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ORIGINAL ARTICLE

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Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline

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Abstract Coastal sand dunes represent one of the most fragile ecosystems in the Mediterranean basin. These habitats naturally suffer the action of several limiting factors such as sand burial, marine aerosol and low soil fertility; on the other hand, they often host species of high conservation value. Over the last decades, they have also experienced a high level of biological invasion. In this study, we sampled psammophilous vegetation in two sites in the northern Adriatic coast belonging to the Natura 2000 network to describe diversity patterns and to identify the main ecological drivers of species diversity. Plant species richness and their abundance were assessed in each plot. Differences in species composition for native and alien species were compared via PERMANOVA analysis. Species complementarity was explored by partitioning beta diversity in its spatial components (richness and replacement). A Generalized Linear Model was also computed to assess the main environmental factors that may promote invasiveness in these ecosystems. For the investigated area, our results highlight the strong differentiation in community composition both in alien and native species: in particular alien species showed on average a lower complementarity among habitats compared to native species. Specifically, communities seem to be more diversified when larger spatial scales were considered. Beta diversity in both groups appears to be more dominated by the richness component with respect to the replacement component. Furthermore, in these habitats, the occurrence of alien species was shown to be related to geomorphological predictors more than climatic variables.

Keywords Alien species · Beta diversity · Diversity partition · Natura 2000 network · PERMANOVA

Introduction

Coastal sand dunes are particular ecosystems that represent natural barriers against waves and windy storms. Three interacting factors are mainly responsible for the biota hosted in these habitats: waves, tides and sand particle size (McLachlan 2001; Šilc et al. 2017). Established plant communities are naturally subject to several limiting factors such as sand burial, sand blasting, marine aerosol and soil fertility. These environments are characterized by strong ecological gradients due to differences in the abiotic conditions that allow for the establishment of a typical spatial arrangement of the plant community along a sea-inland gradient, typically described as "zonation" by plant ecologists, which can be easily reiterated in different sites. Across the globe and particularly in the Mediterranean basin, coastal ecosystems are deemed to be highly endangered (Kutiel et al. 2000) and they have suffered a heavy loss of biodiversity and habitat simplification (Dolan and Walker 2006), mainly due to a steady increase in human pressure over the last decades (Curr et al. 2000; Reidsma et al. 2006; Brown et al. 2013). Usually, these environments naturally cope with stresses; however, recent alterations driven by anthropic disturbances (tourism, urbanization; O'Shea and Kirkpatrick 2000; Feagin et al. 2005), shoreline erosion (Anderson et al. 2015), climate changes (Van der Meulen et al. 2004; Prisco et al. 2013), and biological invasion (Acosta et al. 2009; Carboni et al. 2010), seriously threaten these ecosystems. The latter factor has been widely demonstrated to heavily jeopardize worldwide biodiversity, along with habitat loss and

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fragmentation (DAISIE 2009; EEA 2012). A growing body of literature has shed light on the negative effects that alien species can have in natural ecosystems (e.g. Vilà et al. 2011). They can trigger cascade effects among which it is worth keeping in mind the modification of local species composition (Gaertner et al. 2009; Hejda et al. 2009; Powell et al. 2011) and the alteration of the nutrient cycle (Ehrenfeld 2010). These may even lead to the extinction of native taxa with great ecological value, like endemism and keystone species, through competitive exclusion processes. This can be particularly evident in coastal ecosystems, which are one of the most invaded ecosystems in Europe (Chytrý et al. 2008) in which alien species have the heaviest ecological impacts (see for instance Santoro et al. 2012). In fact, despite their adaptations in tackling stresses, these environments have little resilience capability since modest disturbances may cause long-term alterations and abrupt changes (Carter 1988; Lemauviel and Rozé 2003). Italy has about 7500 km of coastline; among these, coastal dunes occupy only 40% of the total (3300 km, CNR 1999), even though are exploited mainly for touristic purposes. In fact, since the 1950s, sand dune ecosystems along the northern Adriatic coastline have experienced strong habitat fragmentation, trampling and alteration in geomorphological processes, among others, mainly due to a steady increase in tourist activities and urbanization (Nordstrom et al. 2009), resulting in the few natural remnants present along the coastline today. For these reasons, most of the ecosystems hosted are highly threatened and belong to protected areas such as the Sites of Community Importance (SCIs, Natura 2000 Network), due to the dual presence of both priority habitats and species of Community Importance according to EU regulations (Habitats Directive 92/43/EEC). The uniqueness of the flora occurring in the Northern Adriatic area is the result of a ''crossroad'' of species with different origins due to the peculiar biogeographical location. Hence, climatic changes which occurred between the third and first millennium BC led to important floristic migrations: in fact, species with Alpine, Mediterranean and Eastern native range reached the N-Adriatic coast (Lorenzoni 1983; Géhu et al. 1984; Buffa et al. 2012). Thus, in this biogeographic and bioclimatic context, xero-thermophilus species tend to colonize draining substrates, whereas in the interdune lowlands, it is still possible to find hygrophilous and microthermic entities of montane origin. For this floristic uniqueness compared to the rest of the Mediterranean basin, the conservation value of these plant communities goes far beyond the European environmental conservation policies (Sburlino et al. 2013).

For the above-mentioned reasons, there is a need to constantly assess or update the conservation status of coastal dunes ecosystems in order to promote appropriate management strategies to preserve these peculiar environments. At the same time, it is mandatory to determine those biotic/abiotic factors directly or indirectly driving biodiversity patterns in order to propose decisions for coastal protection made using rigorous scientific criteria. In this study, through a systematic sampling design based on belt transects, we sampled psammophilous vegetation in two SCIs along the northern Adriatic coastline with the following specific aims: i) describe the diversity patterns of sand dune plant communities in two coastal sites for both native and alien species components, ii) assess the conservation status of native plant communities in relation to alien invasion and iii) identify the main drivers of native and alien species diversity and testing for the effect of geomorphological, environmental and human-induced factors related with alien species occurrence.

