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Impact of alien species on dune systems: a multifaceted approach

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Abstract We applied a multifaceted approach, in terms of taxonomic, phylogenetic and functional diversity, to study at fine scale how three plant communities occurring in a Mediterranean dune have been affected by the encroachment of alien species. We sampled 81 sites in a Site of Community Importance in Central Italy. Past and present land use/cover data have been derived using GIS and remote sensing tools. Information on plants phylogenesis and functional traits has been gathered from several databases. Ecological variables have been collected. GLMs in conjunction with an Information Based approach were used to model species composition, richness and phylogenetic diversity. Multivariate analysis has been used to study functional diversity. The results outlined how total species richness is related to recent land transformations and to a set of environmental factors. The analyses of functional and phylogenetic diversity support the idea that alien species significantly affect the functional and phylogenetic characteristics of the native plant communities. Habitat filtering seems to be predominant in not-invaded plots, whereas limiting similarity/niche differentiation is predominant in driving community assembly of invaded communities. The attained scenario depicts the spread of a reduced group of alien species phylogenetically and functionally well-differentiated, able to reduce the abundance of native species, not to exclude them though. Ultimately, the multifaceted approach assisted in understanding the community assembly of dune vegetation, and to discern the relative impact of alien species on native plant communities. Such approach represents a crucial

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step to achieve an efficient management of dune habitats, as useful tool to monitor and to effectively protect their biodiversity and functioning.

Keywords Functional diversity · Phylogenetic diversity · Biodiversity conservations · Alien species · Dune systems

Introduction

Ecological processes such as natural disturbance, hydrology, nutrient cycling, erosion control, biotic interactions determine the species composition, habitat structure, and ecological health of every ecosystem on Earth (EPA 2012).

To date, the consensus around the relevant impact of biodiversity loss is quite large within the scientific community (Cardinale et al. 2012). Biodiversity loss is a raising pattern driven by the ecosystem simplification due to the uncontrolled human handling of Earth (Hassan et al. 2005). The menace represented by the encroachment of species in new ecosystems leading to biological invasion is among the most potential threats to biodiversity conservation (EEA 2012). The widening of the natural distribution range of some groups of species has been associated mainly to land use/cover (LULC), climate change and globalization-related phenomena (Brook et al. 2008). The spreading of new species is mostly dangerous for dynamic and fragile ecosystems, already threatened and disturbed by human pressure and climate change (Brook et al. 2008).

A heavy loss of biodiversity and habitat simplification has particularly struck the coastal dunes (Walker et al. 2006). These changes have been extremely amplified by the shift of human population towards the coast (Roberts and Hawkins 1999).

Coastal dune systems are both ecologically-interesting and very fragile environments, and several dangers threaten these environments (Martínez et al. 2008). Well-preserved coastal dunes are protective habitats. They accomplish a set of key ecosystem functions, as defence against storms and sea-level rise, water filters, erosion control and barriers against salty winds (Feagin et al. 2005; Giambastiani et al. 2007). In addition, they mediate the connection between sea and terrestrial ecosystems (Carboni et al. 2009). Therefore, degraded coastal ecosystems are placing people and property at greater risk of damage from coastal hazards (Day et al. 2007; Jolicoeur and O'Carroll 2007; Titus et al. 2009; Sallenger et al. 2012; Shepard et al. 2012), and the likelihood and magnitude of anthropic losses may be reduced by intact coastal vegetation (Arkema et al. 2013).

Since the uniqueness of the environmental niches occupied and supplied by dune habitats, their biota is composed by very specialized species, capable to relate to extremely harsh environmental conditions (Gehu 1985). Plants usually show particular ecological strategies associated to dune conditions due to their low or void mobility, and are considered good indicators of the overall biodiversity, ecosystem integrity of coastal dune (Araújo et al. 2002; Lopez and Fennessy 2002). Dune plant communities are extensively shaped by the sand burial (Davy and Figueroa 1993; Disraeli 1984) which acts as a strong limiting factor, applying a fine-mesh filter to the plant community. However, many other factors cooperate to forge the plants composition in sand dune ecosystems, such as high wind velocity, sand blasting, salt spray and salinity, soil fertility (Martínez and García-Franco 2008; Fenu et al. 2012).

The morphological and biological diversity of coastal dunes is preserved by naturally-occurring patch dynamics, caused by the interaction among the environmental factors, which in combination determine a very dynamic environment (Acosta et al. 2005; Martínez and García-Franco 2008). Despite their stress-based ecological dynamics, coastal dunes are considered low resilient systems because slight disruptions may lead to marked changes and long-term progressive alterations (Carter 1988).

Even though the fragility of dune systems and their multifunctional role in nature, they are under several heavy human-related threats, causing both direct (trampling, grazing, levelling of dunes) and indirect damages (climate change, alien invasions, sea-level rise and alterations in soil, moisture regimes and sediment supply; EEA 2012). Further, different dune habitat types show differential sensitivity to the invasion of alien species (Carranza et al. 2011), requiring additional caution to be effectively protected.

In the last decades, the remnant patches of dune habitats have progressively been placed under protection, since their conservation value and functional importance for other ecosystems and humans have been recognised (Carboni et al. 2009; Feola et al. 2011; Santoro et al. 2012a, b). A recent study by Carboni et al. 2013 in a Mediterranean dune system pointed out the relevance of using an approach which takes into account both phylogenetic and functional information of the plant communities. Such approach should consider the multidimensionality of biological diversity, (Pavoine and Bonsall 2011), aiming to provide a comprehensive survey of biological diversity which could represent the baseline for future management and restoration programmes.

We here apply a multifaceted approach, in terms of taxonomic, phylogenetic and functional diversities, in order to study at a fine scale how a dune plant community has been affected by the invasion of alien species. Our overall goal is to test the impact of alien species on native plant communities from a multidimensional biodiversity viewpoint. Further, we aim to understand the ecological processes ruling the assembly of the dune vegetation (i.e. habitat filtering, limiting similarity; Wilson 2007; De Bello et al. 2009; Laliberté et al. 2013), and how the community assembly might be impacted by the encroachment of alien species. In details, we specifically focus on: (i) determining the role of environmental factors, past LULCs and present human activities in shaping plant community assembly; (ii) identifying the actual status of species composition, phylogenetic and functional diversity; (iii) detecting ecological processes driving community assembly; (iv) quantifying the impact of alien species occurrence on native species and communities.

Methods

Study area

Our research area is placed in a Site of Community Importance (SCI) named “Dune di Capratica” (IT6040021; Centroid coordinates: longitude 13.39E, latitude 41.27N, datum WGS84; Fig. 1), Central Italy. It is a South-East to North-West oriented Holocene dune system, with a maximum distance to the sea of 220 m. The study area is characterized by Mediterranean climate type (Peel et al. 2007). The year average temperature is 17.1 °C (Reconstructed MODIS LST; Metz et al. 2014), while the mean rainfall is 635 mm year^{-1} (ECA&D; Haylock et al. 2008; reference period 2000–2012). These dune system occupies a narrow strip along the seashore, being not very high (8–10 m) and relatively simple in

