Make it simpler: Alien species decrease functional diversity of coastal plant communities

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Abstract

Questions: (a) Are there differences in abundance-weighted functional trait values between native and alien species in coastal plant communities? (b) Which functional traits are associated with a higher level of invasion in these communities? (c) Do functional diversity patterns differ between native and alien species? (d) Is alien species occurrence linked to small-scale functional homogenization effects on the resident native species?

Location: N-Adriatic coastal ecosystems (Marano and Grado lagoon, Friuli Venezia Giulia region, Italy).

Methods: We sampled coastal vegetation within two habitats (foredunes and salt-marshes) along nine belt transects in two sampling sites. Plant species richness and abundance were assessed in 128 plots along with a suite of plant functional traits. We tested for differences in community-weighted means between native and alien species within the two habitats, and Linear Mixed Models provided insights into traits fostering the invasion success among alien species. To check for potential functional homogenization driven by alien species invasion, we explored functional diversity patterns of native and alien species (β and γ functional diversity) and the relationship between α functional diversity and alien cover.

Results: Alien species had lower functional diversity than natives and were characterized by lower leaf construction costs coupled with lower drought resistance and higher water transport efficiency. The most abundant aliens were the ones minimizing carbon investment for leaf construction. In addition, we also found evidence for small-scale functional homogenization driven by alien invasion.

Conclusions: Our results suggested that native species adopt a resource conservative strategy whereas alien species are characterized by a higher resource acquisition capacity (i.e., acquisitive strategy). Our data also confirmed that alien species are less functionally diverse than natives, potentially driving the community towards small-scale functional homogenization, resulting in a loss of species and a reduction in the functional space.

KEYWORDS
biological invasion, community ecology, community weighted mean, functional homogenization, functional rarefaction, functional traits, functional uniqueness, quantitative methods

1 | INTRODUCTION

Coastal ecosystems are among the most fragile habitats in the Mediterranean basin (Kutiel, Eden, & Zhevelev, 2000). These environments are usually characterized by marked vegetation zonation, associated with strong environmental gradients (Acosta, Carranza, & Izzi, 2009), and often host rare species and endemics. Due to the harsh abiotic conditions of these ecosystems (e.g., sand burial, salinity, drought), plant species often display peculiar morpho-functional adaptations (Maun, 2009). Coastal ecosystems are threatened by human-related impacts such as tourism, urbanization, and shoreline erosion (e.g. O'Shea & Kirkpatrick, 2000), along with climate changes and biological invasions (Feagin, Sherman, & Grant, 2005; Prisco, Carboni, & Acosta, 2013; Tordoni, Napolitano, Maccherini, Da Re, & Bacaro, 2018). Specifically, biological invasions are among the most important drivers of biodiversity loss and modification of ecosystem services worldwide (Duraiappah et al., 2005). Invasive Alien Species (hereafter IAS) have negative impacts on natural ecosystems (Vilà et al., 2011), by modifying the species composition (Hejda, Pyšek, & Jarošík, 2009; Powell, Chase, & Knight, 2011) and altering the nutrient cycle (Ehrenfeld, 2010). Alien invasions have also been claimed as the major cause of biotic homogenization, defined as the increase in genetic, taxonomic or functional similarity of two or more locations over a specified time interval (La Sorte et al., 2014; Olden, Poff, Douglas, Douglas, & Fausch, 2004; Qian & Guo, 2010).

Coastal areas are among the most invaded regions worldwide (Dawson et al., 2017), even though invasion rate is strongly context-dependent (e.g. Daehler, 2003; Funk, Standish, Stock, & Valladares, 2016). High propagule pressure along with local abiotic conditions and anthropogenic factors are the main factors leading to high levels of invasion in coastal habitats (Basnou, Iguzquiza, & Pino, 2015; Malavasi, Carboni, Cutini, Carranza, & Acosta, 2014). While previous studies have identified abiotic and anthropogenic factors fostering invasions in coastal habitats, the functional characteristics that promote plant invasions in these ecosystems are still poorly investigated (e.g. Castro-Díez, Pauchard, Traveset, & Vila, 2016; Funk, Cleland, Suding, & Zavaleta, 2008; Pakeman, Hewison, & Lewis, 2017; Stanisci, Acosta, Di Iorio, & Vergalito, 2010). These features are typically summarized by species' functional traits within the community (McGill, Enquist, Weiher, & Westoby, 2006). Recently, Brodribb (2017) suggested to further classify functional traits in "general functional traits" (hereafter GFTs) and "mechanistic functional traits" (MFTs). GFTs (e.g. Specific Leaf Area [SLA], which is the ratio of leaf area to dry mass) represent "syndromes" that can be driven by different physiological functions and associated trade-offs, whilst MFTs are traits whose function can be clearly physiologically defined (e.g. turgor loss point associated with drought resistance). Moreover, GFTs do not always consistently predict eco-physiological features that can promote invasiveness, because they are loosely associated with habitat characteristics (Drenovsky et al., 2012; Grotkopp, Erskine-Ogden, & Rejmánek, 2010). In contrast, MFTs have been shown to be more strongly associated with habitat

characteristics and plant functions (Belluau & Shipley, 2018), and can provide deeper insight into species' physiological features.

