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Spatial patterns of coastal dune plant diversity reveal conservation priority hotspots in and out a network of protected areas

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ABSTRACT

Effective conservation planning requires identifying priority hotspots to allocate resources. To preserve biodiversity, it is crucial to consider α , β and γ -diversity and protect the irreplaceable sites with high ecological uniqueness, which can host uncommon species assemblages that would be lost if only species-rich sites were protected. Coastal dunes, hosting highly specialized plant communities, are among the most threatened ecosystems worldwide. In this study, we identified conservation priority hotspots to assess the effectiveness of the network of protected areas in coastal dunes of Tuscany (central Italy), using data on plant communities collected in 506 plots. We additively partitioned γ -diversity in its α and β components, observing a significant variation at all spatial levels only for dune species. In terms of α -diversity, we found that Northern protected sites were richer in dune species, while synanthropic and alien species were equally present inside and outside protected areas of the region. By partitioning the total β -diversity into its components (replacement and richness difference), we found a prevalence of replacement for dune species, indicating the most unique sites as the ones to favor for conservation. Unique sites were identified through Local Contributions to Beta Diversity and their conservation value was determined by their species composition and the relationship with landscape variables. Unique sites with high conservation value were only partly protected, while some protected sites were altered and required restoration. Our approach proved effective for identifying the most unique

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sites, indicating some issues in the existing protected network, while providing valuable information on sites to prioritize for future conservation actions.

1. Introduction

Identifying conservation priority hotspots is fundamental for the maintenance of biodiversity in an era of unprecedented global biodiversity decline (Pimm et al., 2014). The definition of priorities allows to allocate the limited resources available in the most effective way and is a key component of systematic conservation planning (Margules and Pressey, 2000), the most influential paradigm in conservation (Kukkala and Moilanen, 2013), which overcomes the opportunistic approaches that in the past led to uneven representations of natural features (Pressey et al., 1996). However, multiple priority criteria can be adopted and can lead to different results (Dubois et al., 2020; Belote et al., 2021).

Biodiversity can be measured at different spatial scales: α -diversity is the variation at the local scale within a community, γ -diversity is the overall variation at the regional scale, while β -diversity is the variation among communities within a region (Whittaker, 1960, 1972). Effective conservation strategies should extend beyond the conventional methodologies centered on prioritizing biodiversity hotspots characterized by elevated species richness (α -diversity). As elucidated by Socolar et al. (2016), it becomes imperative to embrace the guiding principle of complementarity for the preservation of diversity at the regional scale: to prioritize sites with complementary species compositions, a concept related to β -diversity. Hotspots of species richness, indeed, do not necessarily host species with conservation priorities (Orme et al., 2005), while some species-poor areas host species with high conservation value (Harper et al., 2022). However, a certain degree of redundancy in the protected network is also necessary for the persistence of biodiversity over time, to maintain species even in case of local extinctions (Walker, 1995).

The analysis of β -diversity allows to understand the phenomena generating the patterns of diversity and has significant implications in conservation planning (Legendre, 2014). Following the approach developed by Legendre and De Cáceres (2013), the total β -diversity of a region can be estimated as the total variance of the community data and can be partitioned into two components, namely species replacement and richness difference, which are respectively described as the substitution of species in one site by different species in another site, and the loss of species from one site to another. From the relative importance of the two components in a region, indications for conservation planning can be derived: in landscapes where richness difference is the dominant component of β -diversity, it is preferable to prioritize the most species-rich sites, while in the other case it is better to prioritize the most unique ones (Socolar et al., 2016). The most ecologically unique sites in a region can be identified by computing the Local Contributions to Beta Diversity (LCBD; Legendre and De Cáceres, 2013), and this approach has been recently adopted by some authors to select priority sites for conservation, mainly for animals in freshwater habitats (Hill et al., 2021; Iacarella, 2022), but to a lesser extent also for plant communities, in wetlands (Dubois et al., 2020), lakes (Heino et al., 2022), forests (Tan et al., 2019), high-latitude ecosystems (Niskanen et al., 2017), and agroecosystems (Fanfarillo et al., 2023). Understanding the drivers of site uniqueness is important to plan conservation actions. However, the same drivers can affect site uniqueness in different ways according to which ecosystem is studied and to which taxonomic group is used to compute LCBDs. For instance, local environmental variables effectively explained the variation in site ecological uniqueness using plant communities in forests (Tan et al., 2019; Yao et al., 2021) and bird communities in agroecosystems (García-Navas et al., 2022) but they were weak predictors of LCBD variation using insect communities in streams (Heino and Grönroos, 2017).

