eLTER site) from 2012 to 2023, assessing the impact of non-indigenous species (NIS) establishment. Seasonal sampling at three sites evaluated diversity and biomass variation through PERMANOVA, PCoA, PERMDISP and Indicator Value (IndVal) analyses. Results reveal significant spatio-temporal heterogeneity: Site 1 remains dominated by native species (>70% biomass), summer peaks of NIS were recorded at Site 3, whereas Site 4 experienced a substantial NIS expansion, reaching 97% of total biomass by 2021. Statistical clustering identified distinct indicator species for each inlet, such as *Amphiroa beauvoisii* in the First Inlet and the NIS *Hypnea corona* in the Second. Water temperature emerged as a primary driver of community shifts. Most species, including both native (*Chondracanthus acicularis*) and several NIS (*Polysiphonia morrowii*, *Osmundea oederi*), exhibited negative correlations with mean thermal values, while *Ulva laetevirens* showed greater tolerance. These findings highlight the importance of LTER monitoring in demonstrating that the Mar Piccolo's resistance to NIS pressure is non-uniform across the basin. Under a global warming scenario, thermal forcing is actively reshaping macroalgal assemblages.

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1. Introduction

As dominant macroscopic autotrophs within coastal ecosystems, seaweeds provide a diverse array of essential ecosystem services, ranging from carbon sequestration to the provision of complex habitats for marine fauna [1,2]. Beyond their role in photosynthetic oxygen production at the base of the marine food web functioning, these organisms facilitate community persistence by serving as a primary food source and providing complex biogenic habitats that function as nurseries for early life-history stages [2]. Furthermore, these organisms represent a versatile resource for advancing multiple Sustainable Development Goals, with applications ranging from human nutrition to diverse industrial biotechnologies [1]. Therefore, the structural and functional persistence of these communities is of paramount importance to the health of the broader marine environment. Given the inherent stochasticity of marine environments, macroalgae have evolved significant adaptive plasticity to mitigate fluctuations in biotic and abiotic stressors. However, taxa exhibiting narrow tolerance ranges for physicochemical variables—including irradiance, thermal regimes, salinity, and nutrient flux—frequently face competitive exclusion or mortality under extreme environmental shifts [1,3,4]. Anthropogenic climate forcing and the introduction of non-indigenous species (NIS) represent dual threats to seaweed communities. Their cumulative impact has generally increasingly compromised population dynamics and physiological fitness in coastal waters [5,6], but this condition is species dependent. The colonization of non-indigenous species (NIS) can drastically alter the architecture of benthic communities [7], since invasive macroalgae often exhibit high phenotypic plasticity and rapid growth rates, allowing them to outcompete native perennial species. On New England rocky reefs, the invasive *Dasysiphonia japonica* (Yendo) H.-S. Kim (Ceramiales, Rhodophyta) (formerly *Heterosiphonia japonica* Yendo) has demonstrated significant competitive superiority over native taxa. This dominance is characterized by accelerated growth rates and a superior efficiency in nitrate uptake, allowing it to rapidly colonize northwestern Atlantic substrates [8]. While the structural integrity of seaweed-dominated habitats is critical for marine biodiversity, empirical research quantifying the impacts of NIS on these native assemblages remains still scarce, regardless of whether it is negative or positive. Evidence from Favignana Island (Egadi Islands, Tyrrhenian Sea) underscores the disruptive potential of *Asparagopsis taxiformis* (Delile) Trevisan (Bonnemaisoniales, Rhodophyta), where its proliferation, starting from 2000, led to the degradation of *Ericaria brachycarpa* (J. Agardh) Molinari & Guiry (Fucales, Heterokontophyta) populations. Beyond the loss of primary producer biomass, the invasion triggered a cascading effect, diminishing the diversity and density of the local epifaunal community [9].

Transitional water systems are highly susceptible to the establishment of NIS due to a combination of inherent environmental stochasticity and intense anthropogenic pressure. In particular, activities such as aquaculture and the global trade of mollusks serve as primary vectors for NIS seaweed introduction in these already fluctuating habitats [10–12]. Within the Mediterranean region, the Venice Lagoon is a critical hotspot for non-indigenous seaweeds, with 33 NIS recorded over the last decade [13]. These species represent a broad spectrum of origins and ecological fates; notably, none have yet been associated with significant environmental disruption, suggesting a complex dynamic between invasion pressure and ecosystem stability. Contrary to typical invasion paradigms, the introduction of *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Gracilariales, Rhodophyta) in 2008 has been linked to improved environmental quality in the Venice Lagoon. Over a 13-year period, it has replaced hypoxia-inducing Ulvales, thereby reducing oxygen stress during summer peaks and fostering increased faunal richness [13]. Notwithstanding the potential for ecological recovery, the high biomass of these NIS interferes with traditional fishing activities. The clogging of nets diminishes harvest yields, and the entrapment of seaweed (e.g., *Sargassum muticum* (Yendo) Fensholt (Fucales, Heterokontophyta)) in outboard engines hinders navigation [13], creating a conflict between biological shifts and anthropogenic lagoon use [14]. In the Atlantic context of the Ria Formosa lagoon (southern Portugal), the invasion of *Caulerpa prolifera* (Forsskål) J.V. Lamouroux (Caulerpales, Chlorophyta) over a decade has proved highly disruptive. By displacing native seagrasses and inhibiting the development of local invertebrate populations — including the echinoid *Paracentrotus lividus* (Lamarck, 1816) — this species has fundamentally altered the lagoon's trophic structure and biological composition. Biodiversity in the lagoon has been further compromised by the arrival of *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotales, Heterokontophyta). This invasion triggered a shift in the local herbivore guild, characterized by the gradual substitution of the native sea urchin *P. lividus* by *Sphaerechinus granularis* (Lamarck, 1816) [15].