From a functional perspective, two mechanisms have been proposed to explain coexistence between resident native species and IAS. According to the "try harder" hypothesis, alien species display more extreme trait syndromes than resident species (see below). In contrast, the "join-the-locals" hypothesis states that alien and native species coexist in the same habitat since they share the same set of traits (Tecco, Díaz, Cabido, & Urcelay, 2010). In a meta-analysis on performance-related traits, Brodribb, Field, and Sack (2010) and Van Kleunen, Weber, and Fischer (2010) demonstrated that IAS tend to outcompete native or non-invasive species due to higher values of functional traits related to growth rate and resource acquisition. However, the same pattern was not found by Daehler (2003), suggesting that there is not a unique suite of traits responsible for invasiveness, but that multiple suites of traits could explain invasion success in different environments (e.g. Funk, 2013; Funk et al., 2016; Tecco et al., 2010). Since variations in functional traits are strongly associated with species composition, taxonomical homogenization (intended as an increased species similarity across space) could result in greater functional trait redundancy. As a result, if IAS tend to share similar values of functional traits, they may lead to functional homogenization of resident communities.

In coastal ecosystems, IAS are generally taller than natives and display a better use of resources (Pakeman et al., 2017; Stanisci et al., 2010). Moreover, IAS have also been found to occupy different temporal and spatial niches with respect to natives, which might suggest lack of competition for the same resources (Stanisci et al., 2010). However, previous studies in coastal ecosystems have focused chiefly on GFTs (Castro-Díez et al., 2016; Pakeman et al., 2017; Stanisci et al., 2010), and only few of them included MFTs, generally limited to few species and not tested for the whole community (e.g. Antunes et al., 2018), thus providing only a partial view of the mechanistic determinants of the invasion process in these habitats.

In this study, through a systematic sampling design based on belt transects, we sampled coastal vegetation and measured leaf traits (both GFTs and MFTs) in two sites on the northern Adriatic coastline aiming at: (a) testing differences in abundance-weighted trait values between native and alien species; (b) assessing morpho-functional traits associated with a higher level of invasion; (c) testing whether functional diversity patterns differ between native and alien species within each habitat; and (d) detecting if alien species occurrence is linked to small-scale functional homogenization effects on the resident native species.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was performed in some of the few remnants of natural vegetation on the northern Adriatic coastline, namely Martignano island and San Andrea island (see Appendix S1). Since the 1950s, these ecosystems have suffered alterations due to an increase in tourism

and urbanization (Nordstrom, Gamper, Fontolan, Bezzi, & Jackson, 2009) The current flora is the outcome of a "crossroad" of species with different origins (Mediterranean, Alpine and Eastern native range), due to the biogeographical location of the study area (Buffa, Fantinato, & Pizzo, 2012). Both sampling sites are part of a network of European natural protected areas (Natura 2000 Network), known as Marano and Grado lagoon (centroid coordinates 45.72216° N, 13.24836° E). Climate in the area is influenced by Bora winds, which decrease thermal limits mainly during the winter. Mean annual temperature averages 12°C and mean annual precipitation sums up to about 1,000 mm (https://www.meteo.fvg.it, reference period 1991–2010 accessed on December 5th, 2017). A portion of the study site is characterized by semidiurnal tides and seasonal tidal inundation, emerging from the sea level during the spring–summer period.

2.2 | Sampling design

Vegetation data were collected on the basis of a square grid of 500 m × 500 m, and one transect per cell was randomly selected in the two study areas. Transects spanned a sea–inland gradient and had variable lengths according to dune extension and coastal morphology (from 16 to 168 m). Transects were partitioned in a set of contiguous squared subunits (plots) 16 m^2 each, where the occurrence and the abundance of each vascular plant species (expressed as cover percentage based on visual estimation) were assessed. Overall, nine transects and 128 plots were sampled (41 plots in Martignano island and 87 in San Andrea island, respectively). After sampling, each plot was assigned to a specific coastal habitat according to the European Habitats Directive (92/43/EEC). For the sake of comparison, plots were further classified in two major categories: (a) foredunes including the upper beach, embryo dunes and mobile dunes; and (b) saltmarshes encompassing habitats associated with tidal flats, salt pans or salt lakes that may be permanently or temporarily wet. On this basis, 97 plots belonged to the foredune and 31 to the saltmarsh habitat. All the vascular plants occurring within each plot were identified following Pignatti (1982), and nomenclature was standardized according to Conti et al. (2005). Plants were classified as native or alien species according to Celesti-Grapow et al. (2009).

Samples to be used for measurements of functional traits were collected following a slightly different procedure. When two or more transects displayed redundant species pools, we discarded the one with the lowest species richness, so that samples were finally collected from six transects out of nine. At least one individual was sampled for each species within each habitat in each transect. In total, functional traits were measured on 45 out of 71 recorded species, accounting for about 96% of the total plant coverage. For the other species, it was not possible to measure functional traits for several reasons (e.g. dried individuals), and only traits derived from the literature were included in the analyses. Leaves or entire individuals were collected, wrapped in cling film, put in humid sealed plastic bags, and stored in cool bags until processing in the laboratory. Fieldwork was carried out in June–August 2017. The whole list of functional traits included in this study is summarized in Appendix S2.

2.3 | Functional traits measurements

The functional traits measured in this study were typically associated with the "leaf economics spectrum" (LES, Wright et al., 2004), reflecting the trade-offs between carbon investment for leaf construction and potential photosynthetic carbon gain (SLA, leaf nitrogen and carbon content). Specifically, higher values of SLA and lower values of carbon content are associated with lower leaf construction and maintenance costs (Wright et al., 2004). According to the trade-offs described in the LES, higher SLA (or lower values of its reciprocal, called leaf mass per unit area, LMA) correlates with shorter leaf lifespan and higher photosynthetic rates. Other MFTs measured in the present study were related to the efficiency of water transport within leaves (leaf venation architecture), water use efficiency (leaf isotopic composition) and drought resistance (leaf osmotic potential and turgor loss point).