Coastal sand dunes are ecosystems of high conservation value (Acosta et al., 2009), located on the narrow band at the interface between land and sea, where a strong environmental gradient determines the presence of unique plant communities (Torca et al., 2019; Tordoni et al., 2019, 2021). Coastal dunes support highly specialized plant species, which are often rare or endangered (Acosta et al., 2009), and provide fundamental ecosystem services (Drius et al., 2019), including coastal defense (Arkema et al., 2013), carbon storage (Drius et al., 2016), and recreation (Everard et al., 2010). However, they are nowadays among the most threatened ecosystems in Europe, due to the impacts of urbanization, touristic pressure, spread of invasive alien species and coastal erosion (Janssen et al., 2016). In Italy, 88 % of coastal sand dunes habitats are in a bad conservation status, while the remaining 12 % is in inadequate conditions, and the trend is deteriorating for almost 70 % of them (Prisco et al., 2020).

Protected areas are essential tools for the maintenance of biodiversity, but their efficacy in terms of habitat and species conservation is being questioned (Watson et al., 2016). A protected area should meet two objectives: representativeness, as it should represent the full variety of biodiversity, and persistence, as it should promote the long-term survival of biodiversity (Margules and Pressey, 2000), which will be increasingly jeopardized by the effects of climate changes (Bellard et al., 2012).

In Italy, the network of protected areas along sandy coasts has been described as fairly representative of the current distribution of dune habitats, and its efficacy has been predicted to drop in the near future due to climate change, especially for the most vulnerable habitats in mobile and fixed dunes (Prisco et al., 2013). Moreover, in a recent resurvey of the coastal dunes of central Italy, the protection status showed no positive effect on habitat loss or trends of focal and alien species over a period of 10 years (Sperandii et al., 2020). However, knowledge about the role of protected areas at the Italian level is fragmented (Prisco et al., 2012), and recent studies found substantial differences in the conservation status of dune ecosystems within the protected areas of southern Tuscany (Landi et al., 2012; Sarmati et al., 2019; Bonari et al., 2021).

To assess the role of protected areas in conservation, a common approach is to compare biodiversity inside and outside protected areas (Gray et al., 2016). In coastal dunes, however, the conservation value is not necessarily related to species richness: species richness varies along the coastal zonation and even species-poor habitats can host endangered or rare elements (Acosta et al., 2009).

Moreover, plant richness and cover tend to be highest in sites with medium disturbance, as was observed in a recent study in Sardinian dunes (Pinna et al., 2019). Thus, in these ecosystems β -diversity could be a more useful criterion for the prioritization of conservation. However, the approach based on β -diversity and LCBD has never been applied on coastal dune plant communities to identify conservation priorities.

As pointed out by several authors, a complete understanding of the conservation status of coastal dunes can only be obtained if the identify of species is taken into account and different groups of species are analyzed separately, in addition to the overall pool (Del Vecchio et al., 2016; Prisco et al., 2016). In particular, dune species, which are stenocious species often restricted to a specific zone of the dune (Angiolini et al., 2018), can serve as indicators of good conservation status (Santoro et al., 2012a). On the other hand, synanthropic species, which are generally favored by anthropic disturbance, are generalist species that do not perform the same functions of dune species, and thus can indicate a degradation of the dune systems (Biondi et al., 2012). Similarly, alien species can directly affect dune habitats through modifications of soil properties (Novoa et al., 2013) and functional homogenization (Tordoni et al., 2019).

The aim of this study is to identify conservation priority areas and to assess the effectiveness of the existing network of protected areas in coastal dune ecosystems of Tuscany (central Italy). Specifically, we will analyze a large set of coastal dune vegetation data collected in the region, with the following main objectives: i) analyze the spatial patterns of regional plant community diversity in coastal dunes to identify conservation priority sites; ii) assess the effectiveness of the existing network of protected areas through the distribution of conservation priority hotspots. These steps are of fundamental importance to search new areas to reach the objectives of the 2030 European Strategy of Biodiversity that plans to arrive at the 30 % of protected territory in each country (European Commission, 2020).