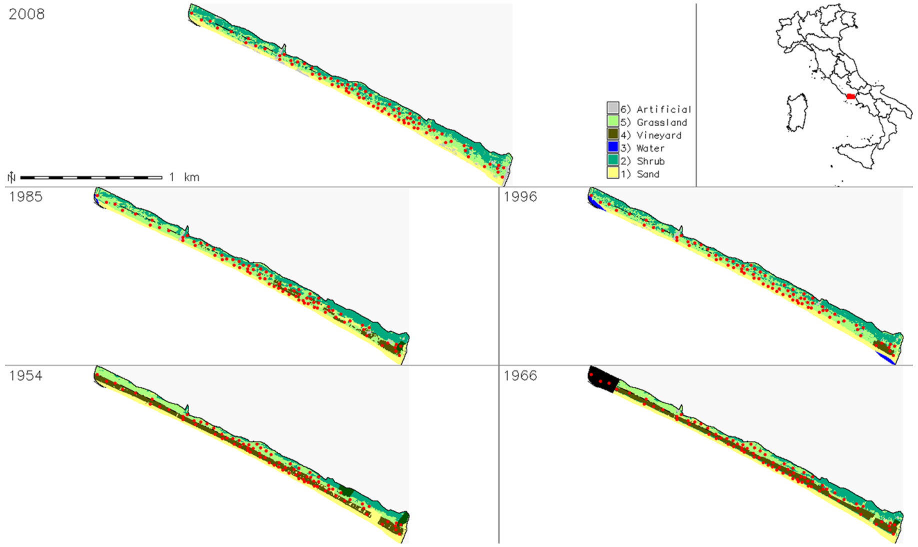

Fig. 1 Location and LULC of the studied area in 1954, 1966,1985, 1996 and 2008. The sample sites are showed as *red filled circles*. (Color figure online)

structure (Fenu et al. 2012). This area is surrounded by perennial crops in his Northern and Eastern parts, borders the Tyrrhenian Sea Westward and another SCI in the Southern part.

Similar Mediterranean dune systems have been recently studied using different approaches (taxonomic, functional and phylogenetic features and metrics) to quantitatively describe plant community assemblage and the impact of invasive alien species on native species and communities (Carboni et al. 2009; Carranza et al. 2011; Santoro et al. 2012a, b). However, our research is using a multifaceted (combined) approach aiming at unifying all these tasks in one analytical framework. In this way we should be able to better understand the ecological mechanisms driving plant community assembles and dynamism, with specific focus on the impact of alien species invasion.

Data collection

Firstly, we divided the study area into different zones on the base of the distance to sea—evaluated through satellite imagery—and on dune morphology. Using these criteria, we selected three sample zones, differentiated by specialized plants communities: (1) embryo dune, characterized by dominant species *Cakile Maritima* and *Elymus farctus* (habitat type 1210 and 2110; EEA 2012; Prisco et al. 2012), (2) fore dune, characterized by the dominance of *Ammophila arenaria (habitat type 2120)* in the seawards side, with marked presence of annual/perennial grasslands in the landward part (habitat type 2230, 2240) and (3) fixed dune, characterized by dominant species *Juniperus oxycedrus* subsp *macrocarpa* and *Crucianella maritima* (habitat types 2210, 2250, 2260). The three dune zones are hereafter abbreviated as DZ1, DZ2 and DZ3, respectively. Then, we performed a random sampling, stratified on each of the three zones. We chose a stratified random sampling since it has been revealed to be optimal for modelling alien species distribution with a low number of samples (Brummer et al. 2013).

Sample points were located in the field using a Garmin GPSMAP60CSx. The sample unit consisted in a 2 × 2 m plot of 4 m^2. The plot size has been selected following similar studies carried out in this kind of habitats (Carboni et al. 2011; Fenu et al. 2012). In each plot the presence of all plant species were collected and the projected cover at ground level of every species was visually estimated (% of cover; hereafter referred as abundance). Moreover, we sampled a series of environmental variables such as slope, aspect, distance to the nearest pathway, distance to the shoreline, mosses and lichens coverage (Fernández and Barradas 1997).

Afterwards, we gathered information on each sampled species from national (Conti et al. 2005; Celesti-Grapow et al. 2009) and international databases (GSID 2012; DAISIE 2013). This step was necessary to achieve an exhaustive alien species list for the studied area, on which basing further ecological analyses. We considered alien species those filed as not-native for the Italian flora in at least one of the consulted databases.

LULC change analysis

To obtain data regarding land cover change occurred on the dune vegetation during the last 60 year we acquired three aerial photos from the Military Geographical Institute relative to three different years (1954, 1966, and 1985). Pictures from 54′ to 85′ were panchromatic photos, while the ones from 1966 own natural colours.

Then, each photo was rectified into WGS84 datum, using *i.rectify* module from GRASS GIS environment (Neteler et al. 2012). In addition, to obtain a temporal series up-to-date, we acquired two further satellite imageries from the National Cartographic Portal, relative to year 1996 and 2008. All orthophotos have 1-m resolution.

To make the information contained into the orthophotos available to the following analyses, we classified each photo using a Supervised Classification Method in GRASS GIS (Lillesand et al. 2008). We used a two-step process: firstly, the *i.gensigset* module was used to extract spectral statistics from each photo, basing on the classification of pixels of a set of training areas. A second module, *i.smap* applied the statistics product by *i.gensingset* to classify the remnant unknown pixels (Neteler and Mitasova 2008). To obtain a useful classification of the two panchromatic photos (54′, 85′), which suffer of a lower level of available information (Short and Short 1987), we used a third GRASS GIS module, *r.texture* (see Rocchini et al. 2012). This tool allows the generation of raster maps with textural features extracted from an initial raster map, reaching more available layers to classify the orthophotos. Following this classification procedure, our photos have been categorised in seven land cover categories: grasslands, shrubs, artificial, water, sand, vineyards, and crops.

Species richness and composition

To test significant differences in species richness between the three DZs at the plot level we used a pairwise Wilcoxon test with Bonferroni p-adjustment. The relationship between a set of variables and species richness was tested using generalized linear models (GLMs) having Gaussian (total species richness) and Poisson-distributed (alien species richness) errors. As response variables we considered, in turn: (i) total species richness; (ii) total species richness in DZ1, DZ2, and DZ3; (iii) alien species richness; (iv) alien species richness in DZ1, DZ2, and DZ3. Therefore, a total of eight GLMs were built.

As predictors we employed different group of variables: (i) historical. LULC maps from 1954, 1966, 1985, and 1996 years assisted in the understanding whether the past heavy utilization as crop of the studied dune affected the present number of species; (ii) environmental. Slope, distance to sea, folded aspect and elevation have been considered to investigate which environmental parameters mostly contribute in shaping plant communities; (iii) disturbance. Distance to nearest road, distance to nearest pathway, moss coverage, lichen coverage and 2008 LULC map were selected to have insights whether and how much human present activities affect species richness.

Then, to avoid over-fitting in the modelling process, we applied a full Information-Criterion-based (IC) model selection approach (Burnham and Anderson 2002; Johnson and Omland 2004; Calcagno and de Mazancourt 2010). We repeated this procedure for each response variable, ranking the models for total species richness through the Akaike information criterion corrected for small samples (AICc), and QAICc (Quasi-Likelihood AIC, adapted for small samples) for alien species richness. Hence, we reported the model beta-weights and their related significances, concerning only the best representative models selected by the IC-based technique.

We also investigated the species composition distribution. We decided to avoid classic multivariate analyses using a model-based framework. Using this approach we escaped a set of issues connected with distance-based multivariate analysis (Wang et al. 2012; Warton et al. 2012). We used the R package *mvabund* (Warton et al. 2012) to represent and to test both the effect of alien species presence, and of habitat differentiation within the dune on the abundance of native species. The *mvabund* package contains a set of functions that allowed us to build multivariate GLMs, testing the statistical significance of the model. In details, we used *manyglm* function to create a negative binomial GLM, considering the abundance of native species as response variable. Further, the uni-variate statistics supplied by *manyglm* served to investigate which alien plant species is a significant indicator of a changed species composition within the invaded plots.