Overall, the following leaf functional and/or mechanistic traits were measured: specific leaf area (SLA, mm^2/mg), major and minor vein length per unit area (VLA$_{maj}$, VLA$_{min}$, mm/mm^2), osmotic potential at full turgor (π_0, -MPa), water potential at turgor loss point (Ψ_{tlp}, -MPa), N and C content (N, %, and C, %), C to N ratio (C:N), and C and N stable isotope composition (δ^{13}C, ‰, and δ^{15}N, ‰).

Specific Leaf Area was calculated as:

$$SLA = (Leaf\ Area)/(Leaf\ Dry\ Weight) [mm^2/mg] \quad (1)$$

Specific Leaf Area is a structural trait correlated with relative growth rate, photosynthetic rate, and nutrient concentration (Cornelissen et al., 2003). Plants adapted to arid and low-nutrient habitats usually have thicker and smaller leaves with lower SLA and increased lifespan (Pérez-Harguindeguy et al., 2013). Leaf area was measured using the software ImageJ (Schneider, Rasband, & Eliceiri, 2012). Leaves were then oven-dried for 48 hr at 70°C and leaf dry weight was measured using an analytical balance.

Leaf venation architecture comprehends several structural features influencing plant performance, and higher VLA is generally associated with higher leaf hydraulic conductance and gas exchange rates (Sack & Scoffoni, 2013). We measured the length per unit area of major and minor veins (VLA$_{maj}$ and VLA$_{min}$) as:

$$VLA = Vein\ Length/Leaf\ sample\ area [mm/mm^2] \quad (2)$$

For VLA$_{maj}$, leaf images were acquired using a desktop scanner, and the ratio between vein length and sample area was measured using PhenoVein software (Bühler et al., 2015). To measure VLA$_{min}$, fresh leaves were cleared in 1 M NaOH solution for 48–72 hr at room temperature, carefully replacing the solution when it turned from transparent to dark-colored. After initial clearance, small portions of the leaves of about 1 cm^2 were cut and bleached in NaClO 5% for 1–2 min. Then, samples were treated in a sequence of ethanol solutions at increasing concentration (25%, 50%, 75%, 100%) and maintained in an alcoholic solution of toluidine blue (3%) overnight. Finally, samples were processed in a series of ethanol solutions at decreasing concentration and microscopic slides were prepared. Images of small portions of leaves

(~5 mm^2) were captured with an optical microscope (4× magnification) equipped with a digital camera (model Syrio-2, Pbinternational), and VLA$_{min}$ was measured using PhenoVein software.

The important mechanistic traits π_0 and Ψ_{tlp} are related to species' drought tolerance, and more negative values are generally associated with greater capability of maintaining turgor under water shortage (Bartlett, Scoffoni, & Sack, 2012). Measurements were done following the method proposed by Bartlett, Scoffoni, Ardy et al. (2012) with some modifications. Leaves were fully rehydrated for 3 hr and then roughly crumbled before being sealed in cling film and immersed in liquid nitrogen (LN$_2$) for 2 min. Leaves (still sealed in cling film) were carefully ground and stored in sealed plastic bottles at −20°C until measurements. Samples were thawed at room temperature for 5 min before measuring π_0 with a dew point potentiometer (Model WP4, Decagon Devices Inc., Pullman, WA, USA). Then, Ψ_{tlp} was calculated according to Bartlett, Scoffoni, Ardy et al. (2012).

δ^{13}C is a proxy of photosynthetic water-use efficiency (lower values indicate greater stomatal aperture) and δ^{15}N reflects the ability of plant species to acquire and use resources (Dawson, Mambelli, Plamboeck, Templer, & Tu, 2002; Lambers, Chapin, & Pons, 2008). Elemental composition, namely percentage N and C, and C:N, is correlated with carbon and nitrogen investment costs, which, in turn, are correlated with SLA and photosynthetic capacity (Gulías et al., 2003). Leaves were oven-dried (70°C for 48 hr) and then pulverized in a mortar. Dried and ground samples were analyzed for carbon and nitrogen contents (% dry weight) and carbon and nitrogen stable isotope composition by means of an elemental analyzer/continuous flow isotope ratio mass spectrometry using a CHNOS Elemental Analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) coupled with an IsoPrime 100 mass spectrometer (Isoprime Ltd, Cheadle, UK). All isotope and elemental composition analyses were performed by the Center for Stable Isotope Biogeochemistry (University of California, Berkeley, CA). Long-term external precision based on reference material "NIST SMR 1577b" (bovine liver) is 0.10‰ and 0.15‰, respectively, for C and N isotope analyses.

Functional traits derived from the literature were mainly associated with phenology and reproductive strategies. Information about life form, flowering time-span, and sprouting was retrieved from Pignatti (1982). The photosynthetic pathway and clonality were derived from online databases such as "eHALOPH" (Santos, Al-Azzawi, Aronson, & Flowers, 2015), "Online Atlas of the British and Irish Flora" (https://www.brc.ac.uk/plantatlas) and "USDA Plant Database" (USDA, 2018). A table showing functional trait values for each species is available in Appendix S3.

2.4 | Statistical analyses

2.4.1 | Testing differences in Community-level Weighted Means between native and alien species in coastal ecosystems

In order to test for differences in abundance-weighted trait values between native and alien species, Community-level Weighted Means (CWMs) per plot were calculated considering native and alien species separately (in the same way Cadotte et al., 2010 applied the same approach to assess phylogenetic patterns of plant communities). We decided to characterize plant community functional composition using CWMs in order to take into account the structure of the vegetation at the plot scale since different species abundances could differently characterize plant communities. In addition, making comparisons without considering species relative abundances may result in an overestimation of the contribution of the rare species, which usually account for a lower proportion of plant biomass within a species assemblage.