In the Mar Piccolo of Taranto, a transitional water system with lagoon features, the implementation of long-term research within the eLTER infrastrucuture has facilitated a robust, high-resolution monitoring framework. This consistent data collection enables not only a continuous update of phytobenthic biodiversity but also the rapid detection of NIS, providing the geographical context necessary to track their colonization dynamics and identify the environmental drivers of their success or decline [12]. However, while several studies have focused on the inventory of NIS in the Mar Piccolo [12], there is still a critical need to understand how these colonizers influence the broader structural dynamics of seaweed assemblages over time [16].

This study investigates the diversity and structure of seaweeds assemblages distributed in the Mar Piccolo, focusing the attention on the changes in biomass of native and alien species and the identification of characteristic taxa of the assemblages, since the functional integrity of phytobenthic communities is essential for long-term ecosystem stability.

2. Materials and Methods

2.1. Study Area

The Mar Piccolo of Taranto is a semi-enclosed transitional water system situated north of the city. The basin is divided into two sub-basins—the First and Second Inlets—forming a roughly elliptical coastal environment (Figure 1). A defining hydrographic feature of the system is the presence of 34 submarine springs, locally termed 'citri'. These springs provide a consistent input of brackish water (mean temperature: 18 °C; salinity: 2.3–4.7 PSU), creating a unique environmental gradient. Consequently, the basin's broader physicochemical profile exhibits significant seasonality, with seawater temperatures fluctuating between 7.5 °C and 32.3 °C and salinities ranging from 33.0 to 37.8 PSU.

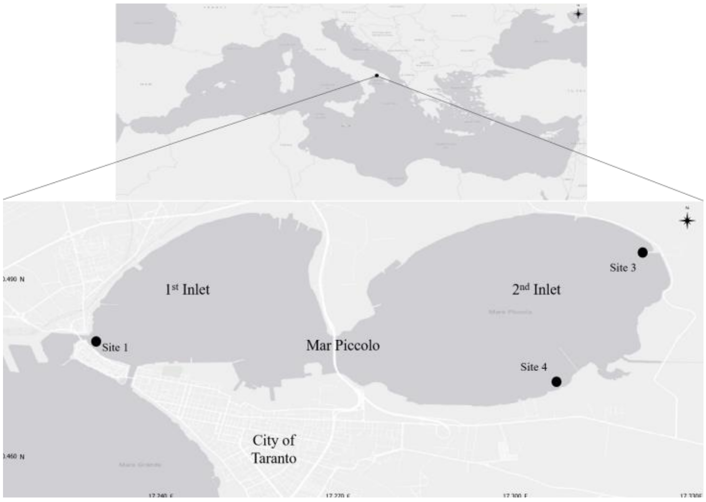

Figure 1. Map of the Mar Piccolo of Taranto with the investigated sites (•). The top pane shows the location of Taranto in Italy.

2.2. Sampling Procedure

From 2012 to 2023, seasonal macroalgal sampling was performed at three designated sites (Figure 1, Table 1) at a maximum depth of 50 cm. At each site, three replicates of 50 × 50 cm quadrats were randomly established, and all phytobenthic biomass within the frames was collected via surface scraping. Harvested material was transported to the laboratory in labeled polyethylene bags and temporarily stored in mesh nets within flow-through seawater tanks. Following manual sorting, taxonomic identification was conducted to the species level using Leica MZ 12 stereomicroscopes and Leica DMR light microscopes (Leica Microsystems GmbH, Wetzlar, Germany). Quantitative biomass was determined as drained wet weight (g ww) using a Sartorius L2200P analytical balance (Sartorius Lab Instruments GmbH, Göttingen, Germany).

Table 1. Coordinates of the investigated sites of the Mar Piccolo of Taranto. Site 1 is located in the First Inlet. Site 3 and Site 4 are located in the Second Inlet.

Site	Lat	Long
Site 1 - Scaletta	40° 28.773′N	17° 13.687′E
Site 3 - Battendieri	40° 29.660′N	17° 19.388′E
Site 4 – Cimino	40° 28.180′N	17° 18.069′E

2.3. Temporal Analysis of Diversity and NIS Fluctuations

Seasonal diversity of macroalgal assemblages was analyzed for the period 2012–2023 across all study sites. Alpha diversity was assessed using Margalef’s richness (d), the Shannon-Wiener index (H’), and Pielou’s evenness (J). Furthermore, seasonal biomass (g m-2) and relative percentage contributions were calculated separately for native species (NatS) and non-indigenous species (NIS). Temporal trends and significant correlations among these indices were evaluated using the non-parametric Mann-Kendall test (tau) [17,18], with significance levels determined via 9,999 permutations. All diversity indices and statistical analyses were performed using PAleontological STatistics (PAST) software, version 4.16 [19].

2.4. Evaluating Spatiotemporal Variation in Macrophytic Communities

Spatial and temporal variations in macroalgal assemblage structure from 2012 to 2023 were evaluated using a multifactorial Permutational Multivariate Analysis of Variance (PERMANOVA) [20]. To refine the dataset, species were filtered based on their frequency of occurrence (FO%), with only those exceeding a 2% threshold included in the final analysis (resulting in 53 selected species). Biomass data were subjected to a fourth-root transformation prior to analysis to minimize the influence of dominant taxa and account for the contribution of rarer species [21]. Multivariate analyses were performed based on a Bray-Curtis similarity matrix derived from a 430 × 53 (Replicates × Species) data structure. A multifactorial PERMANOVA was employed to test the following factors: Site (fixed, 3 levels), Year (fixed, 12 levels), Season (fixed, 4 levels), and Replicates (random, 3 levels). Significance was determined using 9,999 permutations of residuals under a reduced model, testing all main factors as well as the “Year × Site” and “Season × Site” interactions. For significant results ($p < 0.05$), post hoc pairwise t-tests were conducted using Monte Carlo p-values to resolve differences between factor levels [20]. Patterns were visualized via Principal Coordinate Analysis (PCoA) [22], with centroids plotted to represent significant complex interactions. To evaluate seasonal heterogeneity within the macroalgal assemblages at each site, a Permutational Test of Multivariate Dispersion (PERMDISP) [23] was performed. Significance was determined via 9,999 permutations, testing for differences in the mean distance to centroids for the “Site × Season” interaction levels. All multivariate procedures were executed using the PRIMER v6 + PERMANOVA+ software package [20,24].

