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Quantifying plant species diversity in coastal dunes: a piece of help from spatially constrained rarefaction

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Abstract Since coastal dunes are one of the most vulnerable landscapes in Europe, their maintenance requires specific conservation and monitoring programmes. In this paper, the coastal dune systems of two natural parks located in central Italy were analyzed aiming at: (1) assessing diversity patterns of all vascular species, endemic and alien taxa in plant communities along the coast-to-inland gradient; (2) comparing these patterns between coastal sections characterized by different dynamical processes (accreting, stable and erosive coasts); and (3) testing the differences induced by the methodological approach used to characterize these patterns. Twenty-one transects were randomly positioned perpendicular to the shoreline in the whole coastal area (30 km in length), and the full spectrum of plant communities was sampled. Patterns of plant diversity were assessed using spatially explicit methods, namely spatial constrained rarefaction (SCR), able to avoid the confounding effect of spatial autocorrelation. The results show that species richness varied significantly between plant communities along the coast-to-inland gradient with the highest values at the level of mobile dunes and transition dunes. Species richness was significantly higher in stable coastal dunes than those found in accreting and in erosive dunes. In fact, sand dynamics (accumulation as well as erosion) create periodic vegetation disturbances affecting composition variability and succession. The SCR methodology avoided overestimation of species richness when compared to classical rarefaction curves. Our findings pinpointed that coastal plant communities create a highly spatially structured mosaic in which mobile dunes represent the highest compositional heterogeneity. Local managers are encouraged to consider these results for planning adequate conservation strategies.

Keywords biodiversity · coastline dynamic processes · coastal dune vegetation · Natura 2000 · rarefaction curves · spatial autocorrelation

Abbreviations

SCR	spatially constrained rarefaction
MSRM	Migliarino San Rossore Massaciuccoli Regional Park
MP	Maremma Regional Park

Nomenclature Checklist of the Italian vascular flora (Conti et al. 2005, 2007) for plant species.

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Introduction

The term 'biodiversity' is currently used in the literature to cover both the number of different populations and species that exist and the complex interactions that occur among them. Its measurement at all levels is really important for any conservation biology purposes (Pullin 2002). The effects of biodiversity loss or changes in plant community composition on the functioning of ecosystems have been the focus of much ecological research (Schulze and Mooney 1993; Kinzig et al. 2002; Loreau et al. 2002). Species composition, richness, evenness and interactions all respond to and influence ecosystem properties and stability. Unfortunately, the ever-growing impact of human activities is causing biodiversity loss of natural habitats (Hawksworth and Bull 2008).

Coastal sand dune systems are dynamic and heterogeneous habitats characterized by a complex environmental gradient which determines a characteristic coast-to-inland plant community zonation (Ranwell 1972; Doing 1985; Psuty 2004; Wiedemann and Pickart 2004; Frederiksen et al. 2006; Acosta et al. 2007). They contain a high ecological diversity in terms of plant community composition, species rarity and endemism (van der Maarel and van der Maarel-Versluys 1996; van der Maarel 2003; Martínez et al. 2004; Ciccarelli et al. 2014). Unfortunately, coastal dune environments are one of the most vulnerable landscapes in Europe, prone to many stress and disturbance factors such as erosion, global warming and anthropogenic pressure (Cori 1999; Brown and McLachlan 2002; van der Maarel 2003; Coombes et al. 2008; Carboni et al. 2009; Gornish and Miller 2010; Miller et al. 2010; Ciccarelli et al. 2012; Ciccarelli 2014, 2015). Quantifying the number of species that occur along a coast-to-inland ecological gradient could make a valuable contribution to managing the ecosystem.

It should be considered that the examination of species distribution patterns in space can help us better understand the effects of ecological and environmental pressures. To quantify the relative importance of natural and anthropogenic pressures at appropriate spatial scales, both spatial and spatial-temporal analyses are required. The species' spatial distribution and their relationship with the environmental heterogeneity should be explored using specifically developed techniques. Among these, individual and sample-based rarefaction curves are widely recognized powerful tools, also used to evaluate the effectiveness of sampling and to compare species richness in different habitats (Gotelli and Colwell 2001; Moreno and Halffter 2001; Koellner et al. 2004; Crist and Veech 2006; Chiarucci et al. 2008a,b; Acosta et al. 2009; Bacaro et al. 2012a; Chiarucci et al. 2012). Even if this method offers an elegant solution to the interpolation of the number of species observed as a function of sample size, it is affected by various spatial components. However, after Chiarucci et al. (2009) and Bacaro et al. (2012a), the problem related to the lack of independence in the sampling units between samples has been considered thanks to spatially constrained rarefaction (SCR) that incorporates the autocorrelated structure of biological communities into sample-based rarefaction. More specifically, this method addressed the problem of spatial autocorrelation by building the rarefaction curve based on the adjacency of the sampling units. Nevertheless, the use of SCRs has not yet become routine (the only recent ecological application can be found in Janišová et al. (2014) and is expected to be particularly useful in those situations where the spatial structure of biological communities is high, as is the case in coastal dune systems.