Community-level Weighted Means per plot for each functional trait were calculated and analyzed separately for alien and native species pools using the R package "FD" (Laliberté, Legendre, & Shipley, 2014). CWMs were derived by averaging trait values in the community weighted by the relative abundance of taxa bearing each value in the plot (Lavorel et al., 2008). Spearman's rank correlation coefficient among quantitative functional traits of all species sampled (both native and alien species) was calculated. Differences in CWMs between native and alien species within habitat for quantitative functional traits values were tested using Wilcoxon's rank sum test, and p-values were adjusted using Bonferroni correction. The same test was performed for nominal functional traits considering the relative abundance of each individual class.

2.4.2 | Analysis of functional traits fostering invasion success

This analysis aimed at assessing which functional traits of alien species may foster higher levels of invasion (greater alien cover or invasion success) within the community.

Normalized alien cover (N_{alien}) at the plot level was calculated as:

$$N_{alien} = C_{alien}/C_{total} \qquad (3)$$

where C_{alien} is the alien cover in the plot and C_{total} was obtained by summing up native and alien species covers. This procedure was necessary to exclude empty spaces and make CWM values independent of N_{alien}, thus avoiding circularity in the analyses and allowing unbiased parameter estimation in the models relating N_{alien} to CWMs (see below).

Invasion success of alien species was analyzed by means of a Linear Mixed-effect Model (LMM) using the "nlme" package (Pinheiro et al., 2018), after checking for normality of N_{alien} (response variable). This was modeled as a function of alien CWM for each trait (fixed effects) and controlling for the habitat. Transect was added as a random effect to control for the spatial dependence of plots within transects. Furthermore, to account for the effect of spatial autocorrelation in parameter estimation, a matrix was added describing the within-transect correlation structure of the data (Gaussian correlation). Specifically, unlike GLM, which used basically an identity matrix as correlation matrix (1 in diagonals, 0 in off-diagonals), in this specific case off-diagonal values

of the matrix corresponded to the spatial correlation among sampling units. Prior to analysis, quantitative CWMs were standardized (zero mean, unit variance) to obtain comparable coefficients. Starting from a full model including all the CWMs (both GFTs and MFTs), we adopted a stepwise variable selection procedure through AICc minimization criteria plus a backward procedure to avoid multicollinearity among selected explanatory variables in order to find a Minimum Adequate Model (MAM). This was obtained using package "MuMIn" (Barton, 2018). R^2 values were calculated using the "r2glmm" package (Jaeger, 2017). This statistic was based on a standardized generalized variance approach, which is the proportion of generalized variance explained by the fixed predictors.

2.4.3 | Functional homogenization analysis

We tested for a small-scale functional homogenization caused by alien species by comparing functional diversity patterns of native and alien species (expressed by Rao's Quadratic entropy index, Rao's Q) across different components of functional diversity (total or γ functional diversity, between-plot or β functional diversity, and within-plot or α functional diversity). Specifically, we measured the following functional diversity metrics: (a) first, we compared γ functional diversity of alien and native species for a comparable sampling effort using functional rarefaction curves; (b) then, we tested for differences in β functional diversity between alien and native species pool within habitats; and (c) we tested for a possible reduction of α functional diversity in highly invaded communities assessing the relationship between Rao's Q at plot level and N_{alien}. Furthermore, we calculated functional uniqueness at the plot scale, which provided a measure of trait redundancy. In what follows, a detailed description is given of the methods adopted for the calculation of the functional metrics described above.

Rarefaction methods are particularly useful to compare diversity metrics (species richness, functional or phylogenetic diversity) for communities sampled with different sampling efforts (Bacaro, et al., 2012; Bacaro et al., 2016). Plot-based functional rarefaction curves derived from the computation of expected Rao's Q (Ricotta, Pavoine, Bacaro, & Acosta, 2012) were calculated separately for native and alien species using the "adiv" package (Pavoine, 2017). Considering the large difference in the number of native and alien species (62 and 9, respectively), it was trivial to expect a lower functional γ diversity in alien species with respect to native ones using the rarefaction curve. For this reason, we set up a null model to test the potential bias in functional rarefaction curves due to the imbalance in species number in natives and aliens. To be precise, a randomization procedure was adopted: first, nine native species and their related functional traits were randomly selected, and a functional distance matrix was obtained. This trait matrix was then multiplied by the abundance of the observed alien species to calculate Rao's Q statistic as a function of the number of plots (functional accumulation curve). This procedure was repeated 999 times,

and the "average" functional rarefaction curve was then calculated. This curve expressed the expected functional diversity, for a given sampling effort, of an assemblage of native species that resemble the distribution and abundance of the observed alien community. Functional rarefaction curves were computed also at the transect level in order to exclude any effect of the nested data structure.

Community-level Weighted Means at plot level for both native and alien species were used to calculate pairwise functional distances among plots using the package "adiv" (Pavoine, 2017). Considering that some functional traits such as life form were qualitative and CWM analysis returns the most abundant class, we computed a modified version of the Gower distance allowing for the treatment of various statistical types of variables (for more details about methodology see Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). According to the framework for the calculation of β diversity proposed in other studies (Anderson, Ellingsen, & McArdle, 2006; Baiser & Lockwood, 2011), we tested for differences in functional β diversity at group level between native and alien species within each habitat, following the methodology described in Bacaro, Gioria, and Ricotta (2013). This procedure consisted of randomly shuffling within-group dissimilarities (i.e. functional dissimilarities among species of the same group where groups were aliens and natives) disregarding between-groups dissimilarities through 999 permutations, under the null hypothesis that mean within-group dissimilarity is equal for the native and alien species groups. To test whether functional α diversity of the native and total community (RaoQ$_{nat}$ and RaoQ$_{tot}$, respectively) was affected by alien species abundance (N_{alien}), we used second-order polynomial LMMs with transect as random factor. Two separate models were estimated using RaoQ$_{nat}$ or RaoQ$_{tot}$ (response variables) as a function of N_{alien} and controlling for habitat. Each model and related R^2 values (expressing the proportion of generalized variance explained by the fixed predictors) were calculated following the same approach used to test invasion success.