Materials and methods

Study area

Data on sand dune vegetation were collected in two sampling sites (Brussa and Bibione) both located in northeast Italy (Fig. 1). These areas represent two remnants of the primarily sedimentary northern Adriatic coastline where it is still possible to find wide patches of sand dune vegetation that host a great number of rare and endemic species. For this reason, both sites belong to two SCIs named ''Valle Vecchia, Zumelle and Valli di Bibione'' (IT 3250041) and ''Foce Tagliamento'' (IT 3250040). The climate is temperate-subcontinental (Cfa of the Köppen-Geiger classification, Kottek et al. 2006), mean annual temperature is between 10 and 14 °C without a dry phase and mean annual precipitation is ca. 828 mm. Both sites are fiercely influenced by the Bora wind, which dramatically decreases thermal limits mainly during winter. The first study site, called Brussa (45.620554°N–12.942477°E; *datum:* WGS84), represents the longest strip of non-urbanized area in the high Adriatic basin (Provincia di Venezia 2010). It consists of a sandy shoreline east-to-west oriented that divides the

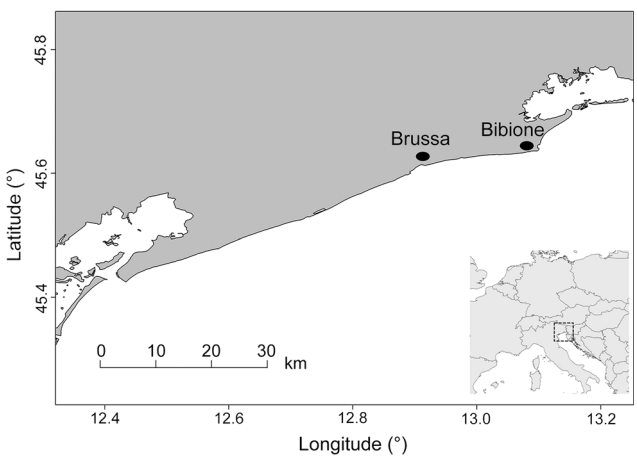

Fig. 1 Location of the two sampling sites in Northeast Italy. On the right, an overview of the sites compared to the Italian peninsula

sea from the lagoon behind (Caorle lagoon). Being not endowed of touristic facilities, it still preserves natural patches hosting plant species of great conservation value, even though trampling may represent an issue especially for rare and endemic species. It is delimited by Porto Falconera to the west side and by Porto Baseleghe to the east. The sedimentary regime of the littoral is determined by a longshore sediment drift towards the southwest (Fontolan 2004) and the recent trend is stable or slightly in accretion (Fontolan et al. 2014). It hosts several plants and animal species included in the Annexes I and II of the Habitat Directive (Directive 92/43/EEC) and 39.74% of the total SCI surface is designated as habitat of Community Importance. During the reclamation of the lagoon in 1960s, an artificial pinewood of *Pinus pinea* L. and *Pinus pinaster* Aiton was planted, which has superseded the potential native vegetation (*Quercetalia ilicis*, Provincia di Venezia 2010). The second sampling site is called Bibione (45.636058°N–13.097145°E; *datum:* WGS84). This site is completely surrounded by a highly urbanized and touristic area; in fact, it has been estimated an average of more than 5 million of tourists per year in the last decade (Fontolan et al. 2014). This place is also famous for the sandy beaches and the many outdoors activities and aquatic sports that is possible to practice (e.g. walking, cycling, windsurfing and kayaking). Here probably trampling and human activities related to beach management may represent the main cause of the reduction or loss of specific habitat features. The sampling area of Bibione is delimited on the east side by the mouth of the Tagliamento River and on the west side by the town of Bibione. The beach is directly influenced by terrigenous deposition; in fact, there is a strong sedimentary input carried by Tagliamento River and in the last years, the sedimentary budget has shown an accretion trend (> 5 m^3 m^{-1} $year^{-1}$, Fontolan et al. 2014).

Sampling design and data collection

The following sampling design was adopted to collect data on plant composition and abundance: first a square grid of 500 m linear dimension was overlaid to each sampling site. In each cell, a random transect was selected following a sea-inland gradient with variable length due to dune width and coast morphology. Transects were partitioned in a set of contiguous squared sub units (plots) of 4 m × 4 m where the occurrence and percentage visual cover estimation of each vascular plant species were assessed. Since this survey is focused on psammophilous vegetation plots, pinewoods and non-sand dune vegetation were not sampled. Fieldwork was carried out during May–August 2016; in total 21 transects and 261 plots were sampled (104 plots in Bibione and 157 in Brussa, respectively). Later on, each plot was assigned to a specific coastal habitat included in the Habitats Directive based on the observed vegetation and on those reported in the SCI habitat map (source https://www.regione.veneto.it). For the sake of simplification and to make these habitats comparable to other studies, plots were classified in three major recognizable classes based on dune dynamics: (i) Foredune including upper-beach, embryo-dunes and mobile dunes (EU Habitat Code 1210, 2110 and 2120), (ii) Fixed dune encompass ing those environments dominated by perennial communities of the inland side (EU Habitat Code 2130 and 6420), (iii) Interdune that include distinctive habi tats mainly constituted by salt marshes and Mediter ranean humid grasslands of tall grasses and rushes (EU Habitat Code 1403 and 7210). It is worth noting that some of these habitats such as 2130 and 7210 are deemed of priority importance by the European Union. All the vascular plants recorded within each plot were identified at the species or subspecies level directly in the field or, most frequently, in the laboratory by using proper identification floras (Pignatti 1982). Nomenclature was standardized according to Conti et al. (2005). Plants were classified as native or alien species, depending on their status as given by Celesti-Grapow et al. (2009).