Phylogenetic diversity

A phylogenetic tree was built considering all collected species using Phylocom4.2 (Webb et al. 2011). The reference tree was R20100701. Branches length was estimated according to (Wikström et al. 2001). Bladj utility aided to produce a pseudo-chronogram, which resulted useful to estimate phylogenetic distance between taxa. Indeed, even having few dated nodes, the resulting phylogenetic distance can be accounted as a marked improvement than simply using the number of intervening nodes as phylogenetic distance (Webb 2000).

We chose to include phylogenetic analysis in our study since related species often show similar functional traits, niches (Wiens et al. 2009) and ecological interactions (Rezende et al. 2007; Bersier and Kehrli 2008; Gomez et al. 2010). Therefore, the phylogenetic diversity may encapsulate many of the functionally important aspects of biodiversity (Srivastava et al. 2012; Carboni et al. 2013). Moreover, phylogenetic diversity is largely recognised as a key feature to enhance ecological interpretation on patterns and processes related to plant species and communities (Hartmann and Jessica 2013).

Phylogenetic diversity has been studied measuring three metrics: the 'classic' Mean Pairwise Phylogenetic Distance (MPD) and two newly proposed indices, phylogenetic evenness-abundance (PAE) and Imbalance of Abundances at higher Clades (IAC), which both incorporate species abundances (Cadotte et al. 2010). MPD measures the mean distance, in branches length, between all possible pair of taxa in a community (Webb 2000). PAE takes into account the phylogenetic-abundance distribution among terminal branches. It gives an indication of the phylogenetic evenness of a community, while IAC quantifies the imbalance in the phylogenetic tree (not among-terminal branches).

Therefore, to test whether the occurrence of alien species affected the phylogenetic patterns we performed two-factors ANOVA, having the three DZs as fixed factor and alien species presence (hereafter AP; levels = presence or absence) as treatment. Furthermore, we tested simple main effects (keeping DZs as a fixed factor) to study in which zones significant changes occurred due to the alien species presence. Phylogenetic analyses were carried out through *picante* (Kembel et al. 2010) and *EcoPD* (Regetz et al. 2009) R packages. Model interactions were tested with *phia* R package (Rosario-Martinez De 2013).

Functional diversity

We selected 29 plant functional traits (see Appendix S1 in Supporting Information), examining thoroughly six on-line databases: BIOLFLOR (Kühn et al. 2004), LEDA (Kleyer et al. 2008), CLOPLA3 (Klimešová and de Bello 2009), ECOFLORA (Fitter and Peat 1994), KEW (Kew 2008) and Plant For A Future (PFAF 2012). Further information on species characters were reached since Pignatti (1982), Tutin (1993) and a set of peer-reviewed scientific papers. The 29 traits have been then classified for each species following their features: (i) nominal; (ii) quantitative; (iii) circular; (iv) ordinal; (v) fuzzy and (vi) multi-choice. Such categorization was necessary for the generation of the trait distance matrix, based on the standardized Gower coefficient (Pavoine et al. 2009). Standardized Gower coefficient was relevant for our study because can take into account non-available data in the trait matrix. Having built the matrix, we calculated four functional metrics for exploring different facets of functional diversity in the multidimensional trait space: functional divergence (FDiv), functional richness (FRic), functional evenness (FEve; Villéger et al. 2008), and Rao's Quadratic Entropy (RaoQ; Botta-Dukát 2005). Each index delves into different aspects of functional diversity. Indeed, FDiv measures how abundance is distributed within the volume of functional trait space occupied by the species (Villéger et al. 2008). FRic relies on presence/absence data and represents the amount of functional space filled by the community (Villéger et al. 2008). FEve quantifies the regularity with which the functional space is filled by species, weighted by their abundance (Villéger et al. 2008). Finally, RaoQ estimates the dispersion of species in the trait space, weighted by their relative abundances, calculated as the mean distance between two randomly selected individuals (Botta-Dukát 2005).

Further, having tested for correlations among traits (assessed using the squared root of the average squared distances between species for all the variables considered; for additional mathematical details see Pavoine et al. 2009), we applied Principal coordinate analysis (PCoA). PCoA has been used both to the global trait distance among species and for single-trait distance of the traits which contributed the most to the final global distance. PCoA allows to discriminate the goodness of the trait distance matrix in representing the trait distribution within communities and to represent the functional relationships among species. To avoid problems in the bi-dimensional species-traits representation, we applied the Lingoes transformation (Lingoes 1971).

Then, we plotted the four functional diversity metrics towards the species distribution in the traits-space (using the fist axis of a double principal coordinate analysis; for details see Pavoine et al. 2009) to test whether the trait variation influenced functional diversity.

Likewise done for the phylogenetic diversity, to test if the occurrence of alien species affected the functional diversity, we performed two-factors ANOVA, with DZs as block and AP as treatment. Furthermore, we tested simple main effects of ANOVA models (keeping DZ as a fixed factor) to study which zones underwent significant changes due to the alien species presence. All indices were calculated using *FD* R package (Laliberté and Legendre 2010).

Results

Land cover changes

The classification and interpretation of aerial and satellite orthophotos revealed a pronounced LULC changing trend from 1954 toward 2008 (Figs. 1, 2). In details, data showed the studied dune endured an intensive viticulture activity since the post-war period. After 1966 we can observe a strong decrease of vineyards and crops, gradually substituted by dry shrubs and grasslands. In 2008 vineyards and crops completely disappeared. Sandy areas have not been subjected to significant variation during the analysed period, while artificial surfaces reported a positive trend, up to cover ~5 % of the dune area in 2008.

Species richness and composition

We sampled a total number of 81 plots and collected 113 vascular plant species. Species belonged to 48 families, of which the most represented were *Poace*ae (18 species) and

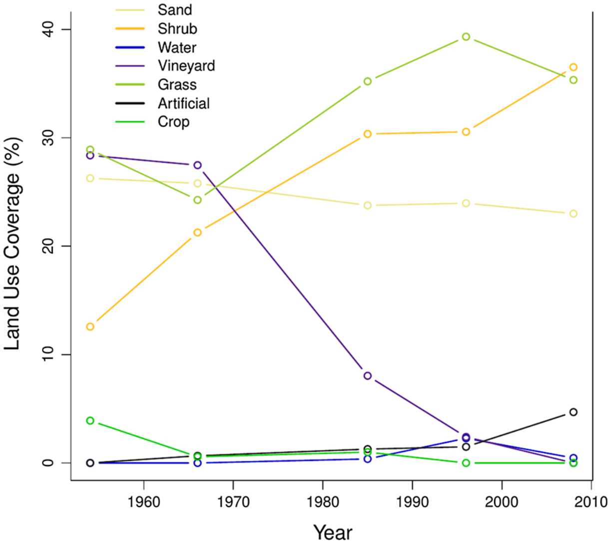

Fig. 2 Trend of LULC change for the studied area during the 1954–2008 time period. *Each coloured line* represents a different LULC. (Color figure online)

Table 1 Descriptive statistics for plant species richness in the study area considering both the total species richness and alien species richness

DZ	NO plot	Total species richness	All species			Alien species		
			Min	Mean	Max	Min	Mean	Max
1	23	32	1.0	5.9a	11.0	0.0	0.7ab	4.0
2	24	50	6.0	9.7b	15.0	0.0	0.8a	2.0
3	34	87	5.0	12.3c	20.0	0.0	0.4b	4.0
Total	81	113	1.0	9.7	20.0	0.0	0.6	4.0

Different letters indicate significant difference ($p < 0.01$) among DZs according to Wilcoxon test; on the contrary the same letter for different DZs means that there are not differences between Dzs; p level was adjusted according to Bonferroni correction