Erosion has a serious impact on some 20 % of the coastline of Europe (Doody 2013). In Italy, 42 % of coasts are largely affected by erosion processes, and in particular the Tuscan coastline reflects this scenario, with 37 % of its sand dune systems being affected by erosion (Gruppo Nazionale per la Ricerca sull'Ambiente Costiero 2006). Although it has been assessed that shoreline erosional processes are one of the major threats for coastal sand dune systems worldwide, little is known regarding plant diversity and coastline erosion (Roman and Nordstrom 1988; Avis and Lubke 1996; García-Mora et al. 1999; Lubke and Hertling 2001; da Silva et al. 2008; Ciccarelli et al. 2012; Ciccarelli 2014).

In this paper, a systematic sampling design based on belt transects was used to sample the full spectrum of coastal dune plant communities. Considering that biodiversity loss is a critical issue in coastal environments, we analyzed the diversity patterns of vascular plant species across the coastal dune systems of two natural parks in Tuscany (Italy) in order to correctly characterize occurring diversity patterns. In detail, we specifically aimed at (1) assessing diversity patterns of all vascular species, endemic and alien taxa in plant community types along the coast-to-inland gradient; (2) comparing these patterns between coastal sections characterized by different dynamical processes (accreting, stable and erosive coasts); and, finally, (3) testing the influence of the methodological approaches used (e.g. regular rarefaction vs spatially constrained rarefaction) for diversity comparisons purposes. This latter point has major implications when conservation actions should be planned and, for this reason, deserves particular attention.

Material and methods

Study area

The present study was conducted in the coastal sand dunes of two protected areas along the Tuscan littoral (Italy): Migliarino-San Rossore-Massaciuccoli Regional Park (MSRM) and Maremma Regional Park (MP; Fig. 1).

The Migliarino-San Rossore-Massaciuccoli Regional Park covers an area of 142 km^2 and is located near Pisa, in the North of Tuscany. The Park hosts 40 km^2 of coastal forest, a sandy beach and inland marshes. This area is characterized by a Mediterranean sub-humid climate, with a mean annual temperature > 15°C and a mean annual rainfall of 800–900 mm (Rapetti 2003).

The Maremma Regional Park is located on the coast near Grosseto, in the southern part of Tuscany. The Park is 90 km^2 and offers a diverse array of landscape types: coastal dunes, inland salt marshes, rocky vegetated foothills, coastal pinewood and farming areas. This area is characterized by a C1 type of climate, Mediterranean sub-arid, with an average annual temperature of 15.6°C and an average annual rainfall of 618 mm (Pinna 1985).

The coastal dune systems of both parks belong to the Natura 2000 network and include the following Sites of Community Importance (SCIs): ‘Coastal sand dunes of Torre del Lago’ and ‘Coastal sand dunes of Uccellina’, respectively. Moreover, these two protected areas are a geomorphological reference system for investigating variability of species richness related to coastal erosion and accretion because sections which belong to the same physiographic unit experience very different and localized dynamical processes (Gruppo Nazionale per la Ricerca sull’Ambiente Costiero 2006; Anfuso et al. 2011).

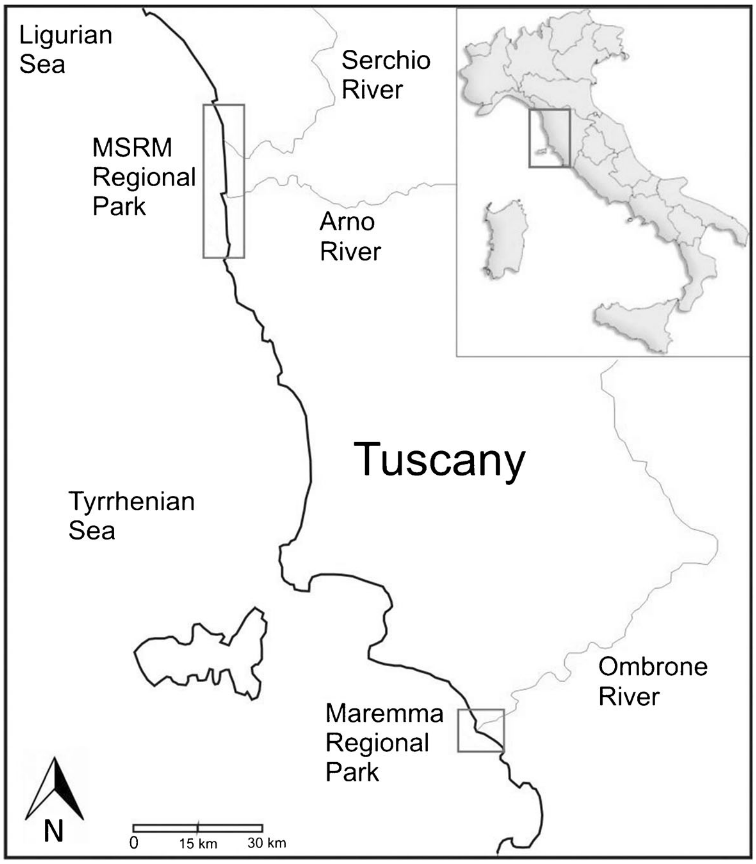

Fig. 1 Location of the Migliarino-San Rossore-Massaciuccoli (MSRM) Regional Park and the Maremma Regional Park in the northern and southern parts of Tuscany (Italy), respectively. On the right a picture of Italy with Tuscany.