Abiotic variables

Climatic data were downloaded from the ARPAV website (http://www.arpa.veneto.it). Averages of mini mal, mean, maximum values along with their range (maximum-minimum) were calculated for temperature (°C) and relative humidity (RH, %). For precipitation (mm), rainy days, and irradiation (MJm^{-2}) only the average values were computed. In this way, a total of 25 climatic predictors were obtained using baseline climatic data spanning from 2008 to 2015 and encompassing a March–October time range. Geomorphological data were derived from the Shape project database (Fontolan et al. 2014); specifically, beach mean width (m), annual deposition rate (m^3 m^{-1}), shoreline variation (m $year^{-1}$), and class of erosion (three levels: accreting, stable and in erosion) were selected. Since these sites are also facing strong human impacts, touristic pressure (number of tourists m^{-2}) was also selected based on the index measured in Fontolan et al. (2014). Finally, Ele vation (m), slope (°), Northness, Eastness and the standard deviation of the slope (as an effective measure of terrain roughness according to Grohmann et al. 2010) were derived using a LIDAR raster at 1 m resolution using QGIS 2.16.3 with GRASS 7.0.4 (Quantum GIS Development Team 2016).

Statistical analysis

Analysis of plant diversity patterns

Latent gradients in species composition for both native and alien species were assessed through indirect gradient analysis (Nonmetric MultiDimensional Scaling). Significant differences in community composition were eval-

uated using multivariate permutational analysis of variance (PERMANOVA, Anderson 2001). Both the analyses were based on a Bray–Curtis similarity matrix on log-transformed species abundances. The following factors were tested in the PERMANOVA design: "Site" (fixed, two levels), "Transect" (random, nested within Site) and "Habitat" (fixed, three levels), along with the interaction "Habitat x Site" and "Habitat x Transect". A posteriori pairwise comparison was applied to assess the effect of habitat when it was found to be significant. All tests were performed with 4999 permutations of residuals under a reduced model using Type I Sums of Squares. Analyses were performed using PRIMER 6 software (Clarke and Warwick 2005) and the PERMANOVA routine in the add-on package PERMANOVA + (Anderson et al. 2008). Subsequently, for each group, plot-based rarefaction curves (hereafter SAC, Gotelli and Colwell 2001; Chiarucci et al. 2008) were computed using the exact method in the "vegan" package (Oksanen et al. 2017) to compare patterns as a function of the sampling effort. We also calculated Spatially-Explicit Rarefaction curves (hereafter SER, Chiarucci et al. 2009; Bacaro et al. 2012) to check the consistency of the SAC due to their ability to account for spatial autocorrelation among plots, especially when the extent of the study areas is different (Bacaro et al. 2011, 2016). Diversity patterns for native and alien species were also compared using classic partition techniques (Lande 1996; Gering et al. 2003; Crist et al. 2003; Chiarucci et al. 2010) that allows for the partition of the three components of the diversity (alpha, beta and gamma) across the different spatial scales of investigation (plot scale, transect scale, site scale and the whole study area). This analysis was also performed by splitting native and alien species by habitat. Mean values of each of these components were reported as the proportion of mean species richness. 999 permutations were used to test if there were deviations from randomness in the observed patterns using null model testing.

Exploring relationships of diversity components between native and alien plant communities

The relationship between alien and native richness was tested using simple linear regression. Species complementarity, namely beta diversity, was split into its basic components in both groups: replacement (β_{repl}, that is a species in one site is substituted by a species in another site) and richness (β_{rich}, the loss or gain of species between sites; for more details about the methodology see Carvalho et al. 2013; Legendre 2014). Beta diversity was further explored using Local Contributors of Beta Diversity (hereafter LCBD, Legendre and De Cáceres 2013) in the R package "adespatial" (Dray et al. 2016). This analysis is useful to highlight the uniqueness of the sampling units in terms of community composition. 999 permutations were performed to test for randomness in species distribution while preserving the species abundance distributions in the observed data. LCBD values have been visually displayed using the "ggmap" package (Kahle and Wickham 2013). In both the analyses the species sampled in the plots were aggregated by transect.

LCBD values were also derived according to habitat in each transect, the presence of significant differences was evaluated using the Kruskal–Wallis rank sum test. When the test resulted significant, adjusted posteriori pairwise comparisons were performed between pairs of habitat using the package "pgirmess" (Giradoux 2017).

Analysis of ecological determinants of native and alien species

The variation partition in the multivariate space of the community matrix for the native and alien compartment was computed with respect to the set of available explanatory variables (Peres-Neto et al. 2006; Legendre and Legendre 2012) in order to assess which group of variables (spatial, climatic and geomorphological) contributed more to explain the variability in the dataset; prior to analysis the species matrix was Hellinger-transformed as suggested by Peres-Neto et al. (2006). Since a very high multicollinearity was detected in our predictors, a subset (Online Resource Tables S1 and S2 for more details) was obtained using multivariate forward selection by permutations of residuals (999) under a reduced model following the double-stopping criterion proposed in Blanchet et al. (2008).