2.5. Identifying Key Taxa in Spatiotemporal Seaweed Patterns

To identify characteristic species within the macroalgal assemblages, the Indicator Value (IndVal) index was calculated [25,26] using seasonal biomass data from 2012–2023. This method was selected to provide a refined characterization of community structure by highlighting species that, while potentially low in biomass, exhibit high site fidelity and occurrence throughout the year. The IndVal score for a given species is determined based on the following equation:

$$IndVal = A \times B \times 100$$

In this formula, Specificity (A) represents the relative biomass of a species within a specific group, while Fidelity (B) denotes its relative frequency of occurrence across replicates within that group. Species were categorized as characteristic if they achieved an IndVal score ≥ 0.25 [26]. Following the hierarchical approach proposed by [25], the maximum Indicator Value ($\text{IndVal}_{\text{max}}$) was identified by nesting samples across five distinct division levels: Level 1 = all sampling sites pooled; Level 2 = Sites partitioned by basin (First Inlet: Site 1; Second Inlet: Sites 3 and 4); Level 3 = Intra-basin partitioning of the Second Inlet (North Zone: Site 3; South Zone: Site 4); Level 4 = Paired contiguous seasons (Winter–Spring and Summer–Autumn) within each site; Level 5 = Individual seasons within each site.

The $\text{IndVal}_{\text{Max}}$ identifies both stenotopic and eurytopic species based on their response to the hierarchical division levels. Stenotopic species, characterized by a narrow niche breadth, serve as indicators for a single division level (e.g., a specific season at a specific site). For these taxa, the indicator value typically increases as the hierarchy narrows toward their specific environmental niche. Conversely, eurytopic species exhibit a broad niche breadth; their indicator values decrease progressively as site groups are subdivided, reflecting their widespread distribution across multiple spatial or temporal clusters [25]. The IndVal analysis was carried out using PAST software (version 4.16) [19].

2.6. Assessing Temperature-Assemblage Correlations

Potential relationships between water temperature (T °C), biomass (NatS and NIS), and diversity indices were evaluated using in situ thermal data collected with TG-4100 - Tinytag Aquatic 2 Datalogger. Continuous recordings were available from 2015 onward for all sites. Following the removal of data anomalies and sensor errors, seasonal temperature metrics—specifically mean (T_{mean}), minimum (T_{min}), and maximum (T_{max}) values—were integrated with the corresponding seasonal biological datasets (Table S2). The Spearman rank correlation coefficient (rs) was employed to assess the strength and direction of associations between variables, with significance levels determined via 9,999 permutations. Furthermore, correlations between T_{mean} and the biomass of individual species were analyzed to identify specific thermal affinities. The analysis was carried out using PAST software (version 4.16) [19].

3. Results

3.1. Dynamics of Community Diversity and NIS Occurrences

At Site 1, species richness (d) exhibited a significant positive temporal trend (tau= 0.342, $p<0.001$), whereas the total biomass of native species showed a negative trend (tau= -0.307, $p<0.01$) (Table 2; Table S3).

Table 2. Correlation coefficients (*tau*) and temporal trends for native species (NatS) biomass, non-indigenous species (NIS) biomass, and alpha diversity indices (Margalef richness, d; Shannon-Wiener diversity, H'; and Pielou's evenness, J) across the study sites. Values below the diagonal (grey cells) represent the Kendall's *tau* and associated p-values determined via Mann-Kendall tests (9,999 permutations) for each pairwise comparison. Blue and red values denote significant increasing and decreasing trends, respectively. Significant p-values ($p < 0.05$) are highlighted in bold.

Site		Time	d	H	J	NatS	NIS
1	Time		>0.001	0.469	0.436	>0.01	0.464
	d	0.342				0.069	>0.001
	H	0.074				0.127	>0.001
	J	-0.078				0.188	>0.05
	NatS	-0.307	-0.181	-0.154	-0.133		0.519
	NIS	-0.078	0.357	0.394	0.243	0.069	
3	Time		0.255	0.309	0.362	0.651	0.548
	d	0.114				0.131	0.078
	H	0.103				>0.001	>0.05
	J	0.092				>0.001	>0.05
	NatS	0.046	0.152	0.365	0.362		>0.01
	NIS	0.061	-0.182	-0.247	-0.220	-0.316	
4	Time		>0.05	0.537	0.773	0.934	>0.05
	d	0.222				0.456	0.675
	H	0.062				0.075	0.080
	J	-0.030				>0.05	0.066
	NatS	-0.009	-0.074	0.181	0.206		0.420
	NIS	0.221	-0.043	0.173	0.186	0.083	

Furthermore, total NIS biomass was positively correlated with all diversity indices (d *tau* = 0.357, $p<0.001$; H' *tau* = 0.394, $p<0.001$; J *tau* = 0.243, $p<0.05$). At Site 3, no significant temporal trends were observed for any of the investigated indices. However, correlation analysis revealed contrasting roles for native and non-indigenous components: total NatS biomass was significantly and positively correlated with both Shannon-Wiener diversity (H', *tau* = 0.365, $p < 0.001$) and Pielou's evenness (J, *tau* = 0.362, $p < 0.001$). Conversely, total NIS biomass exhibited significant negative correlations with both diversity indices ($p < 0.05$) and demonstrated an inverse relationship with total NatS biomass (*tau* = -0.316, $p < 0.01$). At Site 4, significant positive temporal trends were identified for species richness (*tau* = 0.222, $p < 0.05$) and total NIS biomass (*tau* = 0.221, $p < 0.01$). Additionally, a significant positive correlation was observed between NatS biomass and Equitability (*tau* = 0.206, $p < 0.05$). The relative percentage of NatS and NIS allowed to detect distinct spatial and temporal trajectories across the study sites (Figure 2, Table S3).

