

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

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31 **Abstract**

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

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54 **Keywords:** Alien species, Beta diversity, Diversity partition, Natura 2000 network, PERMANOVA.

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64 **Introduction**

65 Coastal sand dunes are particular ecosystems that represent natural barriers against waves and windy
66 storms. Three interacting factors are mainly responsible for the biota hosted in these habitats: waves,
67 tides and sand particle size (McLachlan 2001; Šilc et al. 2017). Established plant communities are
68 naturally subject to several limiting factors such as sand burial, sand blasting, marine aerosol and soil
69 fertility. These environments are characterized by strong ecological gradients due to differences in
70 the abiotic conditions that allow for the establishment of a typical spatial arrangement of the plant
71 community along a sea-inland gradient, typically described as “zonation” by plant ecologists, which
72 can be easily reiterated in different sites. Across the globe and particularly in the Mediterranean basin,
73 coastal ecosystems are deemed to be highly endangered (Kutiel et al. 2000) and they have suffered a
74 heavy loss of biodiversity and habitat simplification (Dolan and Walker 2006), mainly due to a steady
75 increase in human pressure over the last decades (Curr et al. 2000; Reidesma et al. 2006; Brown et
76 al. 2013). Usually, these environments naturally cope with stresses; however, recent alterations driven
77 by anthropic disturbances (tourism, urbanization; O’Shea and Kirkpatrick 2000; Feagin et al. 2005),
78 shoreline erosion (Anderson et al. 2015), climate changes (Van der Meulen et al. 2004; Prisco et al.
79 2013), and biological invasion (Acosta et al. 2009; Carboni et al. 2010), seriously threaten these
80 ecosystems. The latter factor has been widely demonstrated to heavily jeopardize worldwide
81 biodiversity, along with habitat loss and fragmentation (DAISE 2009; EEA 2012). A growing body
82 of literature has shed light on the negative effects that alien species can have in natural ecosystems
83 (e.g. Vilà et al. 2011). They can trigger cascade effects among which it is worth keeping in mind the
84 modification of local species composition (Gaertner et al. 2009; Hejda et al. 2009; Powell et al. 2011)
85 and the alteration of the nutrient cycle (Ehrenfeld 2010). These may even lead to the extinction of
86 native taxa with great ecological value, like endemism and keystone species, through competitive
87 exclusion processes. This can be particularly evident in coastal ecosystems, which are one of the most
88 invaded ecosystems in Europe (Chytrý et al. 2008) in which alien species have the heaviest ecological
89 impacts (see for instance Santoro et al. 2012). In fact, despite their adaptations in tackling stresses,
90 these environments have little resilience capability since modest disturbances may cause long-term
91 alterations and abrupt changes (Carter 1988; Lemauviel and Rozé 2003). Italy has about 7500 km of
92 coastline; among these, coastal dunes occupy only 40% of the total (3300 km, CNR 1999), even
93 though are exploited mainly for touristic purposes. In fact, since the 1950s, sand dune ecosystems
94 along the northern Adriatic coastline have experienced strong habitat fragmentation, trampling and
95 alteration in geomorphological processes, among others, mainly due to a steady increase in tourist
96 activities and urbanization (Nordstrom et al. 2009), resulting in the few natural remnants present
97 along the coastline today. For these reasons, most of the ecosystems hosted are highly threatened and

98 belong to protected areas such as the Sites of Community Importance (SCIs, Natura 2000 Network),
99 due to the dual presence of both priority habitats and species of Community Importance according to
100 EU regulations (Habitats Directive 92/43/EEC). The uniqueness of the flora occurring in the Northern
101 Adriatic area is the result of a “crossroad” of species with different origins due to the peculiar
102 biogeographical location. Hence, climatic changes which occurred between the third and first
103 millennium BC led to important floristic migrations: in fact, species with Alpine, Mediterranean and
104 Eastern native range reached the N-Adriatic coast (Lorenzoni 1983; Gehu et al. 1984; Buffa et al.
105 2012). Thus, in this biogeographic and bioclimatic context, xero-thermophilus species tend to
106 colonize draining substrates, whereas in the interdune lowlands, it is still possible to find hygrophilous
107 and microthermic entities of montane origin. For this floristic uniqueness compared to the rest of the
108 Mediterranean basin, the conservation value of these plant communities goes far beyond the European
109 environmental conservation policies (Sburlino et al. 2013).

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

121

122 **Materials and methods**

123

124 *Study area*

125 Data on sand dune vegetation were collected in two sampling sites (Brussa and Bibione) both located
126 in northeast Italy (Fig. 1). These areas represent two remnants of the primarily sedimentary northern
127 Adriatic coastline where it is still possible to find wide patches of sand dune vegetation that host a
128 great number of rare and endemic species. For this reason, both sites belong to two SCIs named “Valle
129 Vecchia, Zumelle and Valli di Bibione” (IT 3250041) and “Foce Tagliamento” (IT 3250040). The
130 climate is temperate-subcontinental (Cfa of the Köppen-Geiger classification, Kottek et al. 2006),
131 mean annual temperature is between 10 - 14°C without a dry phase and mean annual precipitation is

132 ca. 828 mm. Both sites are fiercely influenced by the bora wind, which dramatically decreases thermal
133 limits mainly during winter. The first study site, called Brussa (45.620554°N – 12.942477°E, *datum*
134 WGS84), represents the longest strip of non-urbanized area in the high Adriatic basin (Provincia di
135 Venezia 2010). It consists of a sandy shoreline east-to-west oriented that divides the sea from the
136 lagoon behind (Caorle lagoon). Being not endowed of touristic facilities, it still preserves natural
137 patches hosting plant species of great conservation value, even though trampling may represent an
138 issue especially for rare and endemic species. It is delimited by Porto Falconera to the west side and
139 by Porto Baseleghe to the east. The sedimentary regime of the littoral is determined by a longshore
140 sediment drift towards the southwest (Fontolan 2004) and the recent trend is stable or slightly in
141 accretion (Fontolan et al. 2014). It hosts several plants and animal species included in the Annexes I
142 and II of the Habitat Directive (Directive 92/43/EEC) and 39.74% of the total SCI surface is
143 designated as habitat of Community Importance. During the reclamation of the lagoon in 1960s, an
144 artificial pinewood of *Pinus pinea* L. and *Pinus pinaster* Aiton was planted, which has superseded
145 the potential native vegetation (*Quercetalia ilicis*, Provincia di Venezia 2010). The second sampling
146 site is called Bibione (45.636058°N – 13.097145°E; *datum*: WGS84). This site is completely
147 surrounded by a highly urbanized and touristic area; in fact, it has been estimated an average of more
148 than 5 million of tourists per year in the last decade (Fontolan et al. 2014). This place is also famous
149 for the sandy beaches and the many outdoors activities and aquatic sports that is possible to practice
150 (e.g. walking, cycling, windsurfing and kayaking). Here probably trampling and human activities
151 related to beach management may represent the main cause of the reduction or loss of specific habitat
152 features. The sampling area of Bibione is delimited on the east side by the mouth of the Tagliamento
153 River and on the west side by the town of Bibione. The beach is directly influenced by terrigenous
154 deposition; in fact, there is a strong sedimentary input carried by Tagliamento River and in the last
155 years, the sedimentary budget has shown an accretion trend ($> 5 \text{ m}^3/\text{m}$ year, Fontolan et al. 2014).