Finally, to highlight which were the main abiotic factors related to alien species spread in sand dune ecosystems, a binomial random intercept model (GLMM) was computed considering the occurrence of alien species in plots, setting the transect factor as the random effect nested in Site. However, the random effect of the transect was not significant according to the likelihood ratio test ($\chi^2(2) = 0$, $P > 0.05$), and a classic Generalized Linear Model (GLM) was then considered. Before building the GLM, all predictors were standardized (z-scores) in order to obtain quantitatively comparable regression coefficients. To reduce multicollinearity in the set of climatic variables, a Principal Component Analysis was performed (Online Resource Table S3). All axes that cumulatively contained greater than or equal to 75% of the variation were considered, this resulted in just the first axis added (91% of the variation explained). The Minimum Adequate Model (MAM) was obtained through model averaging according to AIC reduction using the "glmulti" package (Calcagno 2013). Variable importance was assessed by weighting standardized regression coefficients by AIC-weights and adding them up for all models in which a variable was included (Burnham and Anderson 2002).

All the analyses were performed using R 3.3.3 (R Core Team 2017).

Results

The pooled species richness of the 261 sampled plots is 127 (Table 1). Among these, 116 have been classified as natives (91.4% of the whole sample) and 11 as aliens (8.6%). The most frequent families in the total species pool are represented by Poaceae (17.3% of the sampled species), Asteraceae (16.5%), Cyperaceae (5.5%) and Chenopodiaceae (4.7%). The most frequent species are *Elymus farctus* (Viv.) Runemark ex Melderis (occurring in 36.2% of the sampled plots), *Spartina versicolor* Fabre (30.7%) and *Vulpia fasciculata* (Forssk.) Fritsch (30.4%). Among alien species, the most abundant families are Asteraceae (36.4%) and Fabaceae (18.2%) with *Oenothera stucchii* Soldano (61.8%), *Ambrosia coronopifolia* Torr. & A. Gray (57.6%) and *Xanthium orientale* subsp. *italicum* (Moretti) Greuter (44.7%) as the most frequent species. NMDS analysis for native species provides a fairly good representation of the sampled community (Fig. 2a, stress = 0.17); in fact, plots tend to aggregate according to habitat and sampling site. Conversely, the same unconstrained ordination computed only on alien species (Fig. 2b, stress = 0.18) clearly shows the absence of specific patterns, highlighting the non-specificity with which these species colonize sand dune environments. PERMANOVA outcomes for native and alien species (Table 2) highlight that significant sources of variability in species composition is determined by the spatial scales and habitat: while for native species these differences occurred for each of the considered factors (except for the Habitat x Site interaction), it is interesting to note that as for alien species, the main effect of Habitat was not significant, along with the Site x Habitat interaction, confirming the observed NMDS pattern. The post hoc test reveals a significant difference among all the habitat levels for native species (Foredune *vs* Interdune $t = 1.8576$, $P = 0.0004$; Foredune *vs* Fixed dune $t = 2.0262$, $P = 0.0002$; Interdune *vs* Fixed dune $t = 2.2347$, $P = 0.0002$). The estimated components of variance (expressed as %) are mainly driven by the Site and Habitat component for the native group, whereas for the alien group the factors Site and Transect accounted for most of the variance explained (Fig. S1 in Online Resource).

Rarefaction curves (both SAC and SER, Online Resource Fig. S2) result as being almost asymptotic considering both species groups, suggesting that most of the species pool has been sampled. Once SER and SAC have been calculated separately by habitat type (Fig. 3), the Fixed dunes tended on average to host a higher number of species as expected compared to Foredunes or Interdunes habitats in both groups displaying a greater steepness, however. These results suggest that plant communities closer to the sea are characterized by a lower number of species and are more homogeneous in terms of species pool. It is worth noting how for native species, the SER in Interdune displays different behavior compared to the SAC (Fig. 3a). Proportions of the diversity components (namely α and β), exhibit different patterns according to the investigated species group (Fig. 4). Specifically, alien species present lower levels of beta diversity across plots, transects and sites compared to native ones. Hence, species complementarity decreases substantially moving from the native to the alien group, specifically at plot scale is higher than that expected from the null models. Thus, significant compositional differences exist among plots in each transect, evidently resembling the effect of the sea-inland gradient. Both alien and native species show not significant differences from null expectations across transects, hence highlighting that both these groups essentially share the same species composition within the group. A similar pattern has been observed for alien species at the site level, conversely native species show significant difference between the two sites confirming a difference in the species pools. It is interesting to note how alien species complementarity in the Foredunes show very few differences across sites. A significant positive linear model ($F(2, 259) = 55.77$, $P < 0.001$, $R^2 = 0.17$) was found between native and alien species richness ($b = 1.26$, $P < 0.001$). The analysis of LCBD shows that these values ranged between 0.0337 and 0.0666 for native species with five transects having significant values; whereas for alien species LCBD varied from 0.0118 to 0.1662 with just one significant value (Fig. 5). Kruskal–Wallis test confirms significant differences in LCBD according to habitat both in native ($\chi^2(2) = 25.15$, $P < 0.001$) and alien ($\chi^2(2) = 13.24$, $P < 0.01$). Post-hoc tests show significant values between Foredune *vs* Fixed dune and Foredune *vs* Interdune in native species, whilst alien species display significant differences just between Foredune *vs* Interdune. Decomposition of beta diversity in its two components (β_{repl} and β_{rich}, Online

Table 1 Species richness (Mean ± SD) and number of plots in each habitat for total, native and alien species group; n represents the number of plots in each habitat. Family column displays the most represented family in the dataset for each species group