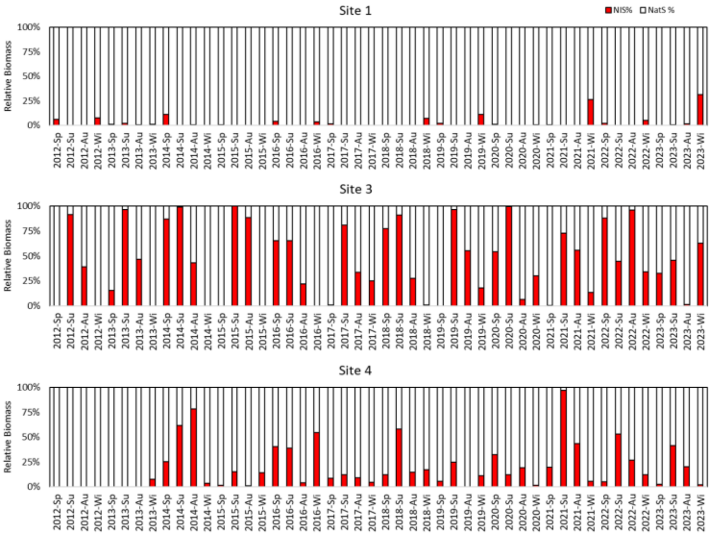

Figure 2. Seasonal percentage contribution of native (NatS) and non-indigenous species (NIS) biomass from 2012 to 2023. Data are expressed as mean percentage values per season.

At Site 1, NatS remained consistently dominant throughout the time series, typically exceeding 70% of the total biomass; NIS reached a maximum contribution of only 31% in winter 2023. In contrast, Site 3 displayed a clear seasonal cycle where NIS biomass peaked during the spring–autumn period—frequently exceeding 70% in summer—while remaining negligible or absent in winter. Notably, this summer dominance weakened in 2022 and 2023, with NIS values falling below 50%. At Site 4, NIS were absent until autumn 2013, after which they showed a progressive increase, reaching a maximum of 97% in summer 2021. The seasonal phenology at Site 4 shifted over time: NIS biomass was concentrated in autumn and winter between 2011 and 2017, whereas the highest peaks transitioned to the summer months during the 2018–2023 period.

3.2. Spatiotemporal Configuration of Seaweed Assemblages

The multifactorial PERMANOVA revealed significant spatial and temporal variations in macroalgal assemblage structure across all primary factors and their interactions, including Site, Year, and Season (Table 3). Notably, no significant differences were detected among replicates, confirming the high degree of internal consistency and representativeness of the sampling units within each site.

Table 3. Multifactorial PERMANOVA results examining the effects of Site (Si), Year (Ye), Season (Se), and Replicates (Rep) on macroalgal assemblage structure. The analysis was based on a Bray-Curtis similarity matrix of fourth-root transformed biomass data. P-values (P_{perm}) were calculated using 9,999 permutations of residuals under a reduced model. df: degrees of freedom; SS: sum of squares; MS: mean sum of squares; Pseudo-F: multivariate F-statistic.

Source of variation	df	SS	MS	Pseudo-F	P perm
Si	2	4.36E+0.5	2.18E+0.5	128.68	0.0001
Ye	11	85633	7784.8	4.5987	0.0001
Se	3	1.04E+05	34799	20.557	0.0001
Rep	2	2321.5	1160.7	0.68568	0.8743
Si x Ye	22	1.30E+05	5901.8	3.4863	0.0001
Si x Se	6	9.68E+04	16136	9.5322	0.0001
Ye x Se	33	1.35E+05	4102.8	2.4236	0.0001
Si x Ye x Se	66	2.16E+05	3278.6	1.9368	0.0001
Residuals	284	4.18E+05	1692.8		
Total	429	1.70E+06			

PERMDISP analysis revealed significant seasonal shifts in multivariate dispersion at Site 3, where the mean distance of replicates to the group centroid—a proxy for assemblage heterogeneity—decreased significantly during the summer and autumn (Figure 3). Conversely, multivariate dispersion remained stable at Sites 1 and 4, with no significant seasonal variations observed.

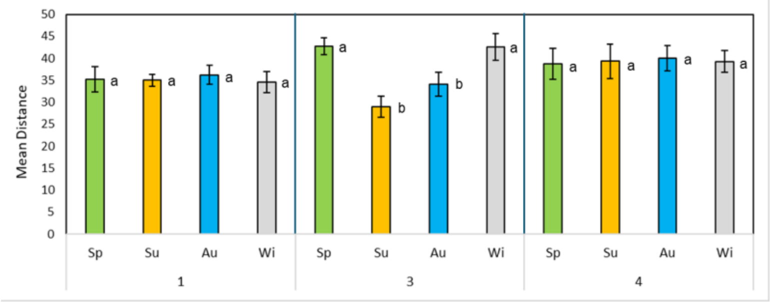

Figure 3. Results of PERMDISP analysis showing seasonal heterogeneity across sampling sites. Mean distances to centroids (bars) and standard errors (vertical lines) are reported for each Site × Season combination. Significant seasonal differences within a site are indicated by distinct lowercase letters ($p<0.05$).

The PCoA ordination of "Site × Year" centroids revealed a distinct spatial separation among the three sampling sites, with the first two axes explaining 70.4% of the total multivariate variance (PCO1: 54.1%; PCO2: 16.3%; Figure 4). Site 1 was characterized by a suite of native taxa, including *Corallina officinalis*, *Dictyota dichotoma* var. *intricata*, *Amphiroa beauvoisii*, and *Ellisolandia elongata*, as well as the NIS *Colpomenia peregrina* and *Grateloupia turuturu*. Sites 3 and 4 were primarily segregated along the second axis, with Site 3 showing a strong correlation with the NIS *Hypnea corona* and the native *Alsidium corallinum*. Conversely, Site 4 was primarily characterized by the presence of *Chondracanthus acicularis*, *Ulva laetevirens*, and *Gelidium crinale*, alongside the NIS *Grateloupia minima* and *Caulacanthus okamurae*. The PCoA ordination revealed high interannual stability at Site 1, evidenced by the tight clustering of centroids, with the exception of 2021 and 2023. In contrast, Site 3 exhibited the highest interannual variability, as indicated by the wide dispersion of centroids. These temporal shifts at Site 3 formed distinct clusters: (i) 2012, 2013, 2016, and 2017; (ii) 2014, 2015, and 2019; (iii) 2018, 2020, and 2023; and (iv) 2021 and 2022. Site 4 exhibited an intermediate level of interannual variability; while its centroids were more dispersed than those of Site 1, they did not form the distinct temporal sub-groups observed at Site 3. In particular 2014 and 2021 emerged as significant temporal outliers in this site. These multivariate patterns were corroborated by the post hoc pairwise t-test results (Table S4), which revealed a gradient of community flux across the study area: the highest number of significant interannual differences was recorded at Site 3 (46 pairs), followed by Site 4 (40 pairs) and Site 1 (28 pairs).