2. Methods

2.1. Study area

The study was carried out along the c. 200 km of sandy coasts of Tuscany (central Italy). The climate is Mediterranean, with upper meso-mediterranean thermotype and ombrotype ranging from lower humid in the North to upper dry in the South (Pesaresi et al., 2017). In this region, coastal dunes are composed of Late Quaternary sand (Carmignani et al., 2013) and generally occupy a narrow stripe, with a maximum extent of 300 m and a height < 10 m (Bertacchi, 2017). Different plant communities usually occur along a well-defined zonation, typical of coastal dune systems, ranging from the annual vegetation of drift lines, through embryonic shifting dunes, to white dunes, stable dune grasslands, coastal dune scrubs, and coastal dune woods (Acosta et al., 2007). The anthropic pressure is uneven in the region: the Northern part is highly frequented by tourists and urbanized, while the Southern part is generally better preserved (Ciccarelli et al., 2014). The study area includes different protected areas, which are partly overlapping (Fig. 1). In particular, there are eight Special Areas for Conservation (SACs) included in the Natura 2000 network, namely “Dune Litoranee di Torre del Lago” (IT5170001, 43.828611 N, 10.253889E), “Selva Pisana” (IT5170002, 43.710278 N, 10.306389E), “Padule di Bolgheri” (IT5160004, 43.224167 N, 10.544722E), “Tombolo da Castiglione della Pescaia a Marina di Grosseto” (IT51A0012, 42.743611 N, 10.942222E), “Dune costiere del Parco dell’Uccellina” (IT51A0015, 42.636100 N, 11.073600E), “Pineta Granducale

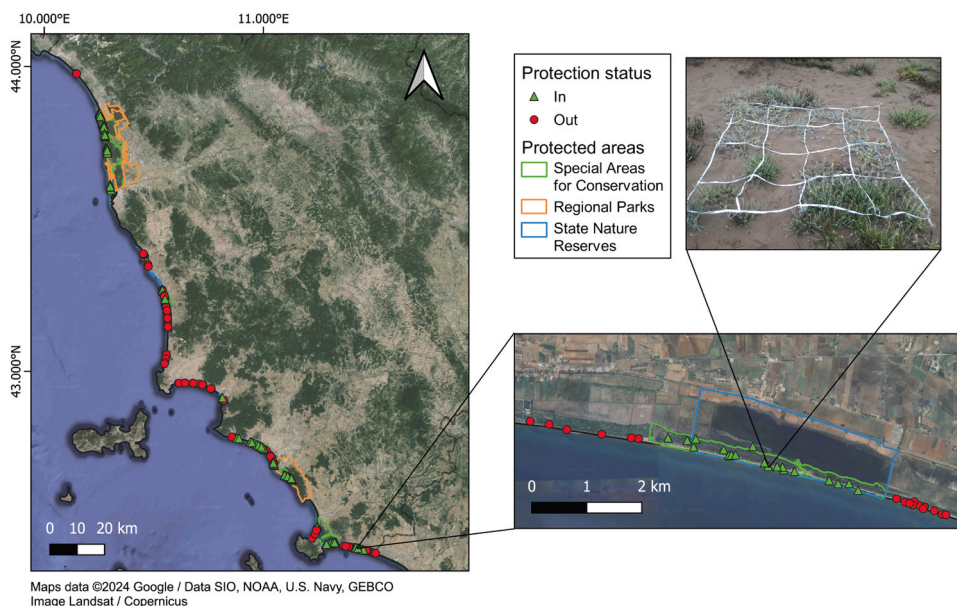


Fig. 1. Location of the surveyed sites in the study area. Image source: Google Earth 2024.

dell'Uccellina" (IT51A0014, 42.653600 N, 11.048300E), "Laguna di Orbetello" (IT51A0026, 42.459722 N, 11.222500E), and "Duna del Lago di Burano" (IT51A0032, 42.398056 N, 11.372222E). Moreover, there are two Regional Parks (the Migliarino-San Rossore-Massaciuccoli Park - provinces of Pisa and Lucca, and the Maremma Park - province of Grosseto), which partly include some SACs within their boundaries, and three State Nature Reserves: "Tombolo di Cecina", "Tomboli di Follonica e Scarlino", and "Duna Feniglia".