Group	Habitat			Family (% of sampled species)
	Foredune $n = 126$	Interdune $n = 42$	Fixed dune $n = 93$	
Total species	6.40 ± 3.54	6.60 ± 3.61	11.81 ± 3.27	Poaceae (17.32)
Native species	4.66 ± 2.81	5.57 ± 2.80	9.31 ± 3.19	Poaceae (16.53)
Alien species	1.75 ± 1.22	1.02 ± 1.33	2.49 ± 0.80	Asteraceae (36.36)

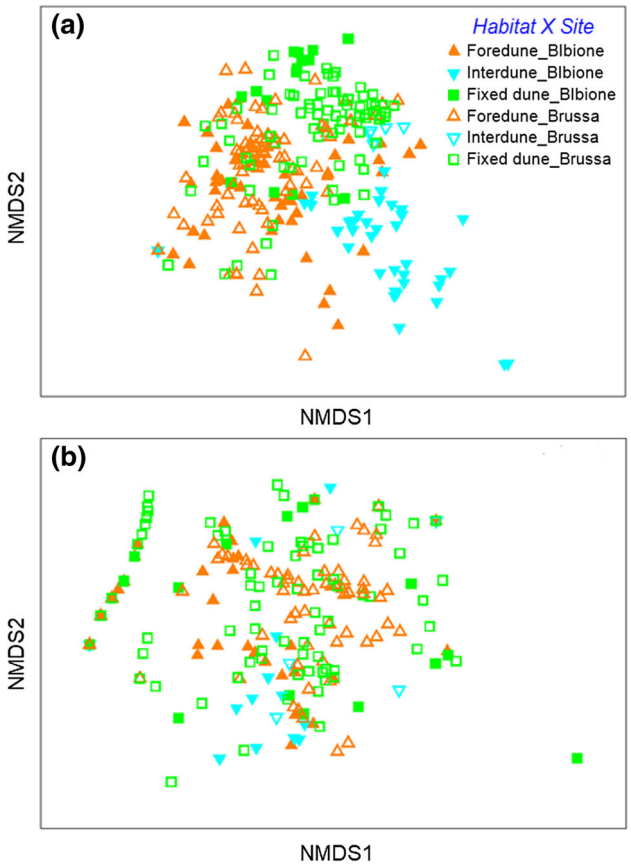

Fig. 2 NMDS output based on Bray–Curtis similarity matrix (log-transformed abundance data) for each habitat and sampling site. **a** Native species **b** Alien species. Please refer to the online version for colors

Resource Fig. S3) highlights that beta diversity in this study area is dominated by differences in species gain or loss among transects for both groups (excluding few transects for native species in which the replacement component dominates). A significant multiple linear regression ($F(2,17) = 3.652$, $P < 0.05$, $R^2 = 0.21$) was calculated between alien β_{rich} and native β_{repl} and the ratio of native $\beta_{repl}/\beta_{rich}$. Model output shows a notable decreasing trend between alien β_{rich} and native β_{repl} ($b = -0.68$, $P < 0.05$, Fig. 6) and a positive relationship with the ratio $\beta_{repl}/\beta_{rich}$ ($b = 0.07$, $P < 0.05$). The variation partitioning approach on species composition data highlights that abiotic variables explain 36% of the total variation for native species and 40% for the alien species (Fig. 7). Notably, climatic and geomorphological predictors in combination encompass most of the variation present in the dataset (32% for native and 34% for aliens), whereas the influence of spatial structure in the dataset is almost completely negligible, likely due to the small extent considered in this study (5% for native and 6% for aliens). Despite climatic and geomorphological predictors accounting for a similar percentage of explained variation in both groups, PERMANOVA analysis points out that observed differences for alien species occur at a finer spatial scale, namely within habitats along each transect. Furthermore, when only the occurrence of alien species is explored, the GLM output shows that the major determinants of alien presence are represented chiefly by the geomorphological dynamics of the beach (Table 3) and, to a lesser extent, by human-induced factors such as touristic pressure. In particular, elevation, class of erosion, beach mean width and deposition rate are the most significant predictors in explaining alien species presence (with a higher likelihood to find alien species according to an increase in these values). Additionally, Northness and Touristic pressure influence alien occurrences with positive and negative slopes, respectively.

Discussion

Community structure along the environmental gradient

The present work aims to describing diversity patterns of plant communities in northern Adriatic sand dune ecosystems, exploring the relationships and the interactions among native and alien species groups and ecological factors shaping their distribution. The number of alien species found is in line with other studies in the same area or ecosystem (Campos et al. 2004; Vilà et al. 2007; Del Vecchio et al. 2015). Despite their apparent low percentage compared to the Italian one (9.4% while the Italian average is 13.4% and that of the Veneto region is 11.8%, Celesti-Grapow et al. 2009) it should be taken into account that these habitats are of great conservation values due to the elevated proportion of

Table 2 PERMANOVA output based on Bray–Curtis similarity calculated for native and alien species

Source of variation	Native species				Alien species			
	df	MS	Pseudo-F	*P*	*df*	MS	Pseudo-F	*P*
Habitat	2	61324	3.98	0.0002	2	11342	1.12	0.1332
Site	1	26739	2.07	0.0214	1	37333	3.53	0.0098
Transect (site)	19	12190	4.50	0.0002	19	10615	4.69	0.0002
Habitat × site	2	8301.7	1.75	0.0830	1	3474.6	0.90	0.4580
Habitat × transect (site)	14	6011.4	2.22	0.0002	12	4368.8	1.93	0.0002
Residual	218	2706.9	–	–	181	2262	–	–
Total	256	–	–	–	216	–	–	–