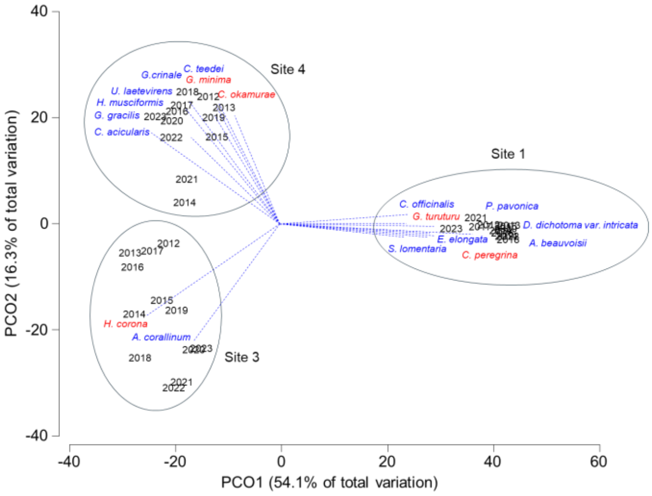

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Figure 4. Principal Coordinate Analysis ordination (PCoA) of "Year × Site" centroids using the Bray–Curtis similarity measure. Blue dashed vectors indicate the primary species driving the ordination (Pearson's $r > 0.7$), with NIS labels shown in red. The percentage of total multivariate variance explained by each axis is reported. Black circles represent the annual centroids for each site across the 2012–2023 period.

3.3. Spatiotemporal Variations in Dominant Seaweed Taxa

IndVal analysis clearly distinguished two distinct groups of characteristic species corresponding to the First and Second Inlets of the Mar Piccolo (Figure 5). Within the First Inlet, *Amphiroa beauvoisii*, *Ellisolandia elongata*, and *Dictyota dichotoma* var. *dichotoma* emerged as perennial indicators, maintained across all seasons. Seasonal associations were also evident: *Jania rubens* characterized the summer–autumn period, while the winter–spring period was defined by *Padina pavonica*, *D. dichotoma* var. *intricata*, and the NIS *Colpomenia peregrina* and *Grateloupia turuturu*. Furthermore, narrow temporal niches were identified for *Scytosiphon lomentaria* and the NIS *Polysiphonia morrowii*, which were exclusive to winter, and *Colpomenia sinuosa*, which was characteristic of spring

Analysis of the Second Inlet identified a stable group of year-round indicators, including *C. acicularis*, *Chaetomorpha linum*, *Spyridia filamentosa*, *U. laetevirens*, and the invasive *H. corona*. In the North Zone (Site 3), *A. corallinum* was the only perennial species, with *Radicilingua mediterranea* (winter–spring) and *Osmundea oederi* (winter) representing the primary seasonal indicators. Conversely, the South Zone (Site 4) hosted a more diverse set of characteristic taxa; *G. crinale*, *Chondracanthus teedei*, *Ceramium gaditanum*, and the NIS *C. okamurae* were present year-round. Seasonal dynamics at Site 4 were marked by *G. minima* (NIS), *Ulva intestinalis*, and *Gracilaria gracilis* in winter–spring, and *Gymnogongrus griffithsiae* and *Ulva rigida* in summer–autumn. Additionally, *Petalonia fascia*, *Ulva prolifera*, and *Ulva flexuosa* emerged as stenotopic indicators for winter and summer, respectively.

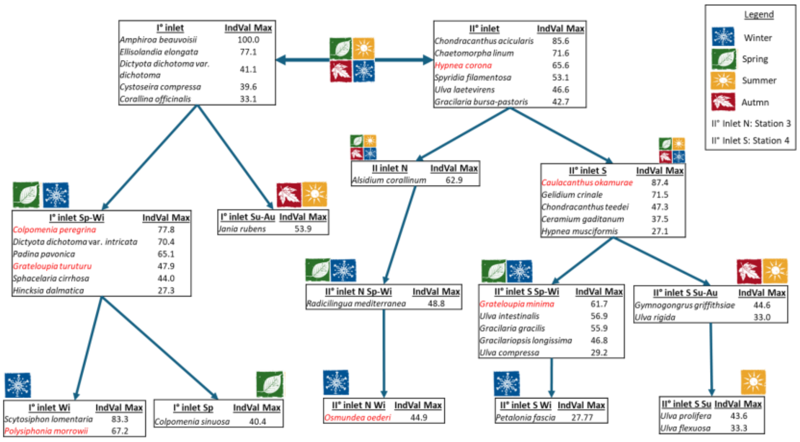

Figure 5. Distribution of characteristic macroalgal species within the Mar Piccolo hierarchical framework. Groups are defined based on $\text{IndVal}_{\text{max}}$ scores calculated for site and seasonal replicates. Non-indigenous species (NIS) and native taxa are categorized by their frequency and specificity to each sampling level.

3.4. Thermal Influence on Seaweed Community Structure

At Site 1, seawater temperatures ranged from 7.44 to 35.07 °C throughout the study period. Correlation analysis (Table 4) revealed that NIS biomass was significantly and negatively associated with both mean temperature ($r_s = -0.410$, $p < 0.05$) and maximum temperature ($r_s = -0.401$, $p < 0.05$). In contrast, no significant correlations were identified between thermal parameters and any of the investigated alpha diversity indices.