Vegetation sampling

We analyzed plant communities on coastal dunes along the Ligurian and Tyrrhenian coast of Italy (Fig. 1). In each study area, the whole coastal system (20 km and 10 km in length for MSRM and MP park, respectively) was divided into sections of 1 km and one random transect was selected within each section. Several sections were excluded from this study because there were practically no more foredunes, as a result of coastal erosion. In May to June 2010 and in May to June 2011, a total of 21 transects (14 for MSRM and 7 for MP park) were positioned orthogonal to the seashore; their length varied depending on dune morphology and width. Along each transect, all vascular plant species were recorded, and the cover percentage of each species was recorded in contiguous 1-by-1-m plots. According to the guidelines of Biondi et al. (2009), all plots were assigned to the coastal habitats (see Ciccarelli 2014 for details on the sampling procedure and habitat classification) included in the Habitats Directive of the Council of European Communities 92/43/EEC (EEC 1992). For this study, we arranged the plots into three main plant community types that are most related to coastal dune zonation (Table 1): (i) upper beach and embryo dunes, which included annual vegetation of drift lines (Habitat code: 1210), and embryonic shifting dunes (Habitat code: 2110); (ii) mobile dunes, identified as shifting dunes along the shoreline with *Ammophila arenaria* (Habitat code: 2120); (iii) transition dunes, which included *Crucianellion maritimae* fixed beach dunes (Habitat code: 2210), and *Malcolmietalia* dune grasslands (Habitat code: 2230). In order to fine-tune the resulting data, we decided to consider as a single group both communities of foredunes – upper beach and embryo dunes – and both assemblages of transition dunes because they tend to grow in a mosaic pattern.

Data analysis

The presence or absence of vascular plant species recorded in each plot was used for data analysis. The first step was to analyze species richness within each plant community type along the coast-to-inland zonation. Secondly, to study the relationships between species richness and coastal dynamics, all plots were classified in dependence to the dynamical processes of the coastal section to which they belonged. The following dynamic classes were considered: CD1 (accreting coastline), CD2 (stable coastline) and CD3 (erosive coastline). These trends of shoreline change were determined using aerial photographs (Gruppo Nazionale per la Ricerca sull'Ambiente Costiero 2006; Anfuso et al. 2011).

Species richness values were calculated at the plot scale for each group of samples (plant community types and coastal dynamic classes), and significant differences were tested using a non-parametric Kruskal-Wallis test, with the Bonferroni correction for multiple comparisons.

For each plant community and coastal dynamic class, spatially constrained sample-based rarefaction curves

Table 1 Plant communities used in this study: distribution along the sea-inland gradient, description of plant communities, habitat code according to the Directive of the Council of European Communities 92/43/EEC (EEC 1992) and main diagnostic species.

Coastal dune zonation	Upper beach and embryo dunes	Mobile dunes	Transition dunes
Plant community description	Formations of annual plants occupying upper beach, and pioneer perennial assemblages representing the first stages of dune construction	Mobile dunes forming the seaward cordon or cordons of dune systems of the coasts	Perennial communities of the inland side of mobile dunes, dominated by chamaephytic species forming a mosaic with annual grasses
Habitat code according to the Directive 92/43/EEC	1210 – Annual vegetation of drift lines 2110 – Embryonic shifting dunes	2120 – Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)	2210 – *Crucianellion maritimae* fixed beach dunes 2230 – *Malcolmietalia* dune grasslands
Main diagnostic species	*Cakile maritima*, *Salsola kali*, *Elymus farctus* subsp. *farctus*, *Sporobolus virginicus*	*Ammophila arenaria*	*Crucianella maritima*, *Pycnocomon rutifolium*, *Seseli tortuosum*, *Malcolmia ramosissima*, *Silene canescens*, *Vulpia fasciculata*

(Chiarucci et al. 2009; Bacaro et al. 2012a) were calculated. In order to calculate SCR, the following framework was used: let *s* be the set of N plots defined in the *d*-coordinates space (in this specific case, *d* equals 2, i.e. the set of projected coordinates of each plot in the Euclidean space). Given a dataset containing the plot identity (label) and the coordinates of each sampling unit, the proposed routine (the R code is available in Bacaro et al. 2012a) calculates the distance between the sampling units, and for each unit, it orders all the others by increasing distance. For each ordered sequence of plots, an accumulation curve is then calculated, and the SCR is obtained as the average of all the accumulation curves. 95 % IC are also computed. Generally, rarefaction curves enable to compare two or more datasets considering the same sampling effort – in this case the same number of grid cells (Gotelli and Colwell 2001; Collins and Simberloff 2009). Spatially constrained rarefaction is suitable for comparing areas of different size because in the sets of samples collected across larger areas the rarefaction curves would increase more steeply due to the distance decay of similarity (for details, see Chiarucci et al. 2009). Bacaro et al. (2012a) developed ‘pointpattern’ and ‘SCR’ routines in the R environment for calculating SCR, making this technique readily available. In order to compare SCRs with classical rarefaction curves (RCs), we used the ‘specaccum’ function in the ‘vegan’ R package to calculate unconstrained and classic rarefaction curves (using the analytical formula proposed by Kobayashi 1974).