Lastly, the functional uniqueness of each plot (U) calculates the functional contribution of a single species to the overall functional diversity of the species assemblage (Ricotta et al., 2016). It was calculated as:

$$U = \frac{\Sigma_i p_i(\Sigma_j p_j \delta_{ij})}{\Sigma_i p_i(1 - p_i)}, \tag{4}$$

where p_i represented the relative abundance of each species and δ_{ij} summarized the pairwise functional dissimilarities between species i and j. U was calculated at plot level for native and alien species separately within each habitat, according to Ricotta et al. (2016) and using the "adiv" R package (Pavoine, 2017). Functional uniqueness ranged between 0 (minimal functional uniqueness) and 1. Specifically, if the n species in a plot were functionally identical, U assumed the value of 0, whereas 1 indicated that all the species were functionally distinct. All statistical analyses were performed using R 3.4.1 (R Foundation for Statistical Computing, Vienna, AT).

A total of 71 species were recorded in the sampled plots, which included nine aliens and 62 natives. The rate of invasion (12.7%) was quite similar to that reported for the total Italian vascular flora (13.4%), but higher than the average for the Friuli Venezia Giulia Region (9.9%; Celesti-Grapow et al., 2009). Among alien species, the most abundant were *Oenothera stucchii* Soldano (54.7% of the sampled plots), *Xanthium orientale* subsp. *italicum* (Moretti) Greuter (46.9%) and *Ambrosia psilostachya* DC. (45.3%). All the alien species found in the survey are deemed invasive according to the Italian alien checklist, with the only exception of *Yucca gloriosa* L., now considered naturalized. Most alien species (78%) originated from North America. Averaged plot species richness for each habitat is

available as online supporting information (Appendix S4) along with the correlation matrix of the quantitative functional traits (Appendix S5). There were significant differences between the alien and native CWMs for most traits analyzed (Figure 1). On average, alien CWMs accounted for higher SLA and VLA_{min} in both habitats, as well as higher π_0 and Ψ_{tlp}. Alien species also displayed higher N content and lower $\delta^{13}C$ and C:N, especially in saltmarshes. The most abundant alien species were mostly not clonal hemicryptophytes, characterized by a C3 photosynthetic pathway. The sprouting period was mainly June–July (Appendix S6).

The MAM minimizing the AICc value (best fit 976.2) showed that foredunes have a higher invasion level than saltmarshes (greater N_{alien}) along with higher CWM of SLA (Table 1, $R^2 = 0.25$).
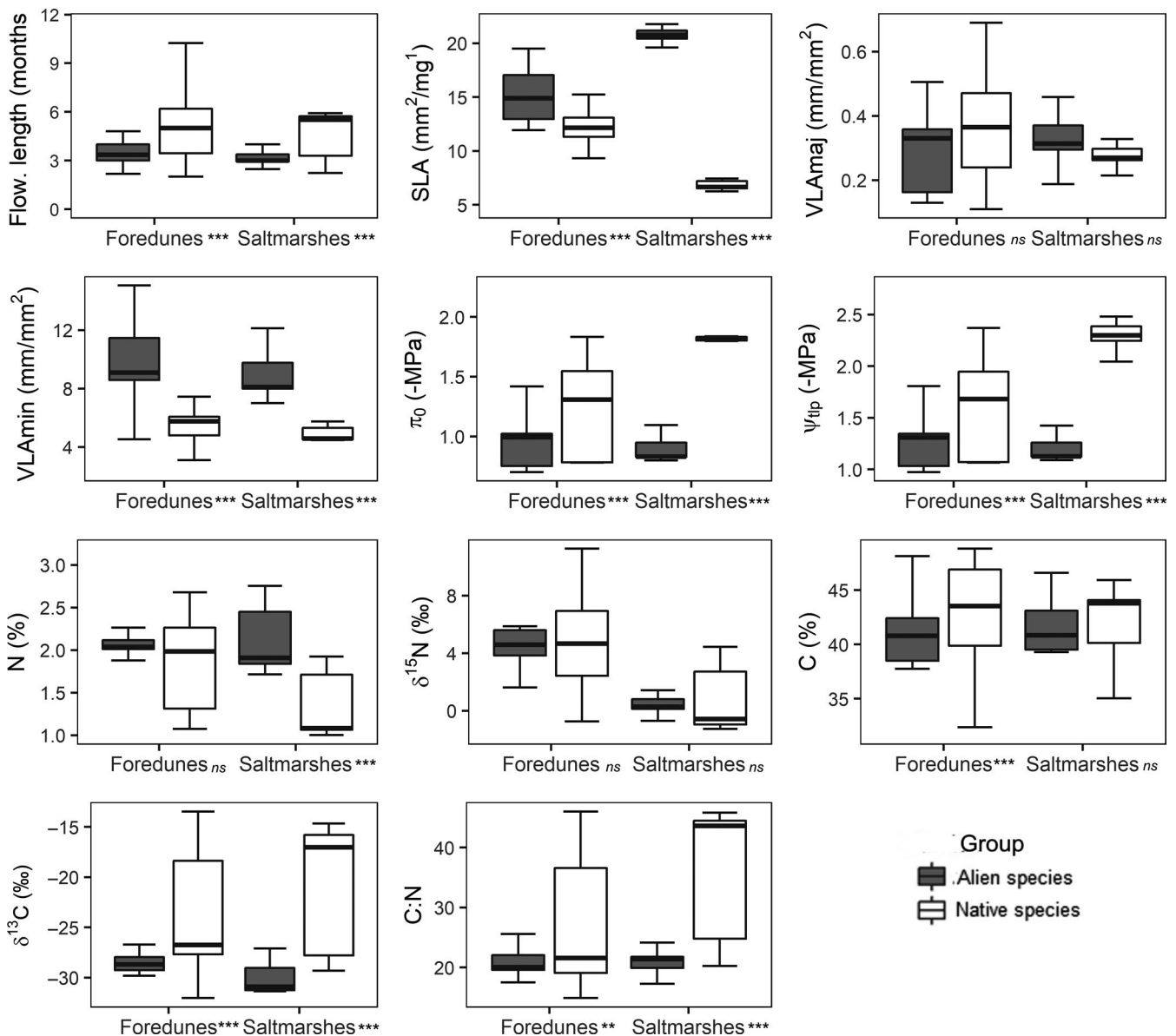
FIGURE 1 Median value, 25th and 75th percentile of the CWMs of quantitative functional traits in native and alien species between habitats. Significance determined using a Wilcoxon test with Bonferroni adjustment is reported (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns = Not Significant)