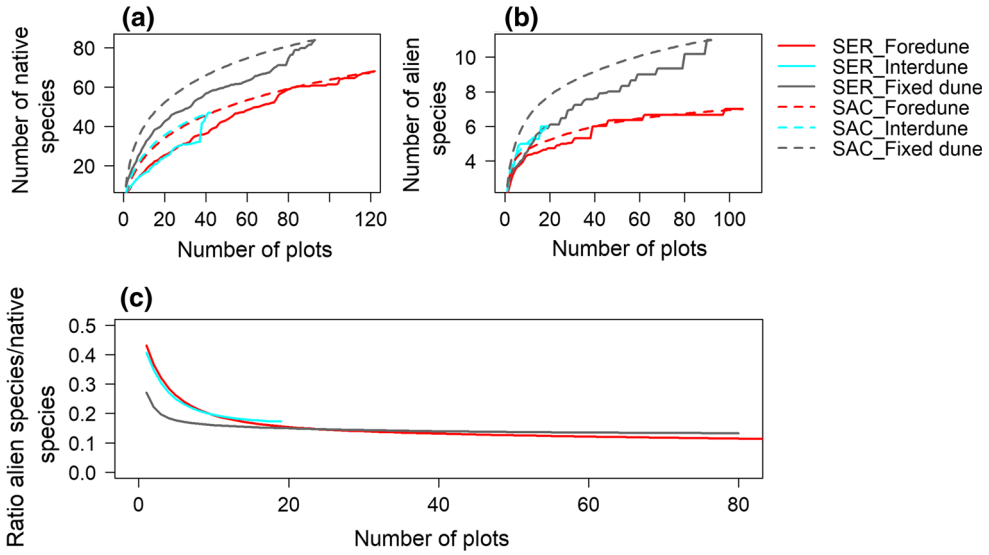

Fig. 3 Rarefaction curve (SAC) and Spatially-explicit rarefaction (SER) for **a** native species and **b** alien species. **c** Ratio between alien and native SAC for each habitat, note that only the first part of the x-axis is reported and that the Foredune curve would continue until 106 plots. Please refer to the online version for colors

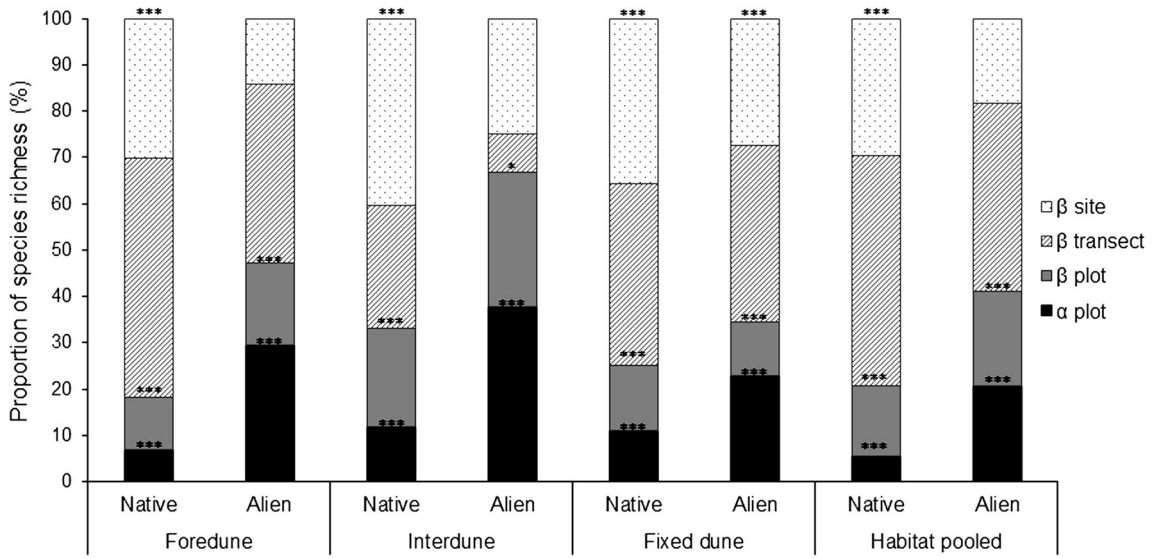

Fig. 4 Diversity components (% of the total) for native and alien species for each habitat and for all habitat pooled. The contributions to the total richness for each scale were determined by the additive partitioning of diversity method (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$)

endangered and exclusive plant taxa they host (Van der Maarel 2003; Acosta et al. 2009). Diversity patterns in native and alien species show very different behaviors according to habitat and to the spatial scale investigated. The concept of scale-dependence between native and alien species richness has already been widely debated (Levine and D'Antonio 1999; Fridley et al. 2007) and, in agreement with this statement, our findings support the idea that it is not possible to directly compare the proportion of aliens across areas without taking into account the effects of the spatial scale or the size of the flora (Gotelli and Colwell 2001; Palmer et al. 2006), as the ratios of SAC of our study also confirm. The observed mean difference between SAC and SER is 3.9 species that can be seen as the outcome of spatial dependence among individuals in the space, acting in the same way in both groups (except for the interdune habitat). In general, rarefaction curves allow us to be satisfied about the goodness of the sampling effort which is crucial in estimating the correct number of species (Acosta et al. 2009; Chiarucci et al. 2012). In case of sampling bias, some rare or endangered species may not have been recognized or underestimated, resulting in relevant implications for conservation programs. Results of NMDS clearly suggest that the gradient in the species composition of native species was only marginally related to that of alien species. The native species pattern could be seen as the outcome of the harsh conditions