2.2. Sampling design and data collection

Vegetation data were collected between 2018 and 2021 according to a stratified random sampling design. Two bands were mapped along the Tuscan coast: band AB, including shifting dunes (EUNIS habitat N14; Chytrý et al., 2020) and stable dune grasslands (EUNIS habitat N16), that could not be separated as they occurred in a fine-grained mosaic, and band C, corresponding to coastal dune scrub (EUNIS habitat N1B). For each band, a number of squared plots of 4 m² proportional to the surface was randomly launched (c. 0.7 plots/ha). Ad hoc plots were added on the field to cover the community of sand beach drift lines (EUNIS habitat N12), for a total of 506 plots (Table 1). In each plot, vascular plant species occurrence and abundance (% cover) were recorded. Nomenclature follows the Portal to the Flora of Italy (2023). Plant species were then classified into three classes according to FloraVeg.EU database (www.floraveg.eu): dune species (i.e., occurring in the broad habitat "Coastal beach, dune or shingle"), synanthropic, and alien species.

2.3. Landscape metrics

To obtain a set of landscape metrics to use for assessing what drives the ecological uniqueness of the communities, a landcover map was produced by photointerpretation of 20 cm resolution orthophotos (GEOSCOPIO, 2022). A total of 11 landcover classes were mapped based on the CORINE Land Cover nomenclature extended to the fourth level of detail: (1) artificial areas (including urban fabrics, industrial units, roads); (2) beach resort facilities and camping; (3) agricultural areas; (4) afforestation (coniferous reforestation with *Pinus* spp.); (5) mixed coniferous-broadleaved forests; (6) Mediterranean maquis (woody dune vegetation); (7) semi-natural woody vegetation (bushy vegetation with scattered trees represented by foredune woodland degradation or forest regeneration/recolonization); (8) semi-natural herbaceous vegetation (grasslands and meadows); (9) open sand (beach pioneer vegetation); (10) herbaceous dune vegetation; (11) wetlands. Note that two of these classes correspond to the bands used for vegetation sampling: herbaceous dune vegetation (EUNIS habitat N14 and N16) and woody dune vegetation (EUNIS habitat N1B). Around each plot, a rectangular buffer of 300 m x 50 m, orthogonal to the coastline, was generated as in Malavasi et al. (2018). For each rectangular buffer, a set of landscape metrics was computed: proportion of artificial landcover (%ART), proportion of bathing facilities (%ARV), proportion of agricultural land (%AGR), proportion of coastal wetlands (%WTC), minimum distance to the centroid of an artificial patch (distART), minimum distance to the centroid of a bathing facility (distARV), Shannon index of diversity of landcover types (LandShan), distance to the shoreline, dune width. Moreover, slope was measured for each plot in the field. Landscape metrics were computed using QGIS 3.28.7 software (QGIS Development Team, 2022) and the R package landscapemetrics (Hesselbarth et al., 2019).

2.4. Statistical analyses

To account for the different levels of anthropic pressure present in the region, the analysis was conducted independently for the Northern and Southern sites. The promontory of Piombino, situated midway along the coast of Tuscany, was delineated as the demarcation point.

For each plot the value of species richness was computed, and differences in mean species richness between protected and non-protected areas were assessed through a Wilcoxon test, considering first the complete set of species and then the individual species groups (dune, synanthropic, alien) separately.

The total β -diversity of the region was computed as the total variance of the community data matrix, which can reach a maximum value of 1 (Legendre and De Cáceres, 2013), and it was partitioned into its two components, replacement and richness difference (Legendre, 2014), both for the complete set of species and for the individual groups, using *beta.div.comp* function in the R package adespatial (Dray et al., 2023). The significance of the three β -diversity components (Total β -diversity, Richness difference, and Replacement) was tested against a null model based on 1000 simulations. This model was obtained through non-sequential swapping and shuffling of the real data matrix to preserve fill, column and row frequencies, as well as either row or column sums. The *commsim* function (*swsh_samp* method) from the R package vegan (Oksanen et al., 2022) was utilized for this purpose. p-values were then calculated under the null hypothesis of no difference between the observed β -diversity component value and values obtained randomly.

Table 1
Number of surveyed plots for each zone of the region inside and outside protected areas.