156

157 *Sampling design and data collection*

158 The following sampling design was adopted to collect data on plant composition and abundance: first
159 a square grid of 500 m linear dimension was overlaid to each sampling site. In each cell, a random
160 transect was selected following a sea-inland gradient with variable length due to dune width and coast
161 morphology. Transects were partitioned in a set of contiguous squared sub units (plots) of 4 m x 4 m
162 where the occurrence and percentage visual cover estimation of each vascular plant species were
163 assessed. Since this survey is focused on psammophilous vegetation plots, pinewoods and non-sand
164 dune vegetation were not sampled. Fieldworks was carried out during May-August 2016; in total 21
165 transects and 261 plots were sampled (104 plots in Bibione and 157 in Brussa, respectively). Later

166 on, each plot was assigned to a specific coastal habitat included in the Habitats Directive based on
167 the observed vegetation and on those reported in the SCI habitat map (source
168 <https://www.regione.veneto.it>). For the sake of simplification and to make these habitats comparable
169 to other studies, plots were classified in three major recognizable classes based on dune dynamics: i)
170 Foredune including upper-beach, embryo-dunes and mobile dunes (EU Habitat Code 1210, 2110 and
171 2120), ii) Fixed dune encompassing those environments dominated by perennial communities of the
172 inland side (EU Habitat Code 2130 and 6420), iii) Interdune that include distinctive habitats mainly
173 constituted by salt marshes and Mediterranean humid grasslands of tall grasses and rushes (EU
174 Habitat Code 1403 and 7210). It is worth noting that some of these habitats such as 2130 and 7210
175 are deemed of priority importance by the European Union. All the vascular plants recorded within
176 each plot were identified at the species or subspecies level directly in the field or, most frequently, in
177 the laboratory by using proper identification floras (Pignatti 1982). Nomenclature was standardized
178 according to Conti et al. (2005). Plants were classified as native or alien species, depending on their
179 status as given by Celesti- Grapow et al. (2009).

180

181 *Abiotic variables*

182 Climatic data was downloaded from the ARPAV website (<http://www.arpa.veneto.it>). Averages of
183 minimal, mean, maximum values along with their range (maximum-minimum) were calculated for
184 temperature (°C) and relative humidity (RH, %). For precipitation (mm), rainy days, and irradiation
185 (MJm^{-2}) only the average values were computed. In this way, a total of 25 climatic predictors were
186 obtained using baseline climatic data spanning from 2008-2015 and encompassing a March-October
187 time range. Geomorphological data were derived from the Shape project database (Fontolan et al.
188 2014); specifically, beach mean width (m), annual deposition rate (m^3/m), shoreline variation
189 (m/year,) and class of erosion (three levels: accreting, stable and in erosion) were selected. Since
190 these sites are also facing strong human impacts, touristic pressure (number of tourists/ m^2) was also
191 selected based on the index measured in Fontolan et al. (2014). Finally, Elevation (m), slope (°),
192 Northness, Eastness and the standard deviation of the slope (as an effective measure of terrain
193 roughness according to Grohmann, et al. 2010) were derived using a LIDAR raster at 1 m resolution
194 using QGIS 2.16.3 with GRASS 7.0.4 (Quantum GIS Development Team 2016).

195

196 *Statistical analysis*

197 *Analysis of plant diversity patterns*

198 Latent gradients in species composition for both native and alien species were assessed through
199 indirect gradient analysis (Nonmetric MultiDimensional Scaling). Significant differences in
200 community composition were evaluated using multivariate permutational analysis of variance
201 (PERMANOVA, Anderson 2001). Both the analyses were based on a Bray-Curtis similarity matrix
202 on log-transformed species abundances. The following factors were tested in the PERMANOVA
203 design: “Site” (fixed, two levels), “Transect” (random, nested within Site) and “Habitat” (fixed, three
204 levels), along with the interaction “Habitat x Site” and “Habitat x Transect”. A posteriori pairwise
205 comparison was applied to assess the effect of habitat when it was found to be significant. All tests
206 were performed with 4999 permutations of residuals under a reduced model using Type I sums of
207 squares. Analyses were performed using PRIMER 6 software (Clarke and Gorley 2006) and the
208 PERMANOVA routine in the add-on package PERMANOVA+ (Anderson et al. 2008).
209 Subsequently, for each group, plot-based rarefaction curves (hereafter SAC, Gotelli and Colwell
210 2001; Chiarucci et al. 2008) were computed using the exact method in the “vegan” package (Oksanen
211 et al. 2017) to compare patterns as a function of the sampling effort. We also calculated Spatially-
212 Explicit Rarefaction curves (hereafter SER, Chiarucci et al. 2009; Bacaro et al. 2012) to check the
213 consistency of the SAC due to their ability to account for spatial autocorrelation among plots,
214 especially when the extent of the study areas is different (Bacaro et al. 2011; Bacaro et al. 2016).
215 Diversity patterns for native and alien species were also compared using classic partition techniques
216 (Lande 1996; Gering et al. 2003; Crist et al. 2003; Chiarucci et al. 2010) that allows for the partition
217 of the three components of the diversity (alpha, beta and gamma) across the different spatial scales
218 of investigation (plot scale, transect scale, site scale and the whole study area). This analysis was also
219 performed by splitting native and alien species by habitat. Mean values of each of these components
220 were reported as the proportion of mean species richness. 999 permutations were used to test if there
221 were deviations from randomness in the observed patterns using null model testing.

222

223 *Exploring relationships of diversity components between native and alien plant communities*

224 The relationship between alien and native richness was tested using simple linear regression. Species
225 complementarity, namely beta diversity, was split into its basic components in both groups:
226 replacement (β_{repl} , that is a species in one site is substituted by a species in another site) and richness
227 (β_{rich} , the loss or gain of species between sites; for more details about the methodology see Carvalho
228 et al. 2013; Legendre 2014). Beta diversities were further compared using Local Contributors of Beta
229 Diversity (hereafter LCBD, Legendre and De Cáceres 2013) in the R package “adespatial” (Dray et
230 al. 2016). This analysis is useful to highlight the uniqueness of the sampling units in terms of
231 community composition. 999 permutations were performed to test for randomness in species

232 distribution while preserving the species abundance distributions in the observed data. LCBD values
233 have been visually displayed using the “ggmap” package (Kahle and Wickham 2013). In both the
234 analyses the species sampled in the plots were aggregated by transect.