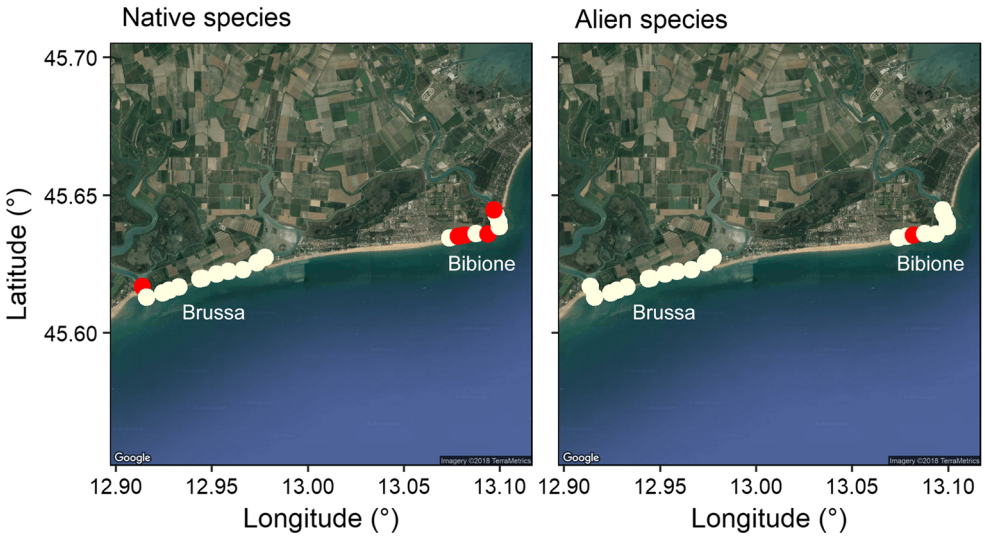

Fig. 5 Map of Local Contributor of Beta Diversity values. In white the non-significant transects ($P > 0.05$); in red, the significant transects ($P < 0.05$). Please refer to the online version for colors

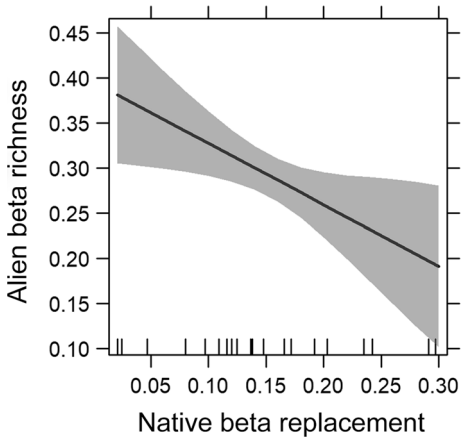

Fig. 6 Relationship between beta replacement of native species and beta richness on alien species. Black line represents the calculated regression trend, shaded area the 95% confidence interval

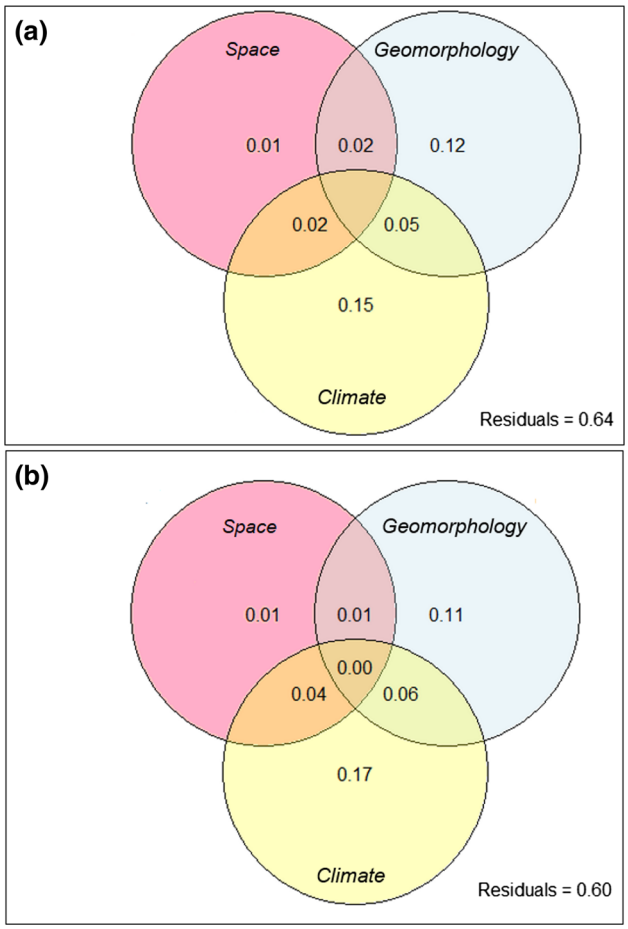

Fig. 7 Partition of the variation of the community matrix according to the three explanatory variable groups. **a** Native species **b** Alien species. Please refer to the online version for colors

naturally present in these habitats that shape plant communities. It is interesting to note how the apparent absence of such structure in the alien species pool may be seen as evidence of a potential shift towards randomness in the community assembly rules (Santoro et al. 2012). Differences in distributional patterns between native and alien species at the local scales have also been reported by some studies on roadside communities (Arévalo et al. 2005) or cultivated systems (Lososová and Cimalová 2009). The presence of strong limiting factors acting in these environments is deemed the main drivers on plant species composition in these ecosystems. Both the native and alien species pool in our dataset share the same ecological drivers though with slightly different proportions and effects, as pointed out in variation partitioning analysis. The Foredune habitat was confirmed as extremely species poor and selective for plant species compared to Fixed dunes. This can be seen as the result of the harsh conditions present closer to the sea such as marine aerosol, lower levels of nutrients and moisture, salt spray (see Perumal and Maun 2006; Carboni et al. 2010; Ciccarelli et al. 2012). On the