Zone	Protection status	Surface (ha)	N° plots
North	In	284.48	202
	Out	134.28	97
South	In	195.43	127
	Out	112.99	80

To get a deeper insight into the role of single sites in regional diversity, subsequent analyses have focused on the complete set of species. The Local Contributions to Beta Diversity (LCBD) were computed for each site and were tested for significance by 999 random permutations, while Species Contributions to Beta Diversity (SCBD) were computed for each species, using *beta.div* function in the R package *adespatial* (Dray et al., 2023). The relationship of LCBD with landscape variables was investigated through a beta regression, which is a modelling tool suitable for variables that assume values between 0 and 1, using the R package *betareg* (Cribari-Neto and Zeileis, 2010). We used beta regression with logit link function to model the relation between LCBD (response variable) and landscape metrics (predictors). Correlation among predictors was checked through Spearman's correlation, and a subset of landscape variables was selected through a forward selection procedure, using function *forward.sel* in the R package *adespatial* (Dray et al., 2023). This function performs a forward selection by permutation of residuals under reduced model, which stops when either the selected variables reach a set value (number of rows – 1 by default), the R^2 or the adjusted- R^2 of the model exceed a threshold (0.99 by default), the p-value of a variable is higher than alpha (0.05 by default), or the difference in model R^2 with the previous step is lower than a threshold (0.001 by default; Dray et al., 2023). Through this procedure, we selected three variables as predictors for the beta regression: distance from the sea, slope, and distance from artificial surfaces. The variation explained by the beta regression model is measured through the pseudo- R^2 , which assumes values between 0 and 1, and is defined as the squared correlation coefficient between the linear predictor and the link-transformed response (Cribari-Neto and Zeileis, 2010).

To understand the reasons why sites with significant LCBD (i.e., unique sites) were different from the others, we analyzed the species composition of sites with significantly different LCBD values through a Nonmetric Multidimensional Scaling (NMDS), based on a Bray-Curtis similarity matrix derived from log-transformed species abundances. Landscape variables having a significant correlation with NMDS axes were overlaid to the ordination plot using the *envfit* function in the R package *vegan* (Oksanen et al., 2022). A NMDS with all sites was also performed to understand the difference in species composition between the significant LCBD sites and the others (Supplementary Materials, Fig. S2).

The total γ -diversity of the region was partitioned across the spatial scales of analysis following the additive partitioning approach (Lande, 1996; Gering et al., 2003; Crist et al., 2003), taking into account first the complete set of species and then the individual groups of species. The levels considered were: diversity within plot (α_{plot}), between plots (β_{plot}), between localities (β_{site}), and between zones of the region ($\beta_{\text{North/South}}$). The significance of each level was tested by 999 permutations, using the function *adipart* in the R package *vegan* (Oksanen et al., 2022).

All analyses were performed using R 4.3.0 (R Core Team, 2023).

3. Results

A total of 192 plant species were found in the study area, of which 73 were classified as dune species, 56 as synanthropic and 14 as alien. The most frequent species were *Thinopyrum junceum* (occurring in 42.68 % of the plots), *Juniperus macrocarpa* (34.78 %) and *Helichrysum stoechas* (34.38 %), which are all dune species. Among synanthropic species, the most frequent were *Cerastium glomeratum* (12.25 %), *Anisantha sterilis* (3.75 %) and *Dittrichia viscosa* (3.75 %), while the most frequent alien species were *Xanthium orientale* (11.66 %), *Oenothera* sp. (3.75 %) and *Ambrosia psilostachya* (2.37 %).

Species richness was significantly higher inside protected areas than outside only in the Northern part of the region (Fig. 2). In particular, this pattern emerged for the whole set of species and for the dune species group, while no significant differences were found for the other groups.

The total β -diversity in the region was 0.47. For the whole set of species and for the dune species group, the replacement was more