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

239

240 *Analysis of ecological determinants of native and alien species*

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

249 Finally, to highlight which are the main abiotic factors related to alien species spread in sand dune
250 ecosystems, a binomial random intercept model (GLMM) was computed considering the occurrence
251 of alien species in plots, setting the transect factor as the random effect nested in Site. However, the
252 random effect of the transect was not significant according to the likelihood ratio test ($\chi^2(2) = 0, p >$
253 0.05), and a classical Generalized Linear Model (GLM) was then considered. Before building the
254 GLM, all predictors were standardized (z-scores) in order to obtain quantitatively comparable
255 regression coefficients. To reduce multicollinearity in the set of climatic variables, a Principal
256 Component Analysis was performed (Online Resource Table S3). All axes that cumulatively
257 contained greater than or equal to 75% of the variation were considered, this resulted in just the first
258 axis added (91% of the variation explained). The Minimum Adequate Model (MAM) was obtained
259 through model averaging according to AIC reduction using the “glmulti” package (Calcagno 2013).
260 Variable importance was assessed by weighting standardized regression coefficients by AIC-weights
261 and adding them up for all models in which a variable was included (Burnham and Anderson 2002).
262 All the analyses were performed using R 3.3.3 (R Core Team 2017).

263

264 **Results**

265 The pooled species richness of the 261 sampled plots is 127 (Table 1). Among these, 116 have been
266 classified as natives (91.4% of the whole sample) and 11 as aliens (8.6%). The most frequent families
267 in the total species pool are represented by Poaceae (17.3% of the sampled species), Asteraceae
268 (16.5%), Cyperaceae (5.5%) and Chenopodiaceae (4.7%). The most frequent species are *Elymus*
269 *farctus* (Viv.) Runemark ex Melderis (occurring in 36.2% of the sampled plots), *Spartina versicolor*
270 Fabre (30.7%) and *Vulpia fasciculata* (Forssk.) Fritsch (30.4%). Among alien species, the most
271 abundant families are Asteraceae (36.4%) and Fabaceae (18.2%) with *Oenothera stucchii* Soldano
272 (61.8%), *Ambrosia coronopifolia* Torr. & A. Gray (57.6%) and *Xanthium orientale* subsp. *italicum*
273 (Moretti) Greuter (44.7%) as the most frequent species. NMDS analysis for native species provides
274 a fairly good representation of the sampled community (Fig. 2a, stress = 0.17); in fact, plots tend to
275 aggregate according to habitat and sampling site. Conversely, the same unconstrained ordination
276 computed only on alien species (Fig. 2b, stress = 0.18) clearly shows the absence of specific patterns,
277 highlighting the non-specificity with which these species colonize sand dune environments.
278 PERMANOVA outcomes for native and alien species (Table 2) highlight that significant sources of
279 variability in species composition is determined by the spatial scales and habitat: while for native
280 species these differences occurred for each of the considered factors (except for the Habitat x Site
281 interaction), it is interesting to note that as for alien species, the main effect of Habitat was not
282 significant, along with the Site x Habitat interaction, confirming the observed NMDS pattern. The
283 post-hoc test reveals a significant difference among all the habitat levels for native species (Foredune
284 vs Interdune $t = 1.8576$, $P = 0.0004$; Foredune vs Fixed dune $t = 2.0262$, $P = 0.0002$; Interdune vs
285 Fixed dune $t = 2.2347$, $P = 0.0002$). The estimated components of variance (expressed as %) are
286 mainly driven by the Site and Habitat component for the native group, whereas for the alien group
287 the factors Site and Transect accounted for most of the variance explained (Fig. S1 in Online
288 Resource).

289 Rarefaction curves (both SAC and SER, Online Resource Fig. S2) result as being almost asymptotic
290 considering both species groups, suggesting that most of the species pool has been sampled. Once
291 SER and SAC have been calculated separately by habitat type (Fig. 3), the Fixed dunes tended on
292 average to host a higher number of species as expected compared to Foredues or Interdunes habitats
293 in both groups displaying a greater steepness, however. These results suggest that plant communities
294 closer to the sea are characterized by a lower number of species and are more homogeneous in terms
295 of species pool. It is worth noting how for native species, the SER in Interdune displays different
296 behavior compared to the SAC (Fig. 3a). Proportions of the diversity components (namely α and β),
297 exhibit different patterns according to the investigated species group (Fig. 4). Specifically, alien
298 species present lower levels of beta diversity across plots, transects and sites compared to native ones.

299 Hence, species complementarity decreases substantially moving from the native to the alien group,
300 specifically at plot scale is higher than that expected from the null models. Thus, significant
301 compositional differences exist among plots in each transect, evidently resembling the effect of the
302 sea-inland gradient. Both alien and native species show not significant differences from null
303 expectations across transects, hence highlighting that both these groups essentially share the same
304 species composition within the group. A similar pattern has been observed for alien species at the site
305 level, conversely native species show significant difference between the two sites confirming a
306 difference in the species pools. It is interesting to note how alien species complementarity in the
307 Foredunes show very few differences across sites. A significant positive linear model ($F(2, 259) =$
308 $55.77, p < 0.001, R^2 = 0.17$) was found between native and alien species richness ($b = 1.26, p < 0.001$).
309 The analysis of LCBD shows that these values ranged between 0.0337 and 0.0666 for native species
310 with five transects having significant values; whereas for alien species LCBD varied from 0.0118 to
311 0.1662 with just one significant value (Fig. 5). Kruskal-Wallis test confirms significant differences
312 in LCBD according to habitat both in native ($\chi^2(2) = 25.15, p < 0.001$) and alien ($\chi^2(2) = 13.24, p <$
313 0.01). Post-hoc tests show significant values between Foredune vs Fixed dune and Foredune vs
314 Interdune in native species, whilst alien species display significant differences just between Foredune
315 vs Interdune. Decomposition of beta diversity in its two components (β_{repl} and β_{rich} , Online Resource
316 Fig. S3) highlights that beta diversity in this study area is dominated by differences in species gain or
317 loss among transects for both groups (excluding few transects for native species in which the
318 replacement component dominates). A significant multiple linear regression ($F(2,17) = 3.652, p <$
319 $0.05, R^2 = 0.21$) was calculated between alien β_{rich} and native β_{repl} and the ratio of native $\beta_{\text{repl}}/\beta_{\text{rich}}$.
320 Model output shows a notable decreasing trend between alien β_{rich} and native β_{repl} ($b = -0.68, p < 0.05$,
321 Fig. 6) and a positive relationship with the ratio $\beta_{\text{repl}}/\beta_{\text{rich}}$ ($b = 0.07, p < 0.05$). The variation
322 partitioning approach on species composition data highlights that abiotic variables explain 36% of
323 the total variation for native species and 40% for the alien species (Fig. 7). Notably, climatic and
324 geomorphological predictors in combination encompass most of the variation present in the dataset
325 (32% for native and 34% for aliens), whereas the influence of spatial structure in the dataset is almost
326 completely negligible, likely due to the small extent considered in this study (5% for native and 6%
327 for aliens). Despite climatic and geomorphological predictors accounting for a similar percentage of
328 explained variation in both groups, PERMANOVA analysis points out that observed differences for
329 alien species occur at a finer spatial scale, namely within habitats along each transect. Furthermore,
330 when only the occurrence of alien species is explored, the GLM output shows that the major
331 determinants of alien presence are represented chiefly by the geomorphological dynamics of the
332 beach (Table 3) and, to a lesser extent, by human-induced factors such as touristic pressure. In

333 particular, elevation, class of erosion, beach mean width and deposition rate are the most significant
334 predictors in explaining alien species presence (with a higher likelihood to find alien species
335 according to an increase in these values). Additionally, Northness and Touristic pressure influence
336 alien occurrences with positive and negative slopes, respectively.