Moreover, aiming at testing differences in beta diversity among sets of plots belonging to different plant community types, the simple analytical procedure proposed by Bacaro et al. (2012b, 2013) was applied. This procedure consists of shuffling within-community dissimilarities among community and disregarding between-community dissimilarities. By repeating this operation many times (999 for the performed analyses), a distribution of the test statistics under the null hypothesis of no differences in mean plot-to-plot dissimilarities within groups was obtained. This analysis was performed for each natural park separately and by pooling in a unique set plots from the two areas in order to test independence of beta diversity patterns to the specific park considered. The ‘betadispersion2’ function was here used (freely available in Bacaro et al. 2013). All the statistical analyses were performed using R version 3.2.0 (R Development Core Team 2015).

Results

Species richness patterns

A pooled species list of 63 vascular plants belonging to 23 Families was obtained from the 980 sampled plots (Appendix **1**). Of these, Poaceae, Asteraceae, Caryophyllaceae, Apiaceae and Fabaceae showed the largest number of species (16, 11, 5 and 4, respectively). One Tuscan coastal dune endemic species (*Solidago littoralis*) was recorded in 38 plots, representing about 4 % of all sampled plots. By contrast, seven alien species – *Arundo donax*, *Cuscuta scandens*, *Elaeagnus angustifolia*, *Erigeron canadensis*, *Oenothera biennis, Pinus pinaster* (dubitative alien in Tuscany, see Arrigoni and Viegi 2011) and *Xanthium orientale* subsp. *italicum* – were recorded on the foredunes of the protected areas (they were present in 236 plots equals to 24 % of the sampled plots).

Species richness varied significantly between the three plant community types for all vascular species (with Kruskal-Wallis statistic of 42.1 and $P < 0.001$), and for both endemics (with K-W – 53.9 and $P < 0.001$) and alien species (with K-W – 26.2 and $P < 0.001$). Regarding all species, upper beach-embryo dunes showed the significant lowest mean value of species richness per plot and the lowest pooled number of species (Table **2**). By contrast, mobile dunes and transition dunes have similar mean numbers of species per plot and the pooled number of species (Table **2**). The highest number of endemics per plot was found in mobile dunes, while upper beach-embryo dunes showed the highest number of alien species per plot (Table **2**), where the most abundant aliens were *Xanthium orientale* subsp. *italicum* and *Oenothera biennis* with a frequency of 19 % and 10 %, respectively.

With respect to coastal dynamic processes, species richness varied significantly for all vascular species (K-W – 31.0 and $P < 0.001$), and for both endemics (with K-W – 99.2 and $P < 0.001$) and alien species (with K-W – 145.8 and $P < 0.001$) between dunes located on littorals affected by different sedimentary dynamics. Stable dunes (CD2) exhibited the highest mean value of species richness per plot, the highest pooled number of species and the highest mean value of endemics per plot (Table **3**), resulting significantly different from both accreting (CD1) and erosive dunes (CD3). By contrast, erosive dunes showed the lowest number of alien species per plot (Table **3**), with a predominance of *Arundo*

Table 2 Species richness, number of endemics and alien species per plot, and their pooled numbers in each plant community type. Means followed by the same letters are not significantly different at 5 % according to the non-parametric Kruskal-Wallis one-way ANOVA after the Bonferroni correction for multiple comparisons.

Plant community type	Number of plots	Number of species per plot (mean ± *SD*)	Pooled number of species	Number of endemics per plot (mean ± *SD*)	Pooled number of endemics	Number of alien species per plot (mean ± *SD*)	Pooled number of alien species
Upper beach and Embryo dunes	429	3.52 ± 1.50a	46	0.01 ± 0.10a	1	0.32 ± 0.49b	5
Mobile dunes	250	4.44 ± 1.92b	47	0.12 ± 0.32b	1	0.18 ± 0.38a	4
Transition dunes	301	4.18 ± 1.90b	47	0.02 ± 0.13a	1	0.18 ± 0.39a	4

Table 3 Species richness. number of endemics and alien species per plot, and their pooled numbers in each coastal dynamic type. Means followed by the same letters are not significantly different at 5 % according to the non-parametric Kruskal-Wallis one-way ANOVA after the Bonferroni correction for multiple comparisons. *SD* – standard deviation.