Table 4. Correlation analysis (r_s) and associated p-values between thermal parameters and assemblage indices. Minimum, mean, and maximum temperatures were correlated against species richness (d), diversity (H'), equitability (J'), and NatS and NIS biomasses. Coefficients (r_s) are shown in the lower-left diagonal, with permutation-derived p-values (n = 9,999) in the upper-right. Significant associations ($p < 0.05$, in bold) are color-coded to indicate increasing (blue) or decreasing (red) trends. >.

Site		T_{min}	T_{mean}	T_{max}	d	H	J	NatS	NIS
1	T_{min}				0.428	0.623	0.783	0.854	0.078
	T_{mean}				0.640	0.806	0.902	0.519	**0.020**
	T_{max}				0.392	0.883	0.973	0.743	**0.024**
	d	-0.144	-0.085	-0.154					
	H	-0.089	-0.046	-0.027					
	J	-0.050	-0.023	0.007					
	NatS	-0.034	-0.115	-0.060					
	NIS	-0.318	-0.410	-0.401					
3	T_{min}				**0.002**	0.256	0.839	0.472	**0.027**
	T_{mean}				**0.001**	0.155	0.544	0.599	**0.041**
	T_{max}				0.072	0.701	0.961	0.166	0.233
	d	-0.513	-0.551	-0.311					
	H	-0.202	-0.250	-0.069					
	J	-0.035	-0.107	-0.009					
	NatS	0.127	0.094	0.240					
	NIS	0.378	0.356	0.209					
4	T_{min}				**0.043**	0.586	0.854	**0.004**	**0.047**
	T_{mean}				**0.029**	0.772	0.741	**0.003**	0.099
	T_{max}				0.078	0.238	0.515	**0.012**	0.196
	d	-0.393	-0.421	-0.343					
	H	-0.107	-0.057	-0.234					
	J	-0.037	0.067	-0.133					
	NatS	0.551	0.568	0.474					
	NIS	0.389	0.321	0.257					

Correlation analysis revealed distinct site-dependent relationships between mean temperature and species-specific biomass (Figure 6). At Site 1, all analyzed NatS and NIS exhibited significant negative correlations with temperature. Among these, *P. morrowii* and *S. lomentaria* demonstrated the highest negative coefficients, reflecting a substantial reduction in biomass as mean temperatures increased. Correlation analysis for Site 3 identified *H. corona* (NIS) and *U. laetevirens* (NatS) as species positively associated with mean temperature. Conversely, *O. oederi* (NIS) demonstrated the strongest inverse relationship with thermal increase, with *C. acicularis* (NatS) also showing a high negative correlation coefficient (Figure 6).

At Site 4, nearly all analyzed species exhibited negative correlations with mean temperature, with the notable exception of *U. laetevirens*, which showed a positive association. The most significant biomass reductions in response to thermal increase were observed in the NIS *P. morrowii*, followed by the native *R. mediterranea* (Figure 6).

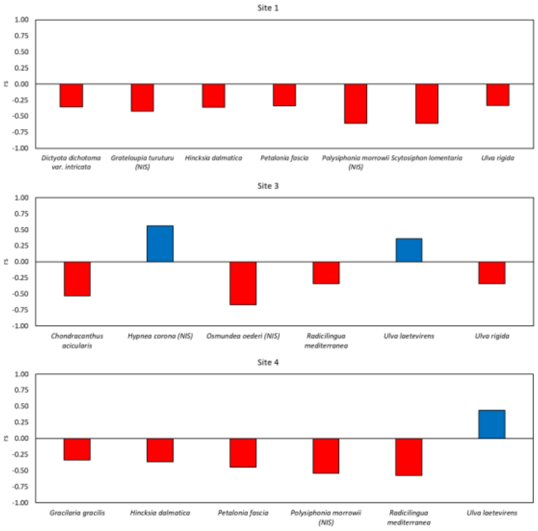

Figure 6. Significant correlations (r_s) between mean temperature and species-specific biomass. Only taxa with statistically significant relationships ($p < 0.05$) are displayed. Bar colors represent the direction of the trend: blue for positive associations and red for negative associations. NIS: non-indigenous species.

4. Discussion

This study identifies a shift in the phytobenthic assemblages of the Mar Piccolo, where the colonization and expansion of NIS seems to be restructuring the basin’s ecological framework, with a spatial heterogeneity in the responses by native communities. Biodiversity indices related to uniformity (Shannon) and equitability (Pielou) of the assemblages remain overall stable over time, while the species richness showed significant increases at Site 1 and 4. In the former site, the effect seems to be due to a significant reduction of native biomass occurred in the last 12 years, while in the latter site, the significant increase in NIS taxa abundance and number contributed to this change. Moreover, the biodiversity condition at Site 3 seems to reflect a stable assemblage over time, where seasonal variations in biomass of NIS species reduced the species diversity and the structural uniformity of assemblage in specific seasons. This would suggest a fundamental reconfiguration of community dynamics, that is the Mar Piccolo could transition from a native-dominated system to one where NIS determine the structural and functional characteristics of the benthic habitat. However, the phytobenthic assemblages of the Mar Piccolo of Taranto exhibit an interesting heterogeneous response to NIS expansion.