337 **Discussion**

338 *Community structure along the environmental gradient*

339 The present work aims to describing diversity patterns of plant communities in northern Adriatic sand
340 dune ecosystems, exploring the relationships and the interactions among native and alien species
341 groups and ecological factors shaping their distribution. The number of alien species found is in line
342 with other studies in the same area or ecosystem (Campos et al. 2004; Vilà et al. 2007; Del Vecchio
343 et al. 2015). Despite their apparent low percentage compared to the Italian one (9.4% while the Italian
344 average is 13.4% and that of the Veneto region is 11.8%, Celesti-Grapow et al. 2009) it should be
345 taken into account that these habitats are of great conservation values due to the elevated proportion
346 of endangered and exclusive plant taxa they host (Van der Maarel 2003; Acosta et al. 2009). Diversity
347 patterns in native and alien species show very different behaviors according to habitat and to the
348 spatial scale investigated. The concept of scale-dependence between native and alien species richness
349 has already been widely debated (Levine and D'Antonio 1999; Fridley et al. 2007) and, in agreement
350 with this statement, our findings support the idea that it is not possible to directly compare the
351 proportion of aliens across areas without taking into account the effects of the spatial scale or the size
352 of the flora (Gotelli and Colwell 2001; Palmer et al. 2006), as the ratios of SAC of our study also
353 confirm. The observed mean difference between SAC and SER is 3.9 species that can be seen as the
354 outcome of spatial dependence among individuals in the space, acting in the same way in both groups
355 (except for the interdune habitat). In general, rarefaction curves allow us to be satisfied about the
356 goodness of the sampling effort which is crucial in estimating the correct number of species (Acosta
357 et al. 2009; Chiarucci et al. 2012). In case of sampling bias, some rare or endangered species may not
358 have been recognized or underestimated, resulting in relevant implications for conservation
359 programs. Results of NMDS clearly suggest that the gradient in the species composition of native
360 species were only marginally related to that of alien species. The native species pattern could be seen
361 as the outcome of the harsh conditions naturally present in these habitats that shape plant
362 communities. It is interesting to note how the apparent absence of such structure in the alien species
363 pool may be seen as evidence of a potential shift towards randomness in the community assembly
364 rules (Santoro et al. 2012). Differences in distributional patterns between native and alien species at
365 the local scales have also been reported by some studies on roadside communities (Arévalo et al.
366 2005) or cultivated systems (Lososová and Cimalová 2009). The presence of strong limiting factors

367 acting in these environments is deemed the main drivers on plant species composition in these
368 ecosystems. Both the native and alien species pool in our dataset share the same ecological drivers
369 though with slightly different proportions and effects, as pointed out in variation partitioning analysis.
370 The Foredune habitat was confirmed as extremely species poor and selective for plant species
371 compared to Fixed dunes. This can be seen as the result of the harsh conditions present closer to the
372 sea such as marine aerosol, lower levels of nutrients and moisture, salt spray (see Perumal and Maun
373 2006; Carboni et al. 2010; Ciccarelli et al. 2012). On the other hand, Fixed dunes tended to be
374 permanent due to the lower exposure to the limiting factors cited above and to the evolution of some
375 adaptations that allow them to survive and reproduce (Wiedemann and Pickart 2004; Acosta et al.
376 2006). Here, higher level of species richness was observed in both groups as reported also in Vaz et
377 al. (2015) and Marcantonio et al. (2014), among others. The higher number of alien species in the
378 Fixed dunes may be seen as a sign that native species assembly have lost their capability to compete
379 with alien species probably due to an effect of human-induced disturbances (e.g. trampling, Del
380 Vecchio et al. 2015) that create gaps in the niche where these species, which are pre-adapted to cope
381 with stresses (e.g. for an urban environment Knapp et al. 2008), can be easily integrated and propagate
382 in the surrounding areas. One of the more hazardous consequences may be the biotic homogenization
383 of these ecosystems, with the resulting loss of endemism or rare species of which these environments
384 are naturally rich.

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

400

401 *Beta diversity patterns*

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

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

428

429 **Conclusions**

430 Sand dune ecosystems represent fragile environments endowed with particular characteristics that
431 make them unique both in terms of species vegetating and habitat features. There is currently an
432 increasing need to monitoring and actively manage these environments through concrete preservation
433 and restoration actions regarding these habitats, where necessary. Thus, coastal ecosystems are

434 currently constrained between human-related threats from one side and shoreline erosion from the
435 other, the so called “coastal squeeze” (Defeo et al. 2009).

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

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

450

451

452

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458

459

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702 **Figure captions**

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

705 **Fig. 2** NMDS output based on Bray-Curtis similarity matrix (log-transformed abundance data)
706 for each habitat and sampling site. a) Native species b) Alien species

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

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

713 **Fig. 5** Map of Local Contributor of Beta Diversity values. In white the non-significant transects ($p >$
714 0.05); in red, the significant transects ($p < 0.05$)

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

717 **Fig. 7** Partition of the variation of the community matrix according to the three explanatory variable
718 groups. a) Native species b) Alien species

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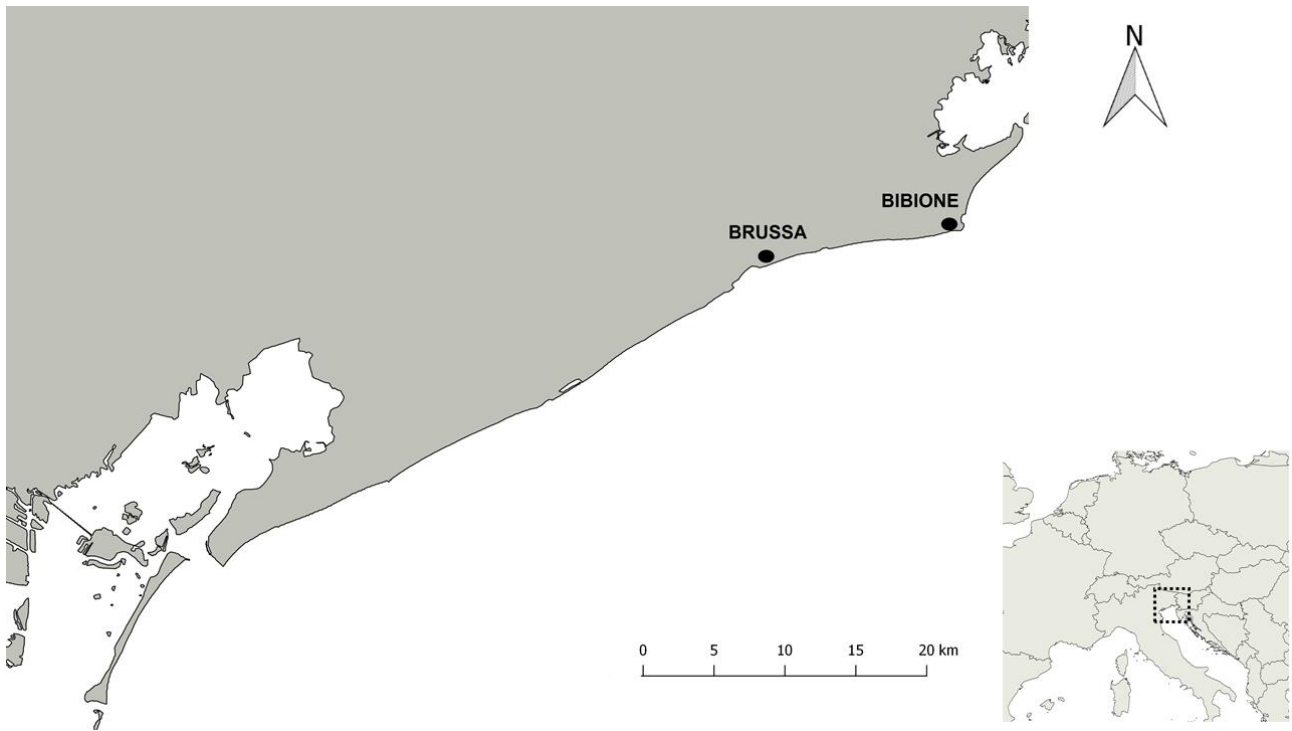
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733 **Figure 1**