Coastal dynamic type	Number of plots	Number of species per plot (mean ± *SD*)	Pooled number of species	Number of endemics per plot (mean ± *SD*)	Pooled number of endemics	Number of alien species per plot (mean ± *SD*)	Pooled number of alien species
CD1 – Accreting	386	3.94 ± 1.70a	34	0.01 ± 0.11a	1	0.41 ± 0.50b	2
CD2 – Stable	217	4.46 ± 1.71b	46	0.16 ± 0.36b	1	0.40 ± 0.56b	6
CD3 – Erosive	377	3.71 ± 1.85a	34	0.00 ± 0.00a	1	0.05 ± 0.21a	3

donax (about 3 %). While accreting dunes and stable dunes have similar mean numbers of alien species per plot, stable dunes showed the highest pooled number of alien species (Table 3). In particular, the most abundant aliens were *Xanthium orientale* subsp. *italicum* and *Oenothera biennis*, which reached a frequency, respectively, of 21 % and 20 % in accreting dunes.

Species rarefaction curves and beta diversity

The rarefaction curves obtained by the pooled sample of plots classified by plant community types showed different patterns of species richness (Fig. 2). For a low number of sampled plots ($N < 100$), no appreciable differences emerged between plant communities. When the number of plots increased, the species RC of mobile dunes was steeper and higher than the one of transition dunes, which was intermediate, and the curve of upper beach-embryo dunes, which was the lowest. All curves showed an asymptotic pattern (Fig. 2). Considering beta diversity, we observed the highest values for upper beach-embryo dunes (for both the MP and MSRM nature areas), while mobile and transition dunes showed comparatively less compositional differentiation (Table 4). Even when plots from the two parks were merged together, the previous observed patters did not change (as expected, however, the mean beta values increased). Interestingly, tests for beta dispersion resulted significant at both the parks and the whole aggregate dataset scales, indicating a substantial difference in plant assemblages occurring in these habitats, independent by the specific area analysed.

The rarefaction curves obtained by the pooled sample of plots classified by the coastal dynamics (Fig. 3) showed no differences between accreting (CD1) and erosive (CD3) sand dune systems. Instead, the curve of stable coastal units (CD2) was the steepest, indicating the highest value of species richness and of compositional heterogeneity. In fact, the curves of CD1 and CD3 were flatter than that of CD2. In both Figs. 2, 3, the SCR curves increased less steeply than the RC curves resulting in lower estimates of species richness at a given extent.

Discussion

In line with existing literature (Acosta et al. 2009; Peyrat and Fichtner 2011; Ciccarelli et al. 2012; Ciccarelli 2014), the total species richness recorded in this study cannot be considered high. In fact, it is well known that in coastal dunes species composition and abundance is reduced by extreme abiotic factors (Ranwell 1972; Roman and Nordstrom 1988; Clark 1977; Hesp 1991; Sykes and Wilson 1991; Maun 1997; Stallins 2002; Stallins and Parker 2003; da Silva et al. 2008; Miller et al. 2010; Ciccarelli et al. 2014).

Both RC and SCR curves calculated for each community type showed an asymptotic pattern (Fig. 2), suggesting that almost all species have been recorded in the study area. This is a good result, because as seen in other

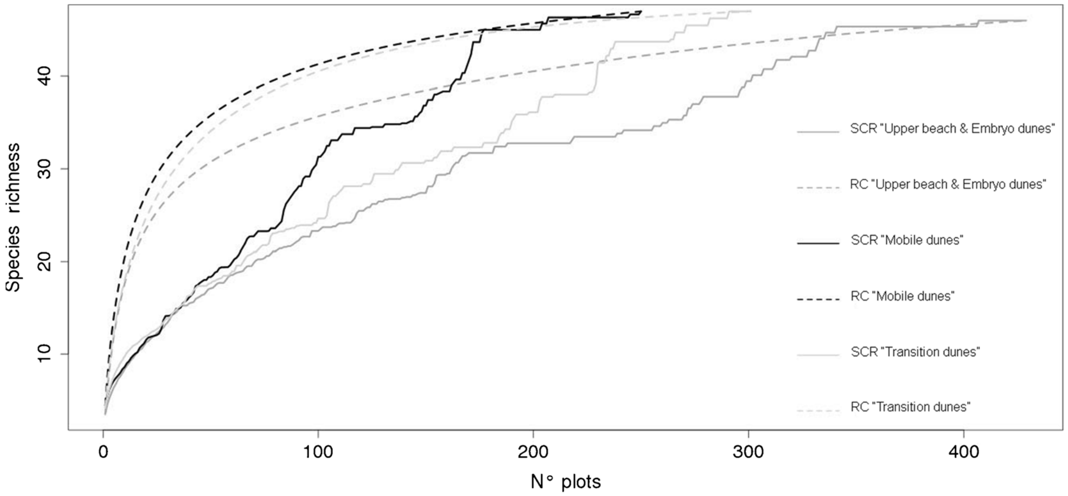

Fig. 2 Plot-based rarefaction curves for the pooled sample of plots classified by plant community type (see Table 1). The SCR curves show a lower amount of accumulated species given the same number of sampled plots, with respect to the traditional exact-based method (RC).