Plot-based functional rarefactions (Figure 2) displayed a very clear pattern, as all the curves reached the asymptote, meaning that sampling effort optimally captured total functional diversity (γ diversity) of the study area. Native species saturated at higher level of Rao's Q index, accounting for a higher functional diversity compared to alien species; this outcome is further supported by the null model. Indeed, despite replacing the functional traits of the alien species with those of nine native species randomly selected and keeping fixed the spatial structure of the alien species pool, the functional diversity of natives still remained higher than that of the aliens. The same pattern was consistent also when aggregating the observations at the transect scale (Appendix S7).

Permutations of functional distances revealed a significant difference in functional β diversity between the two groups of species in both habitats. In particular, foredunes displayed significant differences in functional β diversity between native and alien species ($F_{1,8563}$ = 3,528, p = 0.001) with average β diversity values of 0.28 for aliens and 0.50 for natives. Likewise, a significant outcome was observed in saltmarshes ($F_{1,583}$ = 5.19, p = 0.03), with an average β diversity of 0.31 and 0.37 for alien and native species, respectively.

Significant unimodal relationships derived from LMMs between N_{alien} and both $RaoQ_{nat}$ and $RaoQ_{tot}$ were observed in foredunes (Figure 3). In contrast, these relationships were not significant in saltmarshes (Appendix S8). Additionally, a decrease in functional diversity of the native community (lower Rao's Q) is associated with a peak in alien species coverage (e.g. T6 in foredunes and T9 in foredunes/saltmarshes, see Appendix S9).

A wider range of community-level functional uniqueness (ΔU) was observed in native species, indicating higher plot-to-plot variability in trait values distribution (Table 2). In contrast, alien species traits were highly redundant (lower ΔU, Table 2).

4 | DISCUSSION

4.1 | Functional traits in invaded coastal communities

Our results highlighted that IAS are functionally different from native species due to higher SLA, π_0 and Ψ_{tlp}, suggesting that they minimize leaf construction and maintenance costs (Figure 1). In a low-resource system like sand dunes (Maun, 2009), native species are expected to have a competitive advantage over invasive ones (Daehler, 2003). According to the biotic acceptance theory (Stohlgren, Jarnevich, Chong, & Evangelista, 2006), resource-rich

TABLE 1 Minimum Adequate Model of the Linear Mixed Model computed using N_{alien} as a function of CWMs of alien species group

Variable	Estimate	SE	Pr(>|t|)
(Intercept)	48.58	6.90	***
Habitat (Saltmarshes)	−30.52	8.99	**
SLA	7.50	3.12	*

***p < 0.001; **p < 0.01; *p < 0.05.

environments can potentially host more alien plants. However, it is known that several alien species do occur even in stress-prone ecosystems (e.g. Funk & Vitousek, 2007). According to the LES, pioneer and invasive species are characterized by a "fast-return" (Funk, 2013) or "acquisitive" strategy (Díaz et al., 2016), and our results are in agreement with this pattern. Native species apparently invest more biomass to build "conservative" leaves (lower SLA) more resistant to drought stress (more negative π_0 and Ψ_{tlp}), which in turn may promote longer leaf lifespan and higher survival chances under abiotic and biotic stress (Petruzzellis et al., 2018; Wright et al., 2004). IAS had higher VLA_{min}, which has been suggested to enhance water transport within leaves and is correlated with higher photosynthetic rates (Funk & Vitousek, 2007; Sack & Frole, 2006). The positive relationship between VLA_{min} and water transport efficiency within leaves is particularly apparent in phylogenetically distant species (Brodribb et al., 2010), whilst the trend is not always consistent when closely related species, or species occurring in the same habitat are compared (Nardini, Õunapuu-Pikas, & Savi, 2014; Roth-Nebelsick, Uhl, Mosbrugger, & Kerp, 2001). In the present study, $\delta^{13}C$ was significantly lower in IAS, indicating that these species might have higher gas exchange rates than native ones, supporting the hypothesis that alien plants also display higher photosynthetic rates (van Kleunen et al., 2010).