Table 2 GLMs coefficients and significance levels regarding total species richness and alien species richness

All species						Alien species				
Variable	Estimate	St. error	t	p		Estimate	St. error	z	p	
(Intercept)	3.63	1.42	2.55	0.01	*	0.28	0.25	1.08	0.28	–
Aspect East	2.58	1.03	2.50	0.02	*	–	–	–	–	–
Aspect North-East	−0.49	1.77	−0.27	0.78	–	–	–	–	–	–
Aspect North-West	1.32	1.52	0.87	0.39	–	–	–	–	–	–
Aspect South-East	5.91	1.84	3.21	<0.00	**	–	–	–	–	–
Aspect South-West	−1.41	1.17	−1.21	0.23	–	–	–	–	–	–
Aspect West	−0.33	0.92	−0.36	0.72	–	–	–	–	–	–
us1985-shrub	2.01	1.53	1.31	0.19	–	–	–	–	–	–
us1985-vineyards	3.79	1.45	2.62	0.01	*	–	–	–	–	–
us1985-grass	1.32	1.25	1.05	0.30	–	–	–	–	–	–
us1985-artificial	4.34	3.09	1.40	0.16	–	–	–	–	–	–
us2008-shrub	−2.99	1.39	−2.15	0.03	*	–	–	–	–	–
us2008-grass	−2.67	1.10	−2.44	0.02	*	<0.00	<0.00	−2.94	<0.00	**
Distance to the sea	0.09	0.02	6.21	<0.00	**	–	–	–	–	–
Adjusted-R-squared	0.56	p value < 0.001				Adjusted-D-squared	0.09			

Coefficients concerning only the variables selected by the IC-based approach to model selection are reported. In the last row adjusted model R^2 (or D^2) and p values for both species pools are indicated

ns $p > 0.05$; *$p \leq 0.05$; **$p \leq 0.01$

*Asterace*ae (15 species*)*. Regarding the species life cycle, the vast majority were perennial (71), while annual (37) and biennial (5) were less represented in the communities. 18 species (about 13 % of the total number) have been recognized alien for the Italian flora (see Appendix S2).

The mean number of species per plot was 9.7 (SD = 4.2; Table 1). The three DZs showed a statistically significant difference in total and in alien species number at plot level (Wilcoxon test; $p = 0.01$).

Findings underlined how the number of species throughout the dune was significantly influenced by: plot aspect, LULC of years 1985 and 2008, and distance from the sea (Table 2). Conversely, the number of alien species showed to be significantly affected only by the grassland land cover type.

Considering separately each vegetation zone, either total than alien species richness seemed to be shaped by the same factors affecting the dune as a whole (Appendix S3). Significant differences have been recorded for the impact of dune pathways in shaping alien richness in DZ2, alongside the high influence of slope and 2008 LULC on total species richness in DZ3.

Sampled plots ranged in native species abundance from 11 to 127 %, with a mean of 62.7 % (Fig. 3). DZ1 revealed the lowest median native abundance value, while the DZ2 the highest (Fig. 3). Species reporting the highest abundance were *Scabiosa argentea*, *Clematis flammula* and *Vitis vinifera*, whereas *Carpobrotus edulis* and *Yucca gloriosa* were the most abundant alien species.

Table 3 shows the significant effect of alien species presence (Wald-Test: $p = 0.001$) on native species abundance. The interaction between DZ and AP has resulted significant (Wald-Test: $p = 0.003$), and the effect was uneven across DZs. Table 4 represents the univariate ‘species-by-species’ test statistics of the most abundant native species.

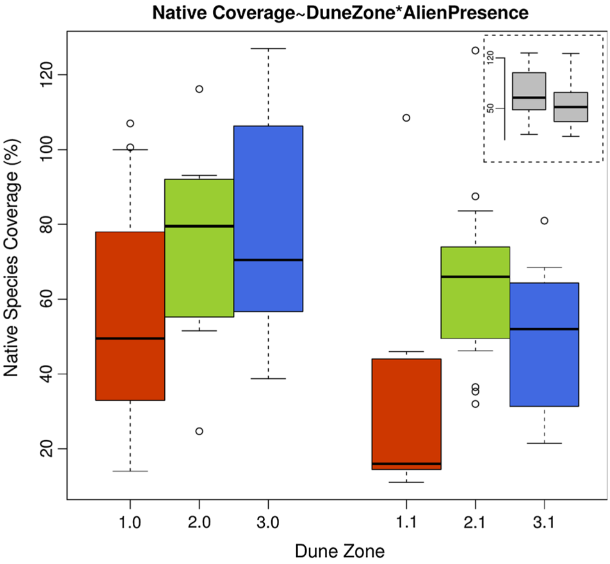

Fig. 3 Boxplot showing the native species abundance distribution for each DZ. The boxplot is divided in not-invaded (*left*) and invaded (*right*) boxes. In the *upper right* it has been reported a further singol boxplot (in *grey*) with the whole area abundance in invaded and not invaded plots. *Red colour* indicates DZ1, *green* DZ2, and *blue* DZ3. (Color figure online)

Table 3 ANOVA table summarising the statistical significance of the multivariate GLM for species abundances

Factor	Res.Df	Df.diff	Val (Dev)	Pr (>F)
DZ	78	2	1,636.3	0.001***
AP	77	1	512.6	0.001***
DZ:AP	75	2	428.6	0.003**

p values were calculated using 999 resampling

$^{**}p \leq 0.01$; $^{***}p \leq 0.001$

Table 4 Univariate statistics from the multivariate GLM which allow to recognize what species significantly contributed to the difference in abundance between blocks (DZ) and treatments (AP)

DZ			AP			DZ:AP		
Species	Dev	*p*	Species	Dev	*p*	Species	Dev	*p*
Agropyron junceum	154.4	0.001	*Juniperus oxycedrus*	30.8	0.113	*Cyperus capitatus*	42.3	0.036
Pteridium aquilinum	97.5	0.021	*Pancratium maritimum*	29.1	0.129	*Vulpia membranacea*	39.2	0.053
Phleum ambiguum	86.3	0.043	*Pistacia lentiscus*	27.0	0.167	*Anacyclus radiatus*	33.5	0.083
Cakile maritima	86.2	0.043	*Phleum ambiguum*	26.0	0.182	*Crucianella maritima*	31.1	0.093
Teucrium polium	83.6	0.054	*Phyllirea angustifolia*	25.7	0.187	*Anthemis maritima*	14.5	0.548
Ononis variegata	65.2	0.152	*Reichardia pricroides*	21.0	0.362	*Teucrium polium*	14.2	0.568
Medicago litoralis	64.6	0.152	*Scabiosa argentea*	20.1	0.414	*Clematis flammula*	11.2	0.712
Cutandia maritima	59.7	0.174	*Cynodon dactylon*	18.0	0.523			

We reported the deviance explained by each species provided with its *p* value

Multivariate GLMs for each single zone revealed that alien species significantly changed the native species abundance in DZ2 and DZ3 (p value $= 0.06$ and <0.09, respectively), but not in DZ1 (p value $= 0.14$; data not reported), coherently with previous findings in similar dune vegetation.