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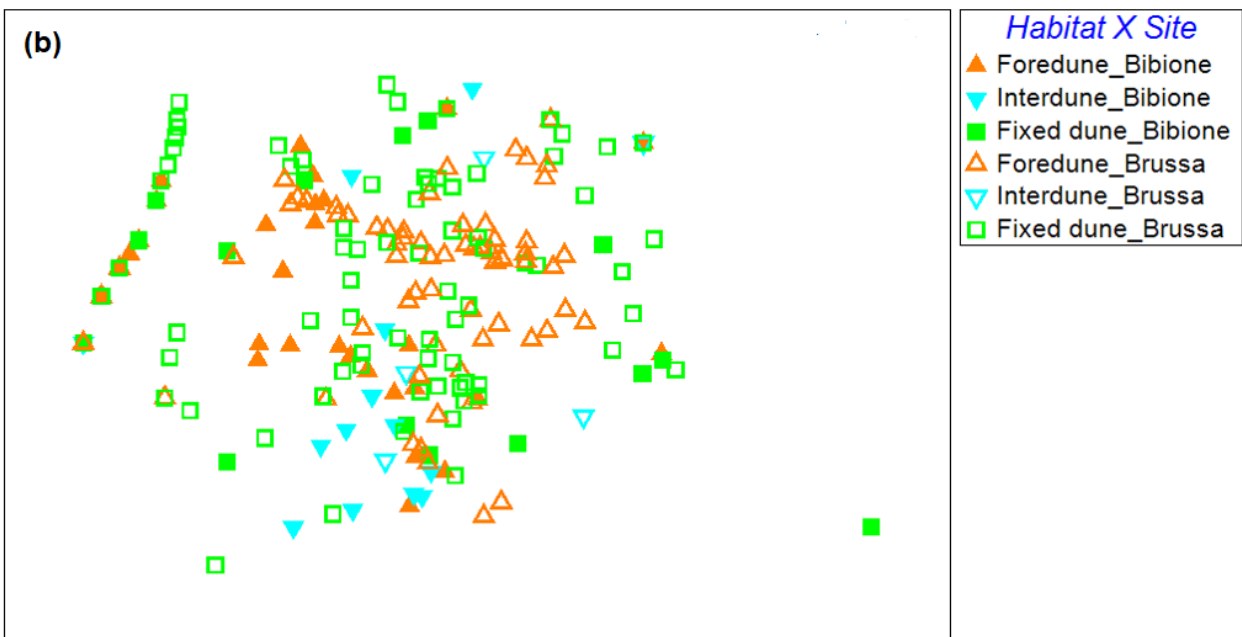
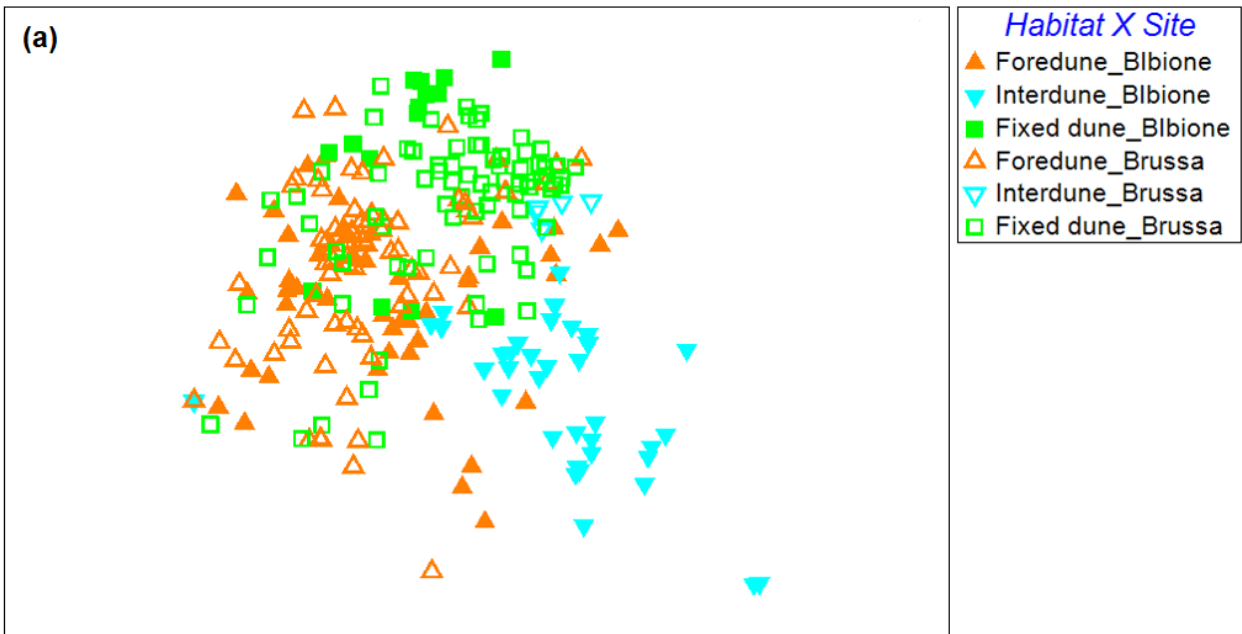
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749 **Figure 2**