Several studies showed that invasive species tend to be more efficient than non-invasive species (e.g. Godoy, Valladares, & Castro-Díez, 2011; van Kleunen et al., 2010), irrespective of biogeographical location or biological factors. This pattern was supported by the output of our model, whereby IAS coverage was mainly related to resource use and acquisition traits such as SLA. In particular, reduction of leaf construction costs apparently made IAS very abundant in the study area (Table 1). Interestingly, only one trait was retained in the final model suggesting that the acquisitive strategy detected in alien species (higher SLA, VLA_{min}, π_0 and Ψ_{tlp}) is consistent across the whole study area and that the most abundant IAS are those that strongly reduce leaf construction costs.

It is also possible that here the IAS do not directly compete with native species, as they mostly grow in summer or may access different nutrient pools (as indicated by the higher N %), highlighting possible niche segregation (Pérez-Ramos et al., 2012; Stanisci et al., 2010). Clearly, measuring below-ground traits may help disentangling alien plant invasion success (Dawson, 2015).

4.2 | Functional diversity in invaded coastal communities

Patterns of functional diversity in coastal communities follow the well-known sea–inland gradient (e.g. Acosta, Izzi, & Stanisci, 2006, for sand dune habitats). Our data showed that functional diversity increased from the drift line to the inner part of the beach (Appendix S9), which is less exposed to harsh abiotic conditions (Ricotta et al., 2012). Accordingly, species growing closer to the sea are more specialized and share the same suite of functional traits, unlike species growing further inland (Acosta et al., 2006).
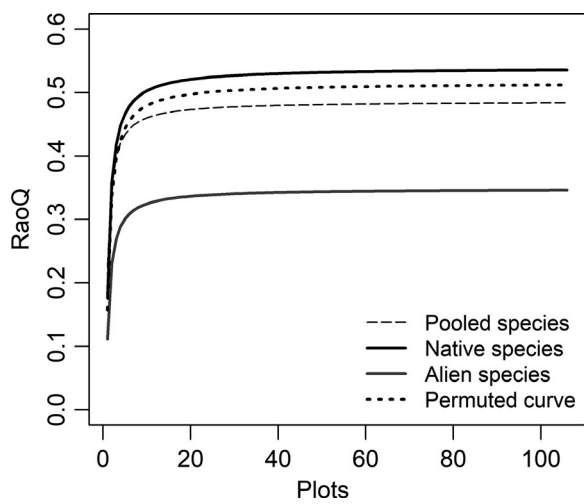
FIGURE 2 Functional rarefaction curves of the expected functional diversity (RaoQ) and cumulative number of plots considering all species pooled (dashed line), native species (black line), alien species (gray line) and the curve averaged from permutations (permuted curve, dotted line). Please note that the x-axis was cut off at 106 plots

Carboni, Acosta, and Ricotta (2013) suggested that differences in species composition alone (and then in phylogeny) should be interpreted with caution as a proxy for functional structure, as this approach may fail to capture the major functional aspects of the community under investigation. Likewise, a simulation study performed by Baiser and Lockwood (2011) revealed that the relationship between taxonomic and functional diversity strongly depends on trait redundancy or overlap, and that the more unique trait

composition a species pool exhibits, the greater is the risk of functional homogenization.

Our findings suggest a potential risk of invasion-induced small-scale functional homogenization. First, we showed that total functional diversity (γ functional diversity) calculated for the alien species pool is lower compared to that of the natives, as shown by functional rarefaction curves (see Figure 2). Moreover, when Rao's Q was calculated for the whole community, the resulting curve was lower than the one calculated on natives only. One possible explanation is the presence of few dominant alien species which may drive community composition and, in turn, functional diversity. Nevertheless, the median value of plot-scale Pielou's evenness is 0.53, suggesting that the pattern observed was chiefly due to greater functional redundancy among alien species, as also shown by the lower ΔU in Table 2.

To the best of our knowledge, whereas several studies have investigated the role of IAS in homogenization of plant communities (e.g. Qian & Guo, 2010), only few of them have explicitly assessed the role of IAS from a functional point of view (Abadie, Machon, Muratet, & Porcher, 2011; Brice, Pellerin, & Poulin, 2017; Tobias & Monika, 2012). Functional homogenization has already been detected in other ecosystems (Brice et al., 2017) and organisms (Villéger, Grenouillet, & Brosse, 2014), and it is generally associated with several triggering causes such as species composition and richness (Baiser & Lockwood, 2011; Smart et al., 2006), land use changes and human disturbances (Brice et al., 2017), and trait redundancy among species.

Under an invasion scenario (Qian & Ricklefs, 2006), we expect to observe a growing number of IAS (or of their abundances) to the