Table 4 Permutational analysis of variance for significant differences in beta diversity between dune habitats in MP (Maremma Park), MSRM (Migliarino – San Rossore - Massaciuccoli Park) and in both parks. The Jaccard dissimilarity for presence/absence data was used for calculating plot-to-plot dissimilarity. *P*-values were obtained by permutation of within-group dissimilarities (999 permutations).

Dataset	Average beta upper beach- embryo dunes	Average beta mobile dunes	Average beta transition dunes	*F* model	*P*-value
MP	0.768	0.612	0.652	580.34	0.001
MSRM	0.711	0.684	0.622	1103.1	0.001
Full dataset	0.784	0.725	0.652	5138	0.001

studies (Chiarucci et al. 2008a,b, 2012; Acosta et al. 2009), the question of ‘sampling effort’ is crucial to quantify species richness in a study area. If underreporting occurred, then many rare and endangered species may not have been recognized, which could have important implications for conservation programmes.

Several studies provided evidence of a correlation between species diversity and the coast-to-inland environmental gradient: Total species richness generally increases as one moves from the annual communities of the upper beach (more unstable habitats) towards the fixed dunes (more stable environments) along the psammophilous sequence (Foster and Tilman 2000; Acosta et al. 2009; Kuiters et al. 2009; Miller et al. 2010; Isermann 2011; Peyrat and Fichtner 2011; Vaz et al. 2013). The present study showed both the lowest values of species richness and pooled number of species for upper beach-embryo dunes confirming the most stressful conditions close to the shoreline. On the other hand, mobile dunes and transition dunes are characterized by higher richness, as already shown by Acosta et al. (2009) for coastal dune systems in central Italy. In particular, the highest frequency of *Solidago litoralis* – the only endemic and threatened species recorded in this study – along mobile dunes can be explained by the preference of this plant to live in association with *Ammophila arenaria* communities that are typical of mobile dunes (Vagge and Biondi 1999). In

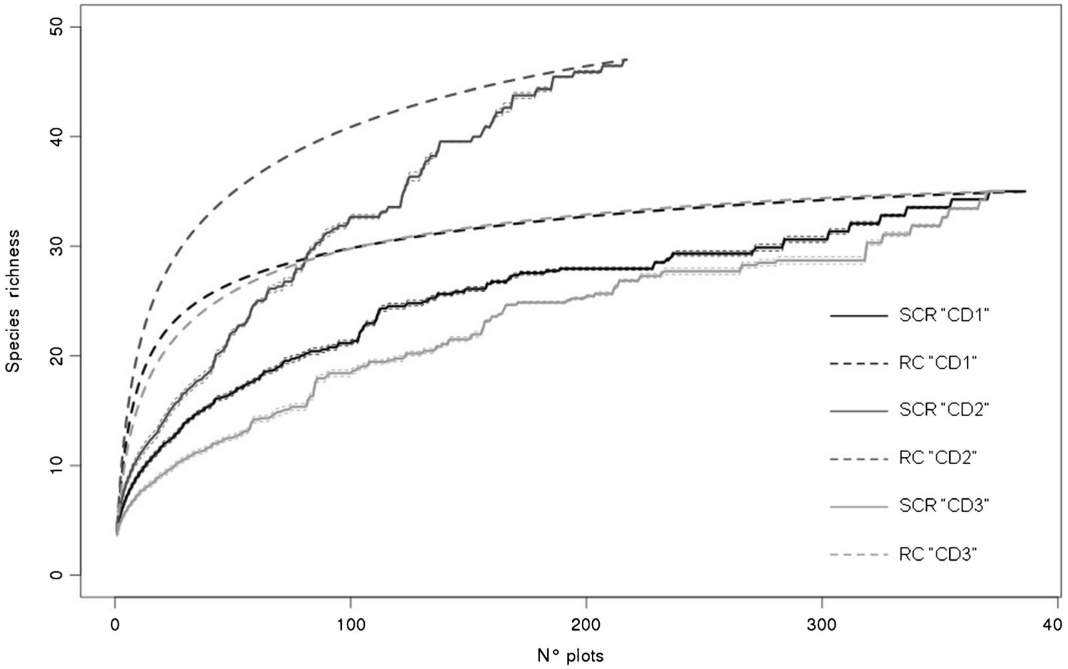

Fig. 3 Plot-based rarefaction curves for the pooled sample of plots classified by the three coastal dynamic types: CD1 (accreting coastline), CD2 (stable coastline) and CD3 (eroding coastline). The SCR curves show a lower amount of accumulated species given the same number of sampled plots, with respect to the traditional exact-based method (RC).

literature it is known that sandy Tuscan coasts are characterized by the presence of three endemics – *Centaurea aplolepa* subsp. *subciliata*, *Limonium etruscum* and *Solidago litoralis* (see Ciccarelli et al. 2014): Only *Solidago litoralis* has been found in our study, because it is distributed along foredunes where transects were placed. Conversely, *C. aplolepa* subsp. *subciliata*, which is present only in MSRM park, has not been recorded because it lives in backdune areas; and *L. etruscum*, a rare endemic taxon occurring in MP park, is typical of humid dune slacks, not included in this study.