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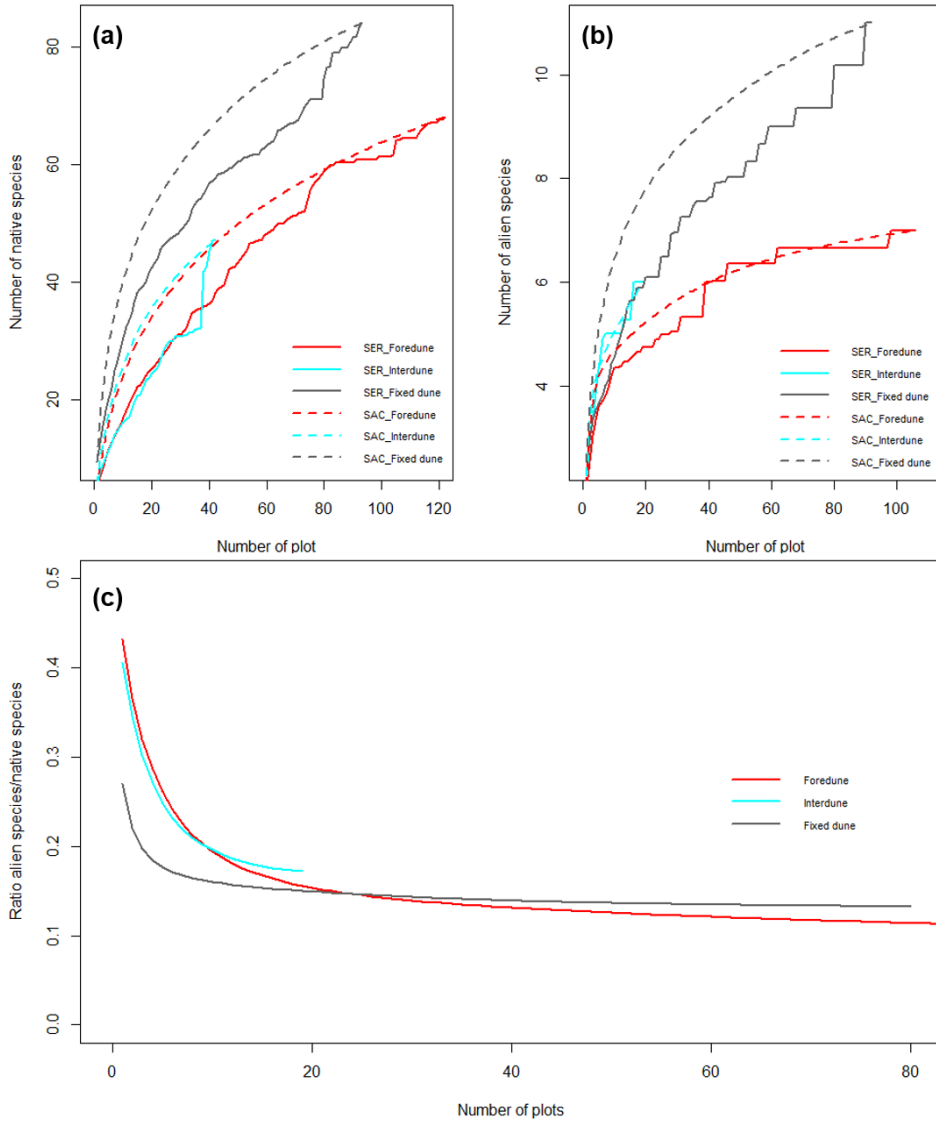
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757 **Figure 3**

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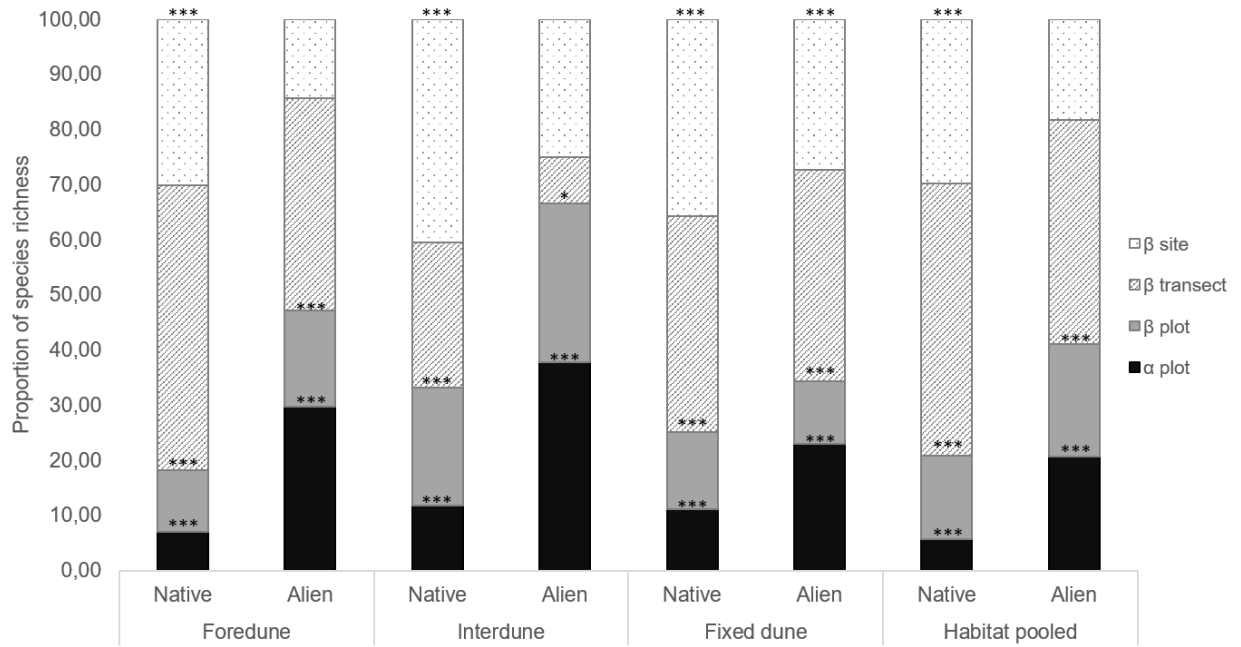
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767 **Figure 4**