4.1. Drivers and Implications of NIS Fluctuations in Native Communities

The observed trends at Site 1, characterized by a significant increase in species richness alongside a decline in native biomass, seem to contradict the common belief that diverse communities resist invaders [27,28]. This would indicate that the environmental conditions facilitating high taxonomic diversity in the Mar Piccolo maybe also lower the barriers for NIS establishment at this site. However, the evaluation of percentage biomass, shows the persistent dominance of native species throughout the time series, confirming a high degree of biotic resistance within the phytobenthic assemblage. Experimental manipulative field studies, carried out in the Tyrrhenian Sea with the invasive NIS *Caulerpa taxifolia* (Vahl) C. Agardh and *C. cylindracea* Sonder (reported as *C. racemosa* (Forsskål) J. Agardh), showed that a well-structured native canopy can act as a physical and biological barrier, limiting the spatial expansion of NIS, especially where the seaweed community is composed by different functional groups [29]. At Site 1, the presence of turf, encrusting and erect species, most likely represents the most effective obstacle to the NIS spatial dominance. The absence of significant variations in equitability of seaweed assemblage at this site suggests a stability of the Mar Piccolo against a complete competitive replacement. The lack of significant temporal trends at Site 3 would indicate a state of apparent community equilibrium; however, the strong negative correlation between NIS and native biomass, with a summer percentage biomass around 70%, would point to an underlying competitive displacement process. This phenomenon is increasingly documented across Mediterranean coastal ecosystems [30]. For instance, the expansion of *Asparagopsis taxiformis* at the Egadi Islands (Sicily) led to a drastic reduction in native macroalgal biomass, with cascading effects on associated epifaunal assemblages [9]. Similarly, the Lessepsian seagrass *Halophila stipulacea* has been shown to directly reduce the shoot density of the native *Cymodocea nodosa* in northwestern Sicily [31], reinforcing the role of NIS as primary drivers of structural reconfiguration. Site 3 is characterized by low levels of urbanization, a factor that likely influenced the observed ecological interactions. This is consistent with experimental evidence from the Tyrrhenian Sea, supporting the hypothesis that the impacts of NIS on the structure of native communities are highly context-dependent. Specifically, NIS effects have been shown to shift from competitive exclusion in pristine environments to facilitative roles in areas heavily degraded by anthropogenic activities [28]. Moreover, this competitive shift may be further mediated by thermal forcing. The documented warming trend in local Mar Piccolo seawater temperatures (G. Denti, unpublished data) likely favors the proliferation of the warm-affinity NIS *Hypnea corona* during peak thermal periods. This occurs at the expense of native taxa ,such as *Chondracanthus acicularis*, which exhibits a narrower thermal optimum for growth and reproduction between 18 °C and 20 °C [32]. Such thermal niche partitioning suggests that climate change may be acting as a catalyst, weakening the competitive standing of temperate native species and facilitating the dominance of thermophilic NIS. At Site 4, the simultaneous positive temporal trends in species richness and NIS biomass suggest a process of species increase rather than immediate competitive exclusion. The positive correlation between native biomass and equitability underscores the importance of community structure for native persistence, since this index is a critical determinant of ecosystem function [33]; a balanced distribution of native species appears to support higher standing crops, potentially offering a degree of functional buffering against the recent ongoing NIS expansion observed at this site.

4.2. Drivers of Spatiotemporal Heterogeneity in Seaweed Assemblages

In transitional waters, benthic macrophyte assemblages exhibit significant spatio-temporal variability driven by fluctuating environmental conditions [4,34]. In the Venice Lagoon, spatial variability in macrophytes is closely tied to sediment grain size and nutrient content. Areas with silt and clay and high phosphorus tend to harbor opportunistic species like the NIS *Agardhiella subulata*, while coarser sediments favor seagrasses [4]. In the Mar Piccolo, at Site 3, PERMDISP analysis identifies a pronounced seasonal shift in macroalgal structure in the 12-year studied period. This is primarily attributed to the proliferation of the NIS *H. corona*, which reduces community heterogeneity during its peak dominance in summer and autumn [35]. In contrast, the macrophytobenthic communities at the remaining two sites appear more homogeneous throughout the study period. The PCoA ordination successfully captured the primary drivers of community structure, with the first two dimensions accounting for a high percentage of cumulative variance. The significant clustering by site centroids, independent of sampling years, suggests that spatial heterogeneity overpowers interannual variability within the Mar Piccolo. This stability is particularly noteworthy given the inherent environmental fluctuations typical of transitional water systems. The persistent, site-specific biological signatures indicate that local environmental filtering exert a more consistent influence on seaweed assemblages than stochastic annual shifts. The environmental gradient within the Mar Piccolo appears to be the primary driver of community assembly, mirroring findings from other Mediterranean lagoons where salinity and nitrate concentrations act as master variables [36]. The PCoA results reflect this transition, with Site 3 close to freshwater inputs and Site 1 closer to marine influence creating a clear spatial hierarchy. Interestingly, the integration of NIS follows this same structured pattern. The distribution of NIS is not chaotic; their alignment with site-specific centroids indicates that their establishment is governed by the same environmental rules as native taxa. This implies that the invasion landscape of the Mar Piccolo is highly structured and predictable based on local abiotic factors. The persistent separation of site-specific centroids, despite the presence of NIS, suggests these invaders have undergone naturalization without inducing biotic homogenization [37,38]. Rather than displacing local assemblages and creating a uniform community across the lagoon, the NIS appear to have integrated into the existing spatial framework. This indicates that the Mar Piccolo maintains a degree of biotic resistance that allows for the coexistence of diverse, site-specific communities even under the pressure of biological invasions.