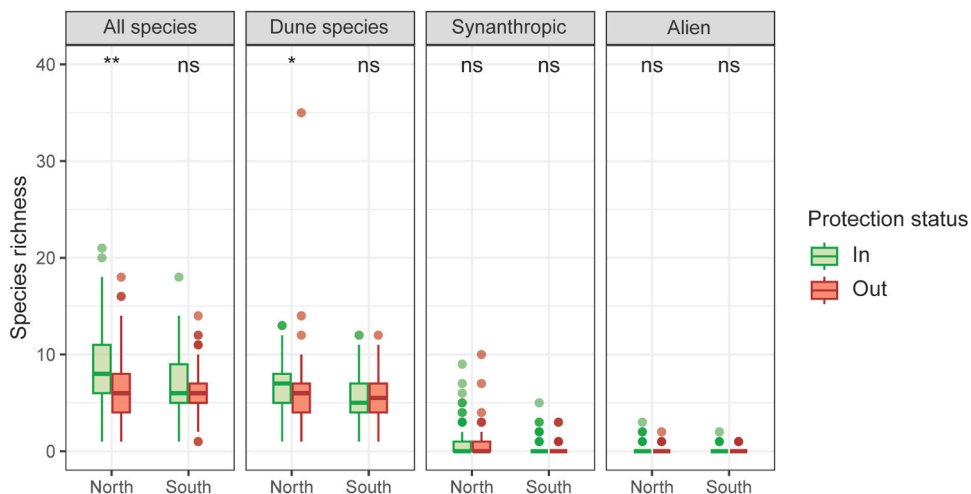


Fig. 2. Values of species richness inside and outside of protected areas. Mean values were compared with a Wilcoxon test (** $p < 0.01$; * $p < 0.05$; ns = non-significant).

important than the other β -diversity component ($> 50\%$), while for synanthropic and alien species the richness difference was prevalent ($> 85\%$). Protected and non-protected areas showed a similar pattern, while Northern and Southern sites differed only in terms of total β -diversity of synanthropic species, which was higher in the North (Fig. 3).

Through the analysis of LCBD, a total of 42 sites with a significant contribution to the β -diversity of the region were highlighted, of which 30 were located inside protected areas (Fig. 4). Generally, highest LCBD values were given by plots with low species richness (LCBD vs. species richness: Spearman's $\text{cor} = -0.45$, $p < 0.05$) mostly located in the herbaceous band. The landscape variables computed to assess the relation with LCBD are reported in Table 2. The beta regression explained a low proportion of the variation of LCBD (pseudo- $R^2 = 0.15$), but revealed a significant negative relation of LCBD with the distance from the shoreline and the slope, and a positive relation with the distance to artificial surfaces (Table 3).

The NMDS ordination of the sites with significant LCBD (Fig. 5; stress = 0.04) showed that species composition in these sites mainly vary along the sea-inland gradient, represented by the first axis of the ordination, ranging from sites with salt-tolerant species of the drift lines on the right (e.g. *Cakile maritima*, *Salsola tragus*, *Convolvulus soldanella*), to sites with scrub species on the left (e.g. *Pistacia lentiscus*, *Smilax aspera*, *Juniperus turbinata*). The second gradient in species composition is a gradient of anthropic disturbance: in the lower portion of the ordination plot, where there is a higher proportion of artificial surface, sites are richer in synanthropic species (e.g. *Papaver rhoeas*, *Avena barbata*, *Anisantha sterilis*). The analysis of differences in LCBD between the North and the South of the region gave only slightly different results, which are reported in Supplementary Materials (Fig. S3).

Values of SCBD are reported in Table 4. The species with the highest contributions to β -diversity were *Juniperus macrocarpa* (0.14), *Calamagrostis arenaria* subsp. *arundinacea* (0.09) and *Thinopyrum junceum* (0.06), which were also among the most frequent ones (SCBD vs. species frequency: Spearman's $\text{cor} = 0.89$, $p < 0.05$). Similar results were also obtained when the analysis was performed separately for Northern and Southern sites (highest SCBD in the North: *J. macrocarpa* 0.16, *C. arenaria* subsp. *arundinacea* 0.10, *Pancratium maritimum* 0.06; in the South: *J. macrocarpa* 0.14, *C. arenaria* subsp. *arundinacea* 0.08, *T. junceum* 0.07).

Finally, the results of the additive partitioning of γ -diversity are represented in Fig. 6: for dune species, all levels of analysis are significant, while for synanthropic and alien species only the plot level is significant.