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783 **Figure 5**

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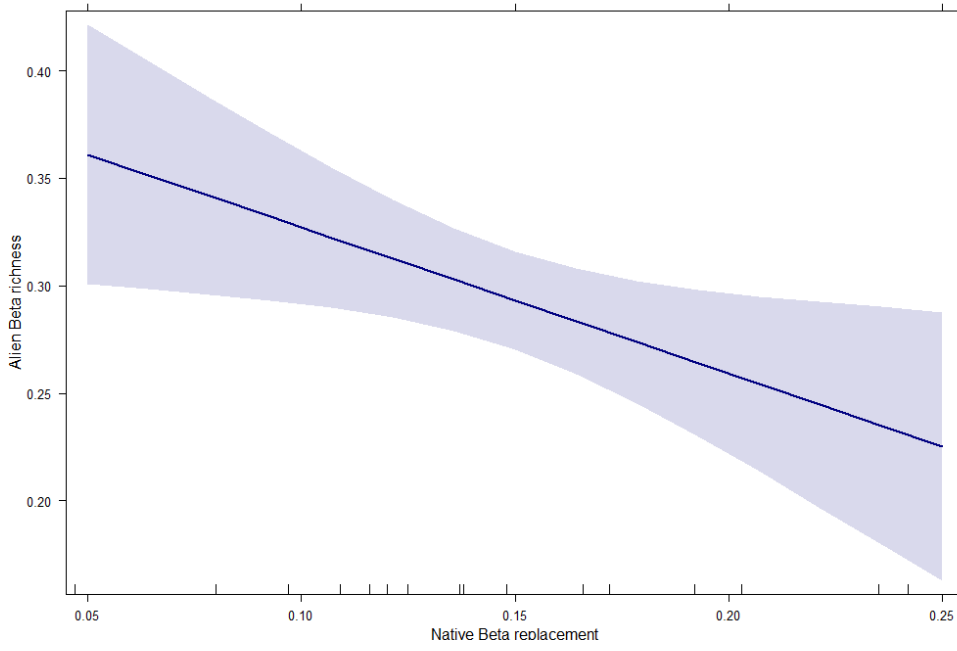
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799 **Figure 6**

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816 **Figure 7**

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Tables

Table 1 Species richness (Mean \pm 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 \pm 3.54	6.60 \pm 3.61	11.81 \pm 3.27	Poaceae (17.32)
Native species	4.66 \pm 2.81	5.57 \pm 2.80	9.31 \pm 3.19	Poaceae (16.53)
Alien species	1.75 \pm 1.22	1.02 \pm 1.33	2.49 \pm 0.80	Asteraceae (36.36)

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 x Site	2	8301.7	1.75	0.0830	1	3474.6	0.90	0.4580
Habitat x 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	-	-	-

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	-

Supplementary materials

Ecological Research

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

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Table S1

Summary statistics (mean, minimum, maximum) of the variables used in variation partition obtained after forward selection using alien species as response variable

	Mean (Min-Max)
<i>Spatial variables</i>	
X (EPSG 3003)	1810894 (1805157 - 1819535)
Y (EPSG 3003)	5060145 (5058462 - 5062760)
<i>Geomorphological variables</i>	
Habitat	1 level (Foredune)
Slope	3.83 (0.10 - 18.34)
Elevation	1.83 (0.08 - 3.45)
Eastness	0.05 (-1.00 - 1.00)
Annual deposition rate	18.00 (-12.40 - 31.70)
<i>Climatic variables</i>	
<i>mean</i> (Rainy days)	6.96 (6.78 - 7.08)
<i>max</i> (Tmin)	13.10 (12.58 - 13.90)
<i>range</i> (Tmin)	0.87 (0.85 - 0.90)
<i>min</i> (Tmean)	17.18 (17.01 - 17.44)
<i>mean</i> (Tmean)	17.91 (17.80 - 18.07)
<i>max</i> (Tmean)	18.51 (18.39 - 18.69)
<i>range</i> (Tmean)	1.33 (1.25 - 1.37)
<i>min</i> (Tmax)	21.57 (21.31 - 21.75)
<i>mean</i> (Tmax)	22.57 (22.20 - 22.83)
<i>max</i> (Tmax)	23.30 (22.76 - 23.66)
<i>max</i> (RH_min)	0.56 (0.54 - 0.58)
<i>min</i> (RH_mean)	0.71 (0.70 - 0.72)
<i>max</i> (RH_mean)	0.80 (0.80 - 0.81)
<i>min</i> (RH_max)	0.93 (0.92 - 0.94)
<i>mean</i> (Irradiation)	559 (552-570)

Table S2

Summary statistics (mean, minimum, maximum) of the variables used in variation partition obtained after forward selection using native species as response variable

	Mean (Min-Max)
<i>Spatial variables</i>	
X (EPSG 3003)	1811930 (1805157 - 1819539)
Y (EPSG 3003)	5060383 (5058462 - 5062762)
<i>Geomorphological variables</i>	
Habitat	2 levels (Foredune, Interdune)
Class of erosion	1 level (Erosion)
Slope SD	1.35 (0.14 - 7.08)
Elevation	1.72 (0.08 - 3.45)
Touristic pressure	0.73 (0.01 - 3.61)
Beach width	119.3 (83 - 193)
Annual deposition rate	15.26 (-12.40 - 31.70)
<i>Climatic variables</i>	
<i>mean</i> (Σ Precipitations)	683.2 (667.9 - 695.4)
<i>mean</i> (Precipitations)	86.47 (85.17 - 87.44)
<i>mean</i> (Σ Rainy days)	55.48 (54.26 - 56.64)
<i>mean</i> (Rainy days)	6.93 (6.78 - 7.08)
<i>min</i> (Tmin)	12.64 (12.31 - 13.00)
<i>mean</i> (Tmin)	13.17 (12.84 - 13.52)
<i>max</i> (Tmin)	13.21 (12.58 - 13.90)
<i>range</i> (Tmin)	0.87 (0.85 - 0.90)
<i>min</i> (Tmean)	17.21 (17.01 - 17.44)
<i>mean</i> (Tmean)	17.93 (17.80 - 18.07)
<i>max</i> (Tmean)	18.53 (18.39 - 18.69)
<i>range</i> (Tmean)	1.32 (1.25 - 1.37)
<i>min</i> (Tmax)	21.53 (21.31 - 21.75)
<i>mean</i> (Tmax)	22.52 (22.20 - 22.83)
<i>max</i> (Tmax)	23.22 (22.76 - 23.66)
<i>range</i> (Tmax)	1.69 (1.45 - 1.91)
<i>mean</i> (RH_min)	0.52 (0.50 - 0.53)
<i>max</i> (RH_min)	0.56 (0.54 - 0.58)
<i>min</i> (RH_mean)	0.71 (0.70 - 0.72)
<i>max</i> (RH_mean)	0.80 (0.80 - 0.81)
<i>max</i> (RH_max)	0.98 (0.98 - 0.99)
<i>mean</i> (Irradiation)	561 (552-570)
<i>mean</i> (Σ Irradiation)	4343 (4338 - 4349)

Table S3

Spearman correlation coefficient of the climatic variables with the first axis of PCA

Variable	Spearman's ρ
<i>mean</i> (Σ Precipitations)	0.98
<i>mean</i> (Precipitations)	0.91
<i>mean</i> (Σ Rainy days)	1.00
<i>mean</i> (Rainy days)	0.99
<i>minimum</i> (Tmin)	-0.99
<i>mean</i> (Tmin)	-0.99
<i>max</i> (Tmin)	-1.00
<i>range</i> (Tmin)	-0.79
<i>minimum</i> (Tmean)	-0.99
<i>mean</i> (Tmean)	-0.99
<i>max</i> (Tmean)	-0.99
<i>range</i> (Tmean)	0.96
<i>min</i> (Tmax)	0.99
<i>mean</i> (Tmax)	0.99
<i>max</i> (Tmax)	0.99
<i>range</i> (Tmax)	0.99
<i>min</i> (RH_min)	-0.94
<i>mean</i> (RH_min)	-0.94
<i>max</i> (RH_min)	-0.93
<i>min</i> (RH_mean)	-0.93
<i>max</i> (RH_mean)	-0.85
<i>min</i> (RH_max)	-0.92
<i>max</i> (RH_max)	0.24
<i>mean</i> (Irradiation)	-1.00
<i>mean</i> (Σ Irradiation)	0.31