Phylogenetic diversity

DZ3 registered a stronger effect on phylogenetic diversity due to alien species than the other two DZs as overall pattern (Fig. 4). However, DZ1 and DZ2 showed generally more differentiated patterns of each phylogenetic metrics as regard DZ3. MPD showed the highest power in discriminating among DZs. Table 5 showed how alien species presence significantly changed PAE (F-test; $p = 0.001$) and MPD (F-test; $p < 0.05$)

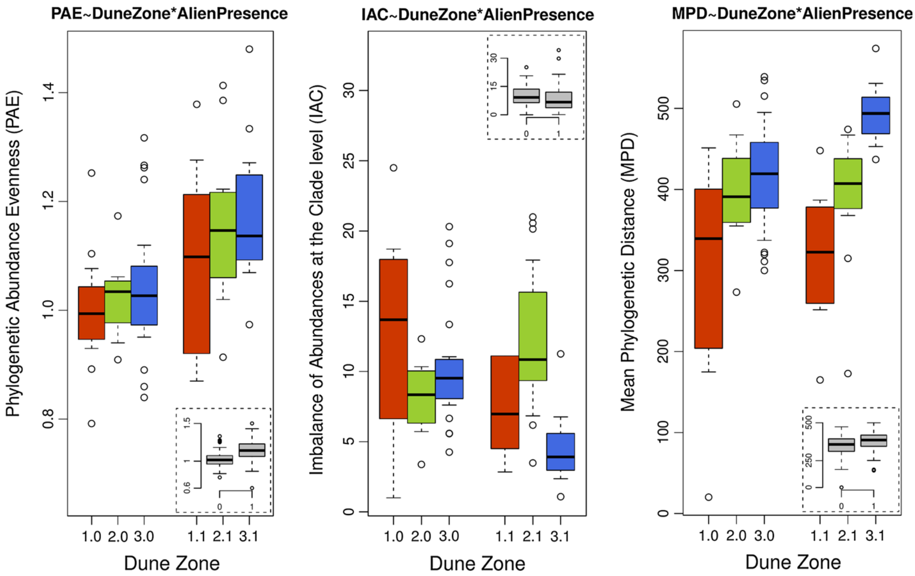

Fig. 4 Boxplots describing the distribution of the three phylogenetic metrics (PAE, IAC, and MPD) between the three DZs (*red* DZ1, *green* DZ2, *blue* DZ3) and in not invaded (*left*) and invaded (*right*) plots. In the little boxes are reported boxplots (in *grey*) reporting the distribution of the different Phylogenetic Diversity metrics in not invaded (*left*) and invaded (*right*) plots, considering the entire area, without discriminating for the DZs. (Color figure online)

Table 5 ANOVA table of the three phylogenetic metrics with DZ as block and AP as treatment

Factor	Df	Sum	Mean	F	Pr (>F)	
PAE						
DZ	2	0.100	0.050	2.570	0.083	
AP	1	0.210	0.210	11.240	0.001	**
DZ:AP	2	0.010	0.010	0.380	0.685	–
Residuals	75	1.420	0.020			
IAC						
DZ	2	181.610	90.800	2.529	0.087	
AP	1	32.780	32.782	0.913	0.342	–
DZ:AP	2	310.290	155.143	4.321	0.017	*
Residuals	75	2,692.580	35.900			
MPD						
DZ	2	229,782	114,891	17.898	0.000	***
AP	1	22,211	22,211	3.460	0.047	*
DZ:AP	2	25,581	12,790	1.992	0.144	–
Residuals	75	481,453	6,419			

ns $p > 0.05$; $*p \leq 0.05$; $**p \leq 0.01$; $***p \leq 0.001$

metrics on the whole area. Indeed, PAE recorded lower value (F-test; $p = 0.08$; Fig. 4) in DZ1 than DZ2 and DZ3. Furthermore, PAE underwent a significant rise in the whole area due to alien species presence (F-test; <0.01; Table 5), showing abundances to be more evenly distributed among lineages in not invaded plots, while individuals are clustered into longer terminal branches (higher PAE) in invaded plots. Such increasing pattern was significant in DZ2 and DZ3 (Appendix S4). Considering the IAC index, a general not significant decrease occurred across the whole dune area. While this metric showed a significant rise ($p = 0.03$) in invaded plots of DZ3, in the other two DZs not significant differences have been revealed (DZ1: $p = 0.9$; DZ2: $p = 0.24$). Finally, MPD showed a highly significant increasing trend from DZ1 toward DZ3 ($p < 0.001$), hence the average phylogenetic distance between species was lower in DZ1 and higher in DZ3, reporting mean values in DZ2. DZ3 registered a significant raise in MPD in invaded plots compared to not invaded ones ($p = 0.008$).

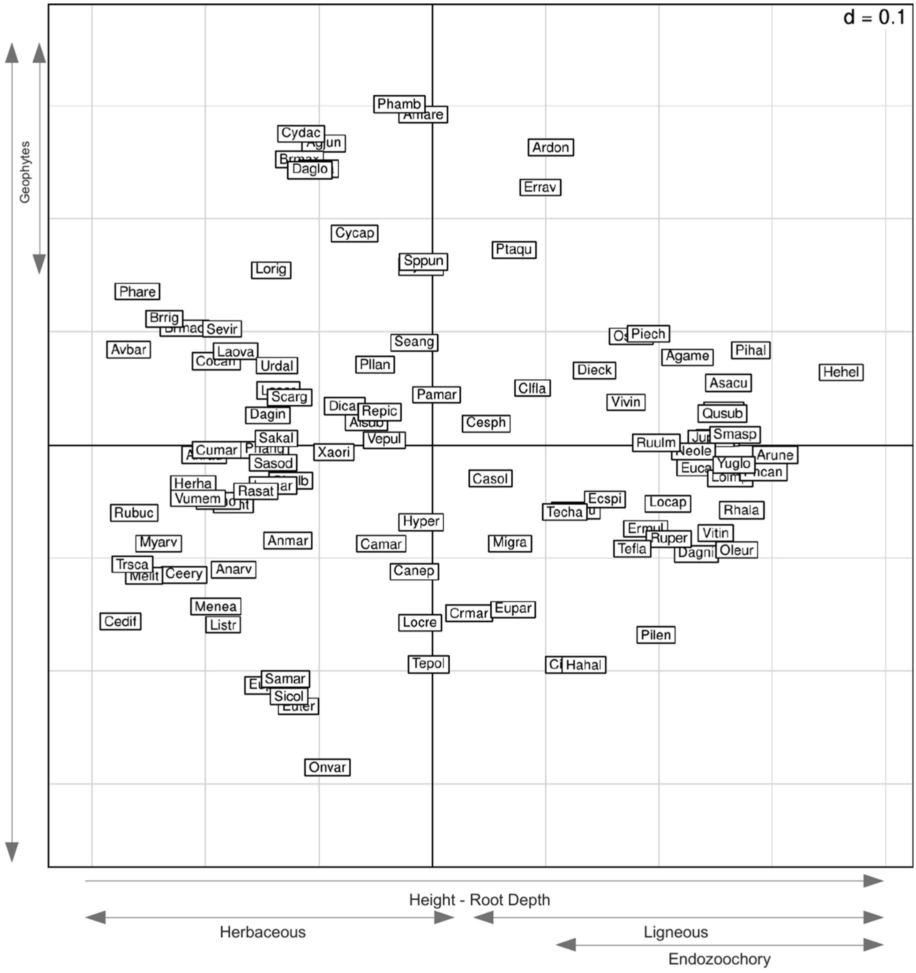

Fig. 5 PCoA biplot reporting the species distribution in the trait-space. Species, were reported using the first two letters of the genus and the first three of the species epithets. On the *bottom* and on the *left* were showed traits range of such traits which mainly influenced the species distribution for both axes. Axis 1 explains 17 % of the variance, while axis 2 expresses 14 of the total variability