FIGURE 3 Relationship between RaoQ$_{nat}$ (left panel) and RaoQ$_{tot}$ (right panel) as a function of N_{alien} in foredunes, The shaded area represents the 95% confidence interval (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns = Not Significant). X1 refers to the coefficient of the linear term, X2 to the to the coefficient of the quadratic one and Rsq. represents the R^2 statistic. Please note that uncertainty of the random effect parameter is not taken into account for confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]
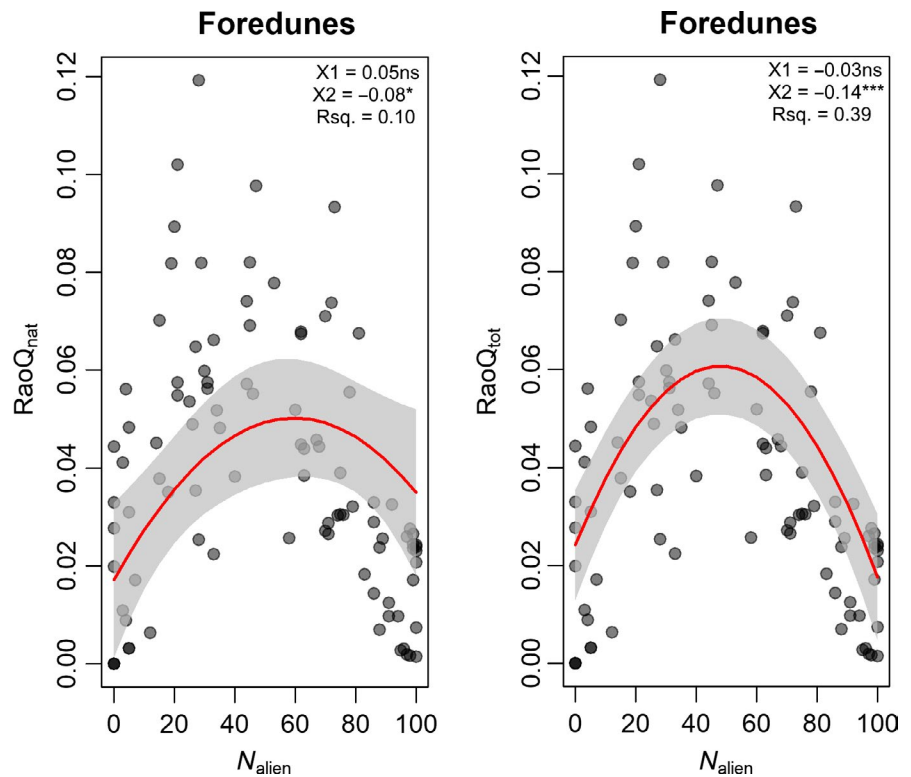
	Alien species		Native species	
	Foredunes	Saltmarshes	Foredunes	Saltmarshes
Min	0.30	0.31	0.28	0.34
Mean	0.40	0.48	0.59	0.57
Max	0.66	0.73	0.84	0.88
ΔU (Max – Min)	0.36	0.42	0.56	0.54

TABLE 2 Summary statistics (minimum, maximum, mean, range) of functional uniqueness metric (U) for each species group within habitat

detriment of native species in the near future. Despite taxonomic homogenization not always being associated with functional homogenization (Sonnier, Johnson, Amatangelo, Rogers, & Waller, 2014), we hypothesize that changes in community composition caused by human-induced ecosystem alterations, along with alien species spread may reduce the functional diversity of native communities, leading to small-scale functional homogenization, as reported also by Lambdon, Lloret, and Hulme (2008). In support of this hypothesis, alien species showed lower functional β diversity in both habitats, suggesting that IAS tend to share more similar values of plot-to-plot functional dissimilarity within habitats, potentially leading to functional homogenization in the study area. In addition, our models suggested that greater IAS cover (>50%, Figure 3) was associated with reduced α functional diversity. In the near future, the loss of rare species that often have specific functions, and the parallel increase of IAS abundance may lead to loss of functional diversity in the native species pool, generating more functionally homogenous communities.

To conclude, we pointed out how alien species may affect the native species pool beyond simple taxa reduction, namely through the reduction of all functional diversity components of the natural communities.

5 | CONCLUSIONS

This is one of the first studies including a large number of functional and mechanistic traits measured in different species in invaded coastal ecosystems. Our results suggest that native species display functional traits associated with stress resistance, whereas alien species are characterized by traits linked to a higher resource acquisition capacity (i.e. acquisitive strategy). Nevertheless, it is worth stressing the concept that the invasion process is strongly context-dependent, and IAS can have distinct impacts on the recipient native community in different ecosystems, both at taxonomic and functional levels (e.g. Funk et al., 2016; Hulme et al., 2013). A signal of potential functional homogenization in coastal ecosystems was detected, due to the lower functional diversity and community-level functional uniqueness displayed by alien species. As pointed out by Tobias and Monika (2012), functional homogenization should be explicitly investigated as an independent phenomenon that might be unrelated to taxonomic homogenization. Increasing the spatial extent of the study area, integrating root and seed functional traits, and considering also intraspecific variability (Petruzzellis et al., 2017), may allow a more comprehensive functional framework of the invasion process to be depicted.

DATA ACCESSIBILITY

Data used in this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. (a) Map of the study area, on the bottom right the geographical position in the Italian peninsula; and (b) specifics of the two sampling sites; red lines represent the transects.

Appendix S2. Description of plant functional traits used in this study.

Appendix S3. Table of the functional traits of each species (* alien species) used in this study. For quantitative traits, means and associated SDs are reported.

Appendix S4. Per-plot species richness (Mean ± *SD*) within each habitat for the whole community and for native and alien species separately; *n* represents the number of plots in each habitat.

Appendix S5. Correlation matrix (Spearman's ρ) of the quantitative functional traits used in this study. In bold the significant coefficients ($p < 0.05$).

Appendix S6. Summary showing CWMs of nominal functional traits in native and alien species in a) foredunes, b) saltmarshes. Significance determined using a Wilcoxon test is reported (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns = Not Significant). Please note that comparisons were performed only for the levels in each trait shared between native and alien species.

Appendix S7. Functional rarefaction curves of expected functional diversity (RaoQ) aggregated by transect considering native species, alien species and the curve averaged from permutations (permuted curve).

Appendix S8. Relationship between functional diversity of the total community (RaoQ$_{tot}$, left panel) and the native community (RaoQ$_{nat}$, right panel) as a function of normalized alien cover (N_{alien}) in saltmarshes.

Appendix S9. Pattern of functional diversity of the native community (RaoQ$_{nat}$, solid lines) and normalized alien species cover (N_{alien}, dotted lines) along each transect. The S below the *x*-axis denotes where the saltmarshes start.