Table 3 Analysis of deviance table (Type III Likelihood-Ratio Test) of the GLM model based on alien species occurrence

Coefficient	LRT (χ^2)	P ($> \chi^2$)	Coefficient sign
Class of erosion	16.08	< 0.001	
Elevation	27.31	< 0.001	+
Beach mean width	13.19	< 0.001	+
Beach annual deposition rate	13.55	< 0.001	+
Northness	9.79	< 0.01	+
Touristic pressure	3.44	0.063	–

other hand, Fixed dunes tended to be permanent due to the lower exposure to the limiting factors cited above and to the evolution of some adaptations that allow them to survive and reproduce (Wiedemann and Pickart 2004; Acosta et al. 2006). Here, higher level of species richness was observed in both groups as reported also in Vaz et al. (2015) and Marcantonio et al. (2014), among others. The higher number of alien species in the Fixed dunes may be seen as a sign that native species assembly have lost their capability to compete with alien species probably due to an effect of human-induced disturbances (e.g. trampling, Del Vecchio et al. 2015) that create gaps in the niche where these species, which are pre-adapted to cope with stresses (e.g. for an urban environment Knapp et al. 2008), can be easily integrated and propagate in the surrounding areas. One of the more hazardous consequences may be the biotic homogenization of these ecosystems, with the resulting loss of endemism or rare species of which these environments are naturally rich.

The model output shows as the geomorphological features rather than climate influence alien species occurrence, most likely due to the indirect effect of the small extent of the study area. The importance of geomorphological predictors in the sand dune plant communities has also been outlined in Prisco et al. (2013), where the beach length was the most important factor influencing their habitat distribution models. Similar results were also described in Fenu et al. (2012), where for the total species pool soil properties more than wind-related variables drive the distribution of plant communities along the sea-inland gradient. Conversely, in Carboni et al. (2010), climatic variables played a key role in shaping alien species richness. The effect of erosive coastal processes on plant community composition and the potential synergic effect between sand dune erosion and invasiveness still remain unclear and would require longer term investigation (e.g. Hill et al. 2010). Ciccarelli et al. (2012) observed that where the instability of the coast was greater there is a disequilibrium in the community and a highly heterogeneous species composition. Moreover, human-related factors such as trampling and coastal erosion are closely related to habitat degradation and loss (Ciccarelli 2014). This confirms the need to preserve costal habitats in order to ensure effective conservation actions regarding these endangered habitats.

Beta diversity patterns

In general, analyses of beta diversity may provide useful insights into drivers and assembly rules of plant communities and of the potential mechanisms of invasion taking into consideration different spatial scales (Leprieur et al. 2009; Marini et al. 2009).

Partition of diversity highlights how most of the diversity can be observed at transect and site scale for native species and at a smaller scale (plot) for aliens. This indicates that alien species tend to share species composition increasing the scale of analyses. A similar pattern has also been described in Tordoni et al. (2017) for a coastal urban context. Although the richness values of native and alien species were correlated at the plot scale, it has been clearly demonstrated that most likely it is the beta diversity of both species groups which regulate equilibrium in the plant community. Decomposition of beta diversity provides a suitable tool to elucidate the mechanisms of assembly of plant sand dune communities along the sea-inland gradient. Our results show how is the difference in richness component more than replacement which dominates in our sampling sites. Practically speaking, this indicates that community change was primarily determined by the loss of species in both groups (originating richness differences among transects) from more dynamic to more stable habitats. Considering alien species, this could be explained as the outcome of the spatial arrangement of the pathways of introduction (e.g. roads and paths, see for instance Marini et al. 2013 for mountain environment, Bacaro et al. 2016 for an oceanic island) thanks to which alien species reflect a similar species pool present in the surrounding areas. On the contrary, the larger proportions of beta replacement observed in native species may be easily interpreted as larger adaptions to the harsh conditions present in these habitats, due to their longer residence time. The relationships between beta components clearly highlight how an increase in native beta replacement significantly reduce alien beta richness. This is in agreement with biotic resistance theory (Levine 2000; Levine et al. 2004), which states that resident species in a community reduce the success of exotic invasion through biotic filters such as competition, pathogens and herbivores. Concerning the significance of LCBD values in native species, this could be mainly explained by the presence of the Interdunes habitat that hosts a characteristic community which share few species with the other habitats.

Conclusions

Sand dune ecosystems represent fragile environments endowed with particular characteristics that make them unique both in terms of species vegetating and habitat features. There is currently an increasing need to monitoring and actively manage these environments through

concrete preservation and restoration actions regarding these habitats, where necessary. Thus, coastal ecosystems are currently constrained between human-related threats from one side and shoreline erosion from the other, the so called "coastal squeeze" (Defeo et al. 2009).

The present study uses quantitative methods to analyze species diversity and their relationships in different coastal plant communities along a sea-inland gradient. A well-structured plant community may cope better with alien invasion that indirectly allows for the protection of endemism or rare species. In order to protect such fragile coastal areas, increase awareness about alien species issue among citizens and tourists is crucial; in addition, it would be advisable to preclude or fence some parts of the beach that host priority habitat, rare or endemic species. Furthermore, we have shown that an increase in the beta diversity of native species may reduce alien species diversity indirectly ensuring the protection of the ecosystems from the potential deleterious effects of biological invasions. Eradication programs may be planned where higher levels of alien beta diversity are observed optimizing time and resources.

At last, in a climate change scenario, it is worth also keeping in mind that the several ecosystem services that coastal habitats provide for such as protection against storms, water purification and other sociocultural aspects (Martínez et al. 2004; Van der Meulen et al. 2004; Worm et al. 2006; Everard et al. 2010).

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