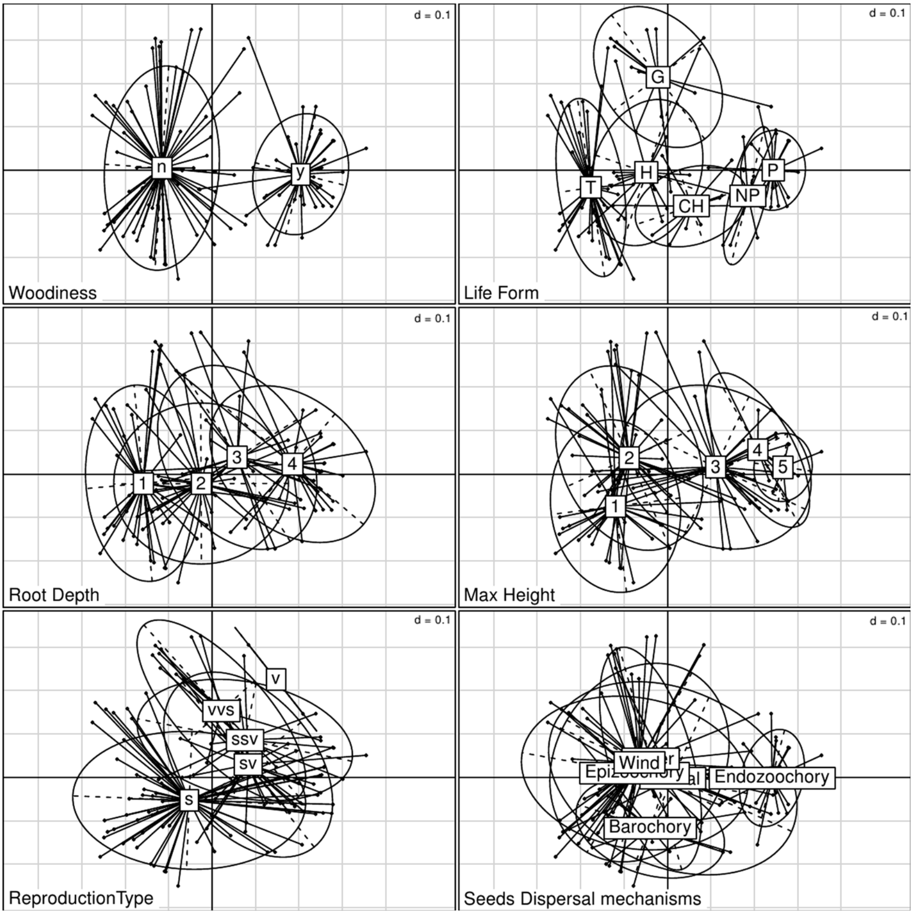

Fig. 6 PCoA outputs of the six most correlated traits: Woodiness (n = non-woody, y = woody), Life Form (Therophytes, Geophytes, Hemicryptophytes, Chamaephytes, Nanophanerophytes, Phanerophytes), Max Height (1 = Minimum height, 5 = Maximum height), Reproduction Type (s = by seeds/by spore; ssv = mostly by seed, rarely vegetatively; sv = by seed and vegetatively; vvs = mostly, rarely by seeds; v = vegetatively =), Seeds Dispersal mechanisms. The small frame in the centre of each trait level represents the centroid of the space occupied by each trait level. Each *line* connects the centroid of the trait level with plots in which it is represented

Functional diversity

Most of the correlations among squared distances obtained by pairs of traits were close to zero (Mean = 0.060, S.D. = 0.197), suggesting low redundancy between traits. However, six traits showed higher correlation with each other and are consequently well represented in the final functional distance: ligneous vs. herbaceous, life form, max height, root depth, favourite reproduction mechanism and seeds dispersal mechanisms. We have therefore considered this set of traits as the most informative ones on plant community assembly. Consequently, we have restricted our further analyses to these six traits.

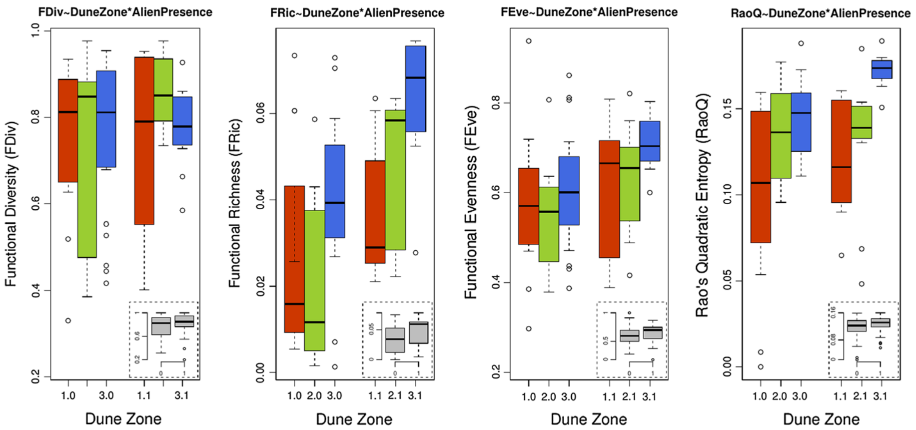

Fig. 7 Boxplots describing the distribution of the three functional metrics (FDIV, FRIC, and RaoQ) between the three DZs (*red* DZ 1, *green* DZ 2, *blue* DZ 3) and in not invaded (*left*) and invaded (*right*) plots. In the little boxes, boxplots (in *grey*) reporting the distribution of the different Functional Diversity metrics in not invaded (*left*) and invaded (*right*) plots, considering the entire area, without discriminating for the DZs. (Color figure online)

The first and the second PCoA's axes explain 17 and 14 % of the variation, respectively (Fig. 5). The first axis substantially separates herbaceous (therophytes) small statured species, with shallow roots exploiting wind, epizoochory and barochory as dispersal ways, from ligneous species, including species having deep root system and mostly using endozoochory (Figs. 5, 6). The second axis mainly separates geophytes species (having vegetative reproduction strategies) from all the other species (Fig. 6).

Regarding the functional metrics, DZ1 showed lower values than the other DZs functional indices, except for FRic and FDiv (Fig. 7). The functional metrics reported invaded plots to be generally more functionally diverse than not invaded plots. In details, considering each of the functional diversity indicator, FDiv in not invaded plots (the less diverse plots, on the bottom of Fig. 7a) reflects mostly herbaceous therophytes plants, especially the two most widespread in the study area: *S. argentea* and *Cutandia maritima*. In addition to ligneous species (mainly *V. vinifera* and *C. flammula*), the most functionally diverse plots recorded many non-therophytes species, rarely found in other plots, including: *Lobularia maritima, Carex flacca* Schreber and *Phleum ambiguum* Ten. Invaded plots were shifted towards higher FDiv values, mainly because of the very functionally diverse plots in DZ2. The not-invaded plots of DZ3 were characterized predominantly by ligneous species and, subsequently, assumed very low FDiv value.