Figure S1

Estimated components of variance (expressed as percentages) calculated for each factor of the PERMANOVA analysis

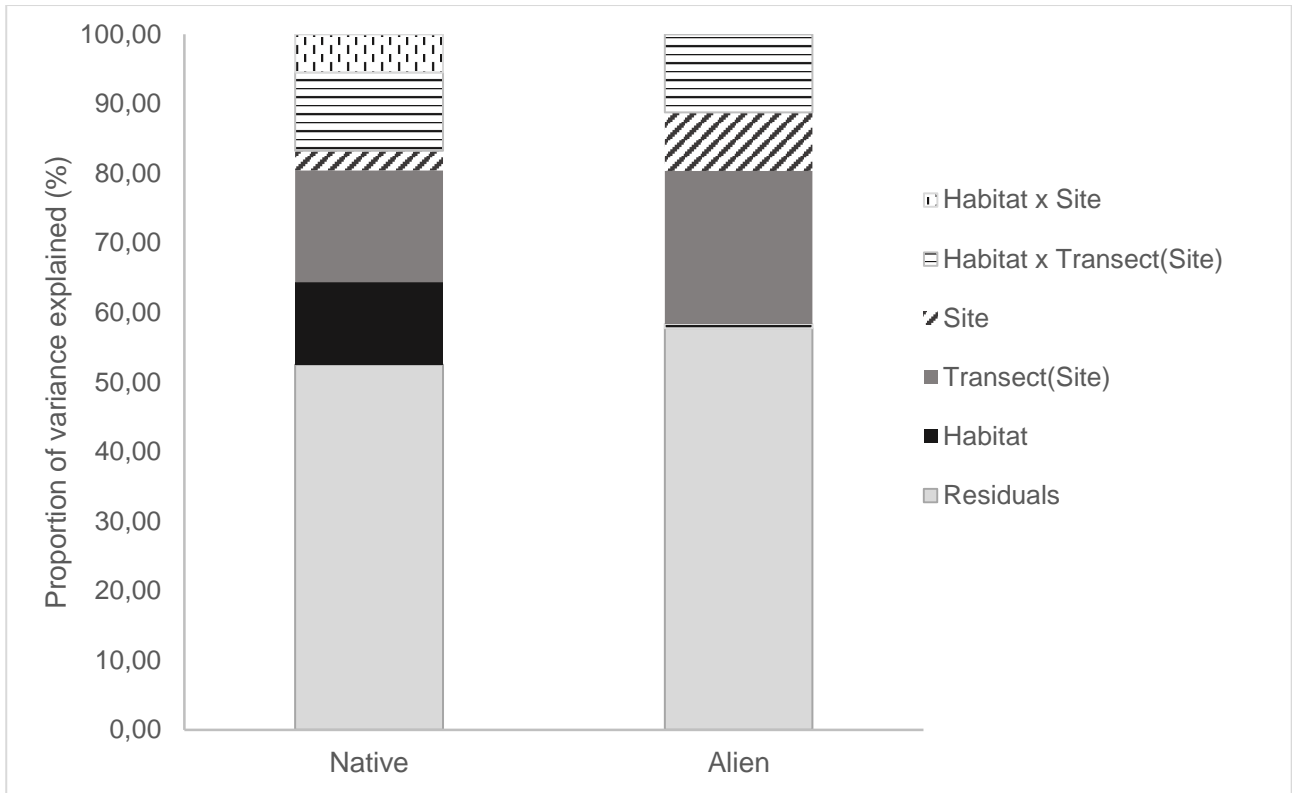


Figure S2

Plot-based rarefaction curves (SAC) and Spatially-explicit rarefaction curves (SER) for native and alien species

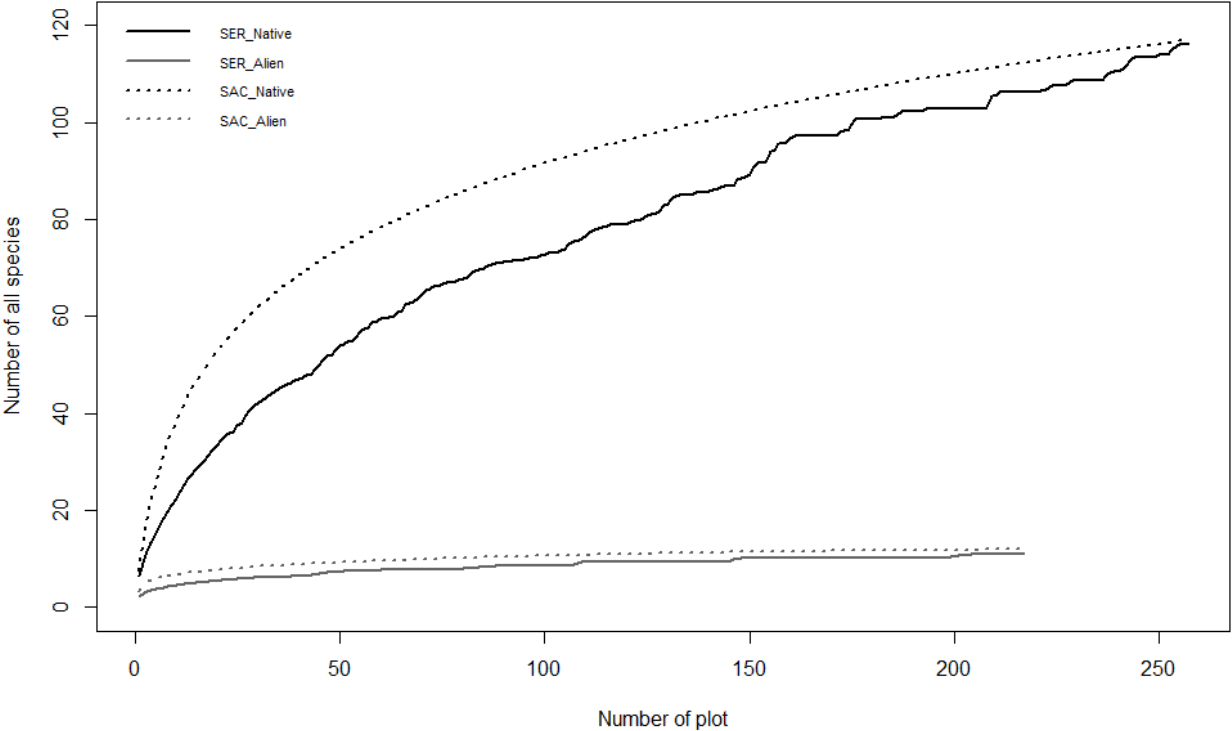


Figure S3

Trend line of beta diversity components (β_{repl} and β_{rich}) for a) native species and b) alien species in each transect; black line represents the trend line of species richness