4.3. Ecological Significance of Characteristic Species Shifts

The IndVal analysis reveals a stark spatial and temporal compartmentalization of seaweed assemblages within the Mar Piccolo of Taranto, highlighting a basin-scale divergence between the First and Second inlets. In the First Inlet, the consistent presence of native indicators (e.g., *Amphiroa beauvoisii*, *Ellisolandia elongata*) throughout the year suggests a relatively stable community structure, mainly made of sensitive species. However, the seasonal emergence of NIS like *Colpomenia peregrina*, *Grateloupia turuturu*, and *Polysiphonia morrowii* during the winter and spring months indicates a temporal window of opportunity for invaders. This pattern suggests that while native species maintain a year-round presence, the cooler seasons allow NIS to grow, temporarily altering the seasonal phenology of the assemblage. Concerning the Second Inlet, despite having some sensitive characteristic species on pair with the First Inlet (e.g., *Chaetomorpha linum*, *Chondracanthus acicularis*), it would exhibit a more pronounced shift toward neutral taxa (e.g., *Gracilaria bursa-pastoris, Spyridia filamentosa*) and opportunistic ones (e.g., *Ulva laetevirens*), reflecting its higher degree of confinement and potential anthropogenic stress. Only one NIS, the neutral *Hypnea corona* is distributed throughout the entire year. In a Sardinian Marine Protected Area, the invasive capacity of *Caulerpa cylindracea* appeared constrained by the presence of well-established native macroalgal canopies. The lack of significant interference with these native populations supports the conclusion that preserving ecosystem climax states is critical to managing marine biological invasions and maintaining community stability [39]. Further noteworthy is the stark difference between the northern Site 3 and southern Site 4 of the Second Inlet, which gives greater emphasis to the local heterogeneity of the basin. Site 3 maintains single indicators, mainly in the cold season, with only one characterising NIS (i.e., *Osmundea oederi*), while Site 4 is heavily characterized both throughout the year and in the spring-winter period by a suite of native species. Here, only one NIS results an indicator throughout the year (i.e., *Caulacanthus okamurae*), and in the spring-winter period (i.e., *Grateloupia minima).* This separation reflects not only the distinct hydrographic and trophic conditions of each sub-basin but also varying degrees of susceptibility to NIS colonization. In a study performed along the Tuscany coasts, the IndVal analysis revealed a significant taxonomic shift between site categories, where *C. cylindracea* (reported as *C. racemosa*) invasion acted as a catalyst for community homogenization [40]. This was evidenced by a marked reduction in beta diversity at invaded sites, which were characterized by a transition from diverse erect and encrusting functional groups to a simplified community dominated by turf-forming species.

4.4. Thermosensitivity and Resilience of Seaweed Assemblages

Correlation analysis between water temperature and ecological metrics revealed distinct spatial patterns between the two Inlets of the Mar Piccolo, although the analysis should be expanded including other sampling sites, especially in the First Inlet, where temperature increases were exclusively associated with a decline in NIS biomass. This negative relationship is likely driven by the presence of NIS originating from cold-temperate regions, most notably *Polysiphonia morrowii*, which may experience physiological stress as temperatures exceed its optimal thermal range. Despite these biomass fluctuations, temperature variations did not yield significant impacts on the overall diversity of this site. This observed thermal sensitivity aligns with previous records in the Mar Piccolo, such as the localized extinction of the cold-temperate seaweed *Undaria pinnatifida* (Harvey) Suringar, which was attributed to rising thermal trends [35]. Similar declines in cold-adapted macroalgae have been documented in the Venice Lagoon, where increasing minimum temperatures threaten stenothermal species. While thermophilic NIS like *Gracilaria vermiculophylla* flourish under warming conditions, cold-adapted taxa, such as *Fucus virsoides* J. Agardh (Heterokontophyta, Fucales) exhibit a strong negative correlation with temperature, often resulting in local disappearance following extreme heatwave events [41].

Conversely, rising temperatures negatively influence assemblage diversity across both sites in the Second Inlet. This reduction in species richness appears to be a direct consequence of increased NIS biomass, largely dominated by *H. corona* at Site 3. As a thermophilic species, *H. corona* reaches peak biomass during the warm season, exerting significant competitive pressure and becoming the dominant taxon, which ultimately leads to a marked decline in overall community diversity. While NatS are often limited by specific environmental constraints, NIS frequently possess eurytopic characteristics, enabling them to exploit a wider spectrum of environmental variables [42], such as the rising temperatures observed in the Second Inlet. Evidence from mesocosm experiments simulating a 14-day summer heatwave indicates a clear disparity in thermal tolerance between NatS and NIS Atlantic seaweeds. While native populations, such as *Fucus serratus* Linnaeus (Heterokontophyta, Fucales) and *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinales) suffered significant declines, the heatwave promoted the development of the NIS *Sargassum muticum* [42]. This suggests that rising frequencies of thermal anomalies may accelerate the displacement of native canopy-forming species by opportunistic invaders.

At Site 4, the expansion of *Ulva laetevirens* in response to warming appears to be a primary driver of reduced community diversity. However, temperature is likely not the sole factor; the interplay between thermal stress and nutrient concentrations warrants further attention. In the Venice Lagoon, for example, the replacement of *Ulva rigida* C. Agardh (Chlorophyta, Ulvales) by *U. laetevirens* (reported as *U. australis*) has been linked to declining nitrogen levels, suggesting that *U. laetevirens* may possess a competitive advantage under specific combined environmental regimes [41]. This demonstrates that native opportunists can be equally disruptive when environmental conditions favor their physiological requirements, and highlights that dominance, regardless of origin (native or alien), is the primary driver of diversity loss in these confined coastal systems.

5. Conclusions

The high-resolution monitoring provided by the LTER framework has been instrumental in moving beyond simple inventories. These data confirm that the Mar Piccolo acts as a “sink” for NIS due to its intense shellfish farming and importation. However, our findings further clarify that the success of these colonizers is not uniform across the basin. The fluctuations in biomass observed between NatS and NIS suggest a highly competitive environment where environmental drivers dictate the seasonal “winners” and “losers” of the assemblage. Moreover, this study indicates that the Mar Piccolo is not responding uniformly to NIS pressure. While some areas maintain high biotic resistance through native dominance, others seem undergoing a functional shift driven by thermal forcing. These findings suggest that monitoring programs in Mediterranean transitional waters must look beyond simple species lists and prioritize biomass-based evenness and thermal niche analysis to accurately predict ecosystem health in a warming sea.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, Table S1: Taxonomical Composition and NIS Status of Mar Piccolo Seaweed Assemblages; Table S2: Summary of Seasonal Thermal Variations and Multi-Index Seaweed Metrics; Table S3: Spatiotemporal Variation of Biodiversity and Biomass Indices (2012–2023); Table S4: Spatiotemporal Pairwise Comparisons and Significance Levels.

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Abbreviations

The following abbreviations are used in this manuscript:

NIS	Non-Indigenous Species
NatS	Native Species
PERMANOVA	Permutational Multivariate Analysis of Variance
FO	Frequency of Occurrence
PcoA	Principal Coordinate Analysis
PERMDISP	Permutational Test of Multivariate Dispersion
IndVal	Indicator Value

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