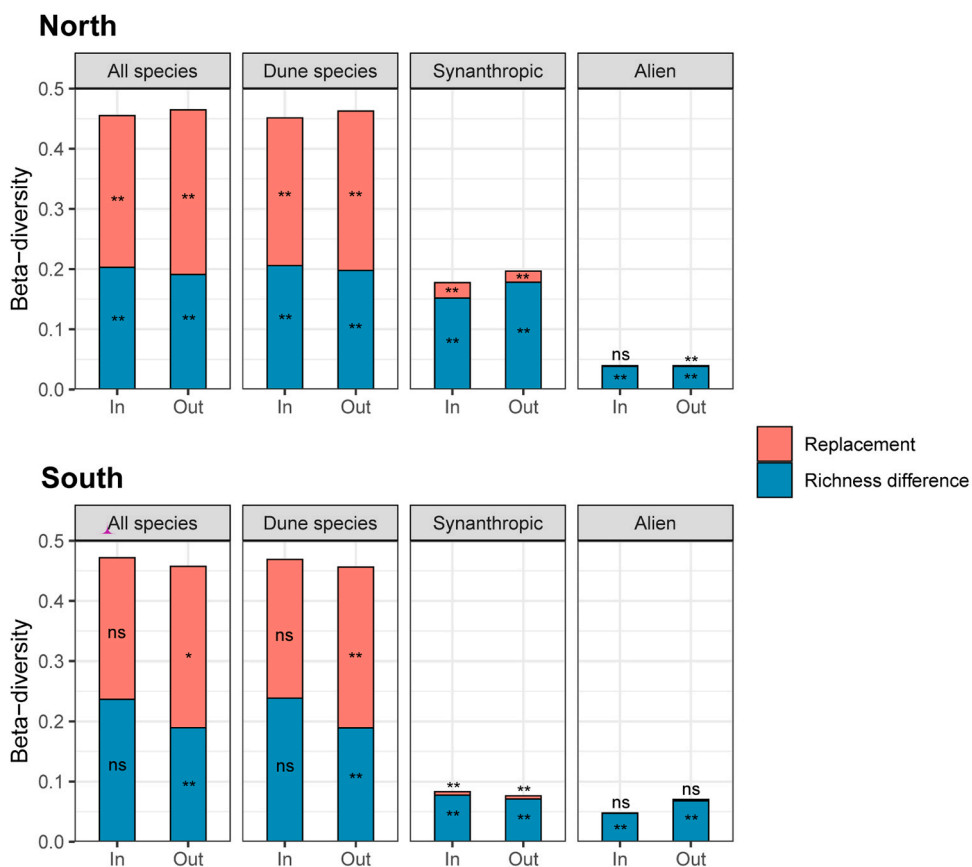


Fig. 3. Partitioning of total β -diversity into replacement and richness difference, computed for the North (a) and South (b) of Tuscany, considering all species together and the single groups of species separately, and distinguishing sites inside and outside protected areas. Significance of β -diversity components was tested against a null model (** $p < 0.01$; * $p < 0.05$; ns = non-significant).



Fig. 4. Local Contributions to Beta Diversity for the plots in the study area, calculated considering all species together. Only the 42 plots with significant LCBD value ($p < 0.05$) are shown, of which 30 are located inside protected areas and 12 outside. Image source: Google Earth 2024.

Table 2

Summary statistics of the environmental and landscape variables computed for each plot.

Variable	Mean	Min-Max	SD
Sea distance (m)	93.19	5.91–398.64	71.28
Dune width (m)	120.74	2.81–467.31	82.38
Slope (%)	2.94	0.00–25.00	7.90
Proportion of artificial landcover (%ART)	0.35	0.00–32.75	2.47
Proportion of bathing facilities (%ARV)	0.11	0.00–28.23	1.37
Proportion of agricultural land (%AGR)	0.32	0.00–36.32	2.39
Proportion of coastal wetlands (%WTC)	0.22	0.00–25.75	1.87
Distance to artificial landcover (m)	221.90	0.00–4143.70	468.17
Landscape Shannon	1.16	0.00–1.97	0.32

Table 3

Results of beta regression analysis of LCBD with landscape variables (pseudo- $R^2 = 0.15$).

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-6.17	0.01	-570.26	< 0.01
Sea distance	-0.01	0.01	-7.51	< 0.01
Slope	-0.01	0.01	-3.75	< 0.01
Distance to artificial landcover	0.01	0.01	4.08	< 0.01

4. Discussion

Our approach has proved effective for identifying the most unique sites on a regional scale relying on the analysis of β -diversity (Dubois et al., 2020; Hill et al., 2021; Heino et al., 2022). By analyzing species composition and exploring the relationship between community uniqueness and landscape variables, we were able to distinguish sites with a high conservation value and prioritize them for protection. Moreover, analyzing the patterns of α -diversity and β -diversity at the different scales, with different groups of species separately, we got a valuable insight on the distribution of dune plant diversity with respect to protected areas, contributing to the assessment of their efficacy in the conservation of coastal dunes of Tuscany.