Functional richness (FRic, Fig. 8) reported the highest values on the centre of the scatterplots, in very species-rich plots located in DZ2 and DZ3 (in both invaded and not invaded plots), characterized by the presence of herbaceous and ligneous species. RaoQ (Fig. 8) assumed similar parabolic shapes in invaded plots reaching the highest values in the centre of the graph and the lowest values on both the sides. On the contrary, not-invaded plots showed linear increasing relationships along the Axis 1 of DPCoA. FEve (Fig. 8) reported a weakly not significant increase (p value 0.11) across the Axis 1 of

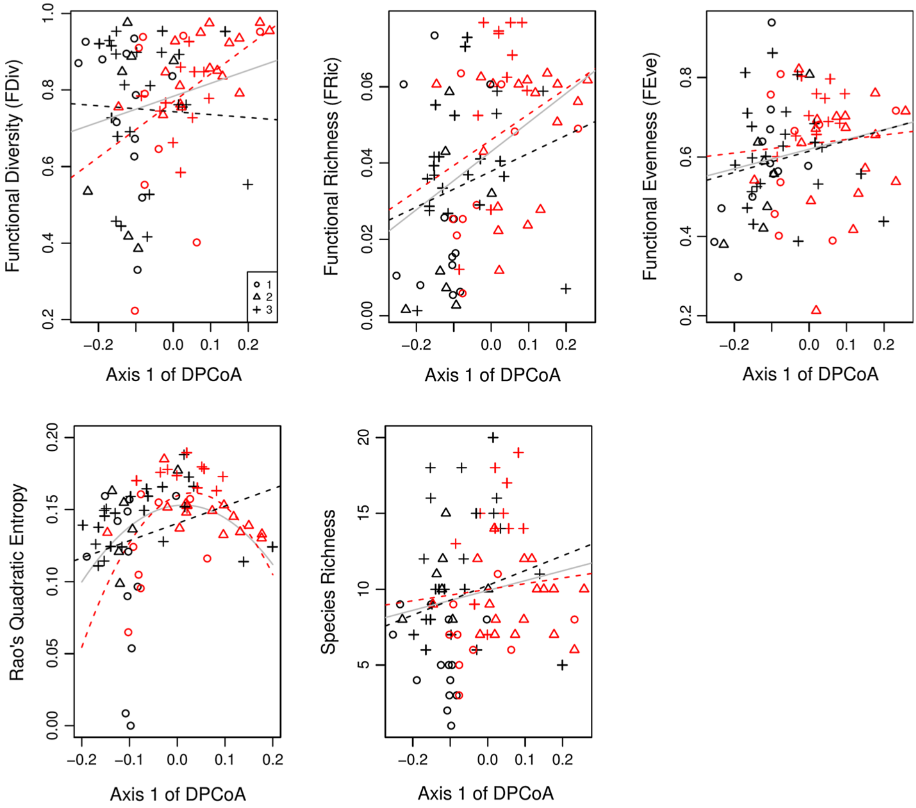

Fig. 8 Scatterplots of the four functional metrics and the species richness ordered along the values from the DPCoA Axis 1. The three zones were represented by different symbols (*circles* DZ1, *triangles* DZ2, *crosses* DZ3) and invaded (*red*) and not-invaded (*black*) plots in different colours. There were reported also least-squared regression lines or predicted lines (for binomial models) regarding the set of all plots (*grey*), not-invaded plots (*black*) and invaded plots (*red*). **a** FDIV (total: R2 = 0.04*; native: R2 = −0.02; alien: R2 = 0.18**); **b** FRIC (total: R2 = 0.15***, native: R2 = 0.02; alien: R2 = 0.08.); **c** RaoQ (total: R2 = 0.25***; native: R2 = 0.05.; alien: R2 = 0.53***); **d** SR (total R2 = 0.02; native: R2 = 0.09*; alien: R2 = 0.01). (Color figure online)

DPCoA, however the absolute highest values where recorded in plots on the left side of DPCoA Axis 1.

All metrics generally assumed higher values in invaded plots, although this trend is not always significant and only when the whole community was considered (Figs. 7, 8). FDiv did not show any significant pattern due to alien species occurrence, whereas FRic, FEve and RaoQ were significantly affected by the alien species (Table 6). In particular, FRic reported significant differences (increasing pattern moving toward invaded plots) in DZ2 and DZ3, (Appendix S5). Finally, Rao's Quadratic Entropy showed a significant increase ($p = 0.02$) between invaded and not invaded plots for all the three zones (Appendix S5). This difference seemed to be entirely underpinned by DZ3 ($p = 0.05$; Appendix S5).

Table 6 ANOVA table for the four functional diversity metrics (FDiv, FRic, FEve, and RaoQ) with DZ as block and AP as treatment

Factor	Df	Sum	Mean	F	Pr (>F)	
FDiv						
DZ	2	0.081	0.040	1.330	0.271	
AP	1	0.023	0.023	0.752	0.389	
DZ:AP	2	0.111	0.055	1.824	0.169	
Residuals	75	2.214	0.030			
FRic						
DZ	2	0.000	0.002	4.100	0.021	*
AP	1	0.010	0.010	15.180	0.000	***
DZ:AP	2	0.000	0.000	0.830	0.440	
Residuals	74	0.030	0.000			
FEve						
DZ	2	0.060	0.030	1.500	0.230	
AP	1	0.080	0.080	4.400	0.040	*
DZ:AP	2	0.020	0.010	0.570	0.570	
Residuals	75	1.350	0.020			
RAOQ						
DZ	2	0.028	0.014	13.350	0.000	***
AP	1	0.005	0.005	5.000	0.028	*
DZ:AP	2	0.002	0.001	1.160	0.318	
Residuals	75	0.078	0.001			

*$p \leq 0.05$; ***$p \leq 0.001$

Discussion

The results of this work indicate that ‘historical’ LULCs (before 1980) did not affect species assemblages. Indeed, species richness is related to more recent land transformations (Pino et al. 2005) and to a set of environmental factors (slope and distance to the sea; Stallins and Parker 2003; Forey et al. 2008). This pattern might have been determined by two causes: (i) the relatively harsh environmental conditions and ecological dynamism acting in dune habitats (Acosta et al. 2006, 2009; Martínez et al. 2008) and (ii) the rapid transformation of LULCs which happened since the ‘80 s. The former drivers allowed fast re-naturalization of the dune system heavily exploited by viticulture in the past (until the ′70 s). In detail, the intensive viticulture activity carried out during the ′50 s, the ′60 s and the ′70 s led to the complete removal of the original dune plant community, erasing any effect of previous LULCs in shaping species richness. Then, when cultivated species have no longer been sustained by external nutrients and water supplies, they may have disappeared faster due to the harsh environmental conditions, being substituted by a pool of specialized species. The latter factor is related to the increasing exploitation of the study area for tourism purposes occurred in the last three decades. Indeed, the surface of man-transformed surface increased five-fold since then. Artificial area sprawl is even more difficult to face for natural systems than agricultural sprawl, because of the irreversible transformation involved (soil isolation, pollutants, waste, etc.; AEA 2011). Moreover, the spread of artificial surfaces is followed by an increase in human density and habitat disturbance that, in turn, favours higher species richness also due to a richer flora of alien species (Stadler et al. 2000; Chocholoušková and Pyšek 2003).

We revealed 18 alien species, an amount which is in line with other studies in dune habitats in Central Italy (Carboni et al. 2010a, b; Carranza et al. 2010a, b). Back dune habitats might supply suitable environmental conditions to alien and grassland species to spread out. Grasslands have rapidly replaced vineyard however they convey the invasion of several alien species typical of intensively cultivated lands (e.g. *V. vinifera*, *Conyza canadensis*, *Setaria viridis*, *Raphanus sativus*, *Euphorbia prostrata*). This trend can be explained by the functional similarity of grasslands with cultivated or mown lands. Indeed they are more prone to sustain and perpetrate the load of invasive species from farmland. Furthermore, grasslands on historically agricultural sites are characterized by the availability of a higher amount of nutrients (overall calcium and phosphorus) derived from farm amendments (liming and fertilization, Compton and Boone 2000). Moreover, grasslands are threatened by tourism activities which in summer crowd the dune without any restrictions. Indeed, grasslands of unprotected dune habitats are crossed by numerous pathways, created by livestock to graze (trampling) and by tourists, carrying with them a burden of alien species propagules (for instance *Agave americana*, *C. edulis*, *Senecio angulatus*). This pattern is particularly pronounced in DZ2, covered by grasslands, where the spatial proximity to the nearest path significantly and positively affected the presence of alien species.