Alien species – especially *Xanthium orientale* subsp. *italicum* – seem to prefer upper beach-embryo dunes habitat, where *X. orientale* subsp. *italicum* competes against *Cakile maritima,* which is the native psammophilous species of these environments (EEC 1992). This alien species could take advantage of the local enrichment in organic matter and nitrogen content – caused by natural or human factors – in the pioneer habitats of the foredune zone, which are generally characterized by poor soils. In fact, previous studies performed in the Mediterranean region on coastal sand dunes highlighted the link between soil modifications of poor substrates and alien species invasions (Santoro et al. 2011; Del Vecchio et al. 2013). Future research on this topic would greatly benefit from a comparison between diversity patterns for the different species groups here considered (total, endemic and alien taxa, for an example see Bacaro et al. 2015), as it would allow identifying those species groups that are facilitated, mediated or inhibited by environmental factors (such as disturbance regime, stress gradients) associated with coast coarse scale variation.

When analyzing species rarefaction curves obtained by the plots classified as plant community types (Fig. 2), differences emerged especially between mobile dunes and the other plant assemblages. In particular, when the number of accumulated plots increased, the SCR curve of mobile dunes was the steepest and highest, while the SCR curve of upper beach-embryo dunes was the flattest (Fig. 2). These results suggest that plant communities of upper beach-embryo dunes are characterized by a lower number of species and by a homogeneous species composition within the different coastal sections. By contrast, plant communities of mobile dunes showed a higher species richness whose composition is not always the same, but it depends on the coastal section considered. These results are in accordance with Jiménez-Alfaro et al. (2015), who found that space was the strongest factor influencing metacommunity structure in shifting dunes (identified as habitat 2120 – shifting dunes along the shoreline with *Ammophila arenaria*) across the Iberian coastline.

Interestingly, at the plot level, patterns of beta diversity were substantially different: when pairwise dissimilarities were averaged, in fact, upper beach-embryo dunes showed the highest beta diversity values (for both parks and also for the pooled set of plots, see Table 4). The observed patterns might be explained by the intrinsic nature of these patchily fragmented and very sparse plant communities: On average, smaller sampling units can exhibit (by chance) either higher or lower similarity than the actual similarity characterizing the whole community composition at larger spatial scales, thus introducing a type of stochastic noise (Bacaro et al. 2012c). Generally speaking, smaller sampling units ‘will have only a subset of the possible species and will contain identical species lists only a portion of the time’ (Nekola and White 1999) and will exhibit, on average, higher pairwise dissimilarity. From an ecological perspective, observed patterns express the high environmental heterogeneity that varies dynamically within the coastline area, resulting in a highly differentiated local plant community composition consequently characterized by very diverse structural and functional vegetation types.

As suggested by Honrado et al. (2009), beta diversity may act as reliable indicator of disturbance in foredune vegetation, especially under transgressive dynamics, which characterize dune fields where sand is blowing over vegetated to semi-vegetated terrain (Hesp and Walker 2013). In our study area, the presence of intermediate levels of stress and/or disturbance could promote complex variations of environmental conditions at fine scales (see Lomba et al. 2008; Vaz et al. 2013; Ciccarelli 2015).

Moreover, our research found evidence that species richness was higher in stable coastal dunes than in accreting and erosive dunes (Table 3, Fig. 3). In fact, it is widely accepted that in dunes, sand dynamics (accumulation as well as erosion) creates periodic vegetation disturbances affecting composition variability and succession (Jungerius et al. 1995; Isermann 2011). These results are partially reflected in the findings of Gallego-Fernández and Martínez (2011), who observed that species richness and diversity were significantly lower on accreting foredunes than on stable or erosive foredunes along the Gulf of Mexico. Recently, Honrado et al. (2009) found that under transgressive dynamics, the species *Ammophila arenaria* becomes dominant along the northern coastline of Portugal, not only because of its ability to tolerate deep sand burial (Maun 1997; Levin et al. 2008), but also for the reduction or disappearance of other species. Similarly, Ciccarelli et al. (2012) showed that coastal tracts of the Migliarino-San Rossore-Massaciuccoli Regional Park affected by high levels of erosional processes were characterized by unstable plant communities with the predominance of *Ammophila arenaria*. In this study, the highest mean number of endemics per plot and the highest pooled number of alien species in stable dunes could suggest that shoreline accretion as well as erosional processes may disturb both endemic survival and alien plant invasion. Interestingly, the most frequent alien species found in erosive dunes was *Arundo donax*, which is an invasive tall perennial cane (Arrigoni and Viegi 2011), highly resistant to disturbance.