We then investigated whether alien species' occurrence influenced the native species assemblage. Consistently with other findings (Santoro et al. 2012a, b), our results highlighted that the presence of alien species into the sampling plots heavily altered native species abundance, generally showing a lower value. This circumstance might be due to: (1) competitive exclusion; (2) feedback effect of disturbance favouring alien species encroachment (Santoro et al. 2012a, b); (3) a mixture of the two previous causes (Gurevitch and Padilla 2004; Gooden and French 2014). As highlighted by previous correlative studies, caution is needed when interpreting such results (Rentéria et al. 2012; Jucker et al. 2013). Since we have no information on the floral composition of invaded plots prior to invasion we cannot determine what is the phenomenon underpinning the decreased native abundance. The influence of alien plants on species composition is not observed in the fore dune, likely related to the extreme specialization needed to survive in this harsh habitat, which may have prevented drastic transformation led by alien species (Becker et al. 2005; Carranza et al. 2011; Santoro et al. 2012a, b; Bellard et al. 2013). These severe ecological conditions are softened by the first dune segment (DZ1; Acosta et al. 2009; Fenu et al. 2012), explaining the power in shaping plant assemblages by alien species in the back dune (DZ2) and in the fixed dune (DZ3). Here, alien species can find more fertile ground where the arrival, the germination, the establishment and the potential for further spreading in the surroundings is possible. Moreover, until the '70 s these areas were cultivated and intensively fertilized. Hence, the alien species richness might be favoured by the enhanced soil fertility (ruderal species, sensu Grime 2001), and by the past LULC. Indeed, soil characteristics, in particular fertility, have been advocated as the most important factor regulating the abundance of non-natives species (Von Holle and Motzkin 2007; Fenu et al. 2012).

Another interesting result was the highly significant difference in the community composition between invaded and not invaded plots which seemed to be related to the whole species assemblage rather than to any particular species. The aforementioned reduction in abundance of native species is generalized and independent from species ecological function. Indeed, in our case study, various alien plant species reduced the abundance of native species. This might be seen as a combined result from the whole set of alien species, which are almost evenly distributed in the invaded plots. This is in contradiction with Jucker et al. (2013), who studied the effect of *C. edulis* on the taxonomic diversity of Central Italy dune habitats. The authors found that iceplant competitively excluded those species with peculiar life-history traits from the plant community, acting as a filter in the process of community assembly (see also Gaertner et al. 2009). However, such a contrasting outcome may be explained considering that in our study area *C. edulis* is not-dominant as it is in the case reported by Jucker et al. (2013) (occurring only in 4 plots out of 81) with low local abundance (mean abundance in the invaded plots 27 %).

From the functional analyses outputs, we evince alien species encroachment significantly affected the functional characteristics of the native dune plant communities. Strictly spoken, the incoming of alien species in the dune system enhanced the values of the functional diversity. Such pattern is similarly revealed for the phylogenetic metrics (increasing trend in invaded plots). The similar parallel pattern of phylogenetic and functional metrics is in accordance with the “phylogenetic signal” concept (sensu Blomberg et al. 2001; Swenson and Enquist 2009). It assumes that traits of closely related species are more similar than those of species which are more distant in a phylogenetic tree because of trait conservatism (Blomberg et al. 2001; Carboni et al. 2013). In other words, species being closely related phylogenetically should also require similar ecologically parameters (Carboni et al. 2013). Consistently with species composition and abundance pattern found in this study, alien species heavily impacted the phylogenesis and functioning of native species and communities. However, alien species do not seem to competitively exclude natives, probably as a result of the incoming of phylogenetically and functionally differentiated species from native ones (Gerhold et al. 2011). On the other hand, our results are not in line with other findings from similar studies in urban landscapes, e.g. Ricotta et al. 2010 regarding phylogenetic relatedness of alien species to native ones where alien and native have been found to be closely phylogenetically related.

Generally, the multifaceted approach also assisted in the detection and understanding of the dune community assembly, and to discern the relative impact of alien species on native plant species and communities. We can deduce that vegetation growing in almost undisturbed conditions has been environmentally constrained for a reduced combination of traits, also associated to limited phylogenetic diversity (Grime 2006; de Bello et al. 2009). Thus, more environmentally stressed plant communities seemed to be predominantly ruled by habitat filtering, as trait convergence is mainly related to this ecological process (Weiher and Keddy 1995; Cornwell et al. 2006). Therefore, in void or low level of disturbance condition (not-invaded plots) we can consider biotic and abiotic constraints to be the major drivers in shaping dune plant community assembly. On the other hand, invaded plots showed a clear phylogenetic and functional differentiation. Alien species might be carrying distinct and different phylogenetic and functional characteristics, affecting the main ecological processes which drives the plant communities structuring. As a result, invaded vegetation should be experiencing trait divergence (associated also with phylogenetic divergence), related to a limiting similarity/niche differentiation process (Chesson et al. 2004; Stubbs and Wilson 2004; Wilson 2007). In this context, biotic interactions, such as competition, and resource partitioning mechanisms might be acting as major players in driving plant community assembly of disturbed/invaded plots. Summarising, we suggest that the two diversely disturbed dune communities are likely to be mainly ruled by two different ecological processes.

Finally, our study accomplished the proposed research targets, as we obtained results which help in better understanding the impact of alien species on native dune plant species and communities. Further, we attained prominent results on plant community assembly shaping dune vegetation systems, under different levels of disturbance (i.e. alien species invasion). Besides, we gathered information on biotic and abiotic constraints structuring species composition and insights on phylogenetic and functional characteristics of invaded and not-invaded dune communities. In the light of the outcomes of this paper we argue that the integration of taxonomic, functional and phylogenetic diversity when defining conservation priorities is compelling (Rolland et al. 2011; Cadotte et al. 2010; Jucker et al. 2013; Carboni et al. 2013). Concluding, we support the idea that multifaceted approach assists in forwarding the ecological understanding of dune vegetation dynamism, also allowing more informed-management of such priority habitats for biodiversity conservation.

Conclusion

This study showed the relevance of applying a multifaceted approach in understanding biodiversity patterns linked to alien species invasion, supplying an overview on on-going ecological phenomena. This is a crucial step to achieve an efficient management of dune habitats, and a useful tool to monitor and to effectively preserve their biodiversity and related ecological functions.

This research underlined that the encroachment of alien species and the recent LULC changes strongly affected the biodiversity patterns in the studied dune. The environmental changes generated interruptions of ecological processes. Concerning global change, coastal flooding and sea level are expected to increase significantly by mid-century and habitat loss would double the extent of coastline highly exposed to storms and sea-level rise (Arkema et al. 2013; IPCC 2007). Besides, population growth and human flow towards coasts will increase the hazard for coastal communities. Therefore, coastal ecosystems are fundamental habitats to protect. The conservation and restoration of these ecologically complex and fragile environments will play a crucial role in the next decades.

After the analysis in this paper have been performed, a new tool to produce robust, repeatable and defensible phylogenesis has been developed (Phylogenerator; Pearse and Purvis 2013). Using DNA sequences from GenBanck (Benson et al. 2011), Maximum likelihood and Bayesian approaches Phylogenerator is able to reduce the number of polytomies in the generated phylogenetic trees, which can influence measures of phylogenetic diversity (Ricotta et al. 2012). We encourage the readers to use Phylogenerator when the number of species into each family is high.

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