Finally, regarding the method for calculating species rarefaction curves, we observed a general overestimation of species richness by the traditional way to calculate rarefaction (Figs. **2**, **3**): Observed divergences between classic rarefactions and SCRs represent the manifest effects of the spatial dependence in the distribution of individuals in the space. While RCs are based on too restrictive statistical assumptions (i.e. the spatial distribution of individuals in the environment is random; for a complete list of assumption see also Gotelli and Colwell 2001), their spatially explicit counterparts allow ecologists and conservation biologists to produce curves which compare actual patterns of species richness and composition. Too often rarefaction curves have been used to compare biodiversity between areas in order to plan conservation strategies but, if their spatial component are not explicitly measured, their use could completely reverse the ranking of protected areas based on species richness value obtained by their calculation, leading to an erroneous prioritization of sites. In our analyses, once the spatial autocorrelation in the distribution of data was taken in account, we observed that the MP resulted more diversified than MSMR (see Bacaro et al. 2016 for a specific discussion on this and other examples). From a practical point of view, this example shows how the inclusion of spatial autocorrelation into rarefaction analyses can alter conclusions and eventually even change the way we might prioritize or manage nature reserves. Similar patterns were also observed by Kühn (2007) analysing data on a study that explored the relationship between plant species richness and environmental correlates in Germany: A dramatic change in sign (from positive to negative) effect was observed when a spatial simultaneous linear error model was applied to describe the relationship between the altitudinal gradient and species richness.

Conclusions

The present study highlights that quantitatively comparing the species diversity of different plant communities along the coast-to-inland zonation and of coastal sections affected by different dynamics by using spatial constrained rarefaction techniques is a useful method to assess biodiversity for coastal dune ecosystems. In particular, for a successful biodiversity conservation programme in these coastal ecosystems, it is recommended to preserve all the habitats of the whole coast-to-inland succession because all of them contribute to its functioning. The fact that several plant communities are characterized by a higher beta diversity suggests that conservation programmes need to consider local-scale variability in order to maintain regional diversity. Moreover, it emerges from this study that erosion is an important factor of disturbance that causes the loss of biodiversity. Hence, managers are encouraged to find the most appropriate techniques to protect eroding foredunes. Lastly, we can conclude that it is fundamental to preserve the natural dynamics of these ecosystems in order to maintain their biodiversity and sustain ecosystem services, such as coastal protection (Martínez et al. 2004, 2006; Provoost et al. 2004).

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Appendix 1

Floristic List of the Vascular Species, in Alphabetical Order, Found in All Transects. Information on the Status of Alien Species, Endemic or Red List Species Followed Rossi et al. (2013) and Ciccarelli et al. (2014).

Achillea maritima (L.) Ehrend. & Y.P.Guo subsp. *maritima*

Ammophila arenaria (L.) Link subsp. *australis* (Mabille) Laínz

Anthemis maritima L.

Arundo donax L. [alien species]

Avena sterilis L. s.l.

Briza maxima L.

Bromus sterilis L.

Cakile maritima Scop. subsp. *maritima*

Calystegia soldanella (L.) Roem. & Schult.

Catapodium balearicum (Willk.) H. Scholz

Cerastium ligusticum Viv.

Chamaesyce peplis (L.) Prokh.

Crucianella maritima L.

Cuscuta scandens Brot. subsp. *cesattiana* (Bertol.) Greuter & Burdet [alien species]

Cutandia maritima (L.) Barbey

Cynodon dactylon (L.) Pers.

Daphne gnidium L.

Dittrichia viscosa (L.) Greuter s.l.

Echinophora spinosa L.

Elaeagnus angustifolia L. [alien species]

Elymus farctus (Viv.) Runemark ex Melderis subsp. *farctus*

Erigeron canadensis L. [alien species]

Eryngium maritimum L.

Euphorbia paralias L.

Helichrysum stoechas (L.) Moench

Hypochaeris radicata L.

Juniperus oxycedrus L. subsp. *macrocarpa* (Sibth. & Sm.) Neilr.

Lagurus ovatus L. s.l.

Limbarda crithmoides (L.) Dumort. s.l.

Lolium rigidum Gaudin s.l.

Lotus hirsutus L.

Matthiola sinuata (L.) R. Br.

Medicago littoralis Loisel.

M. marina L.

Odontites luteus (L.) Clairv.

Oenothera biennis L. [alien species]

Ononis variegata L.

Pancratium maritimum L.

Parapholis incurva (L.) C.E. Hubb.

Phleum arenarium L. subsp. *caesium* H. Scholz

Pinus pinaster Aiton s.l. [dubitative alien species]

Plantago coronopus L. subsp. *coronopus*

P. arenaria Waldst. & Kit.

Polygonum maritimum L.

Pseudorlaya pumila (L.) Grande

Pycnocomon rutifolium (Vahl) Hoffmanns. & Link

Raphanus raphanistrum L. s.l.

Reichardia picroides (L.) Roth

Rubia peregrina L.

Salsola kali L.

Seseli tortuosum L.

Silene canescens Ten.

S. niceensis All.

S. otites (L.) Wibel s.l.

Smilax aspera L.

Solidago litoralis Savi [endemic, status EN]

Spartina versicolor Fabre

Sporobolus virginicus Kunth

Tamarix gallica L.

Teucrium polium L. subsp. *polium*

Verbascum sinuatum L.

Vulpia fasciculata (Forssk.) Fritsch

Xanthium orientale L. subsp. *italicum* (Moretti) Greuter [alien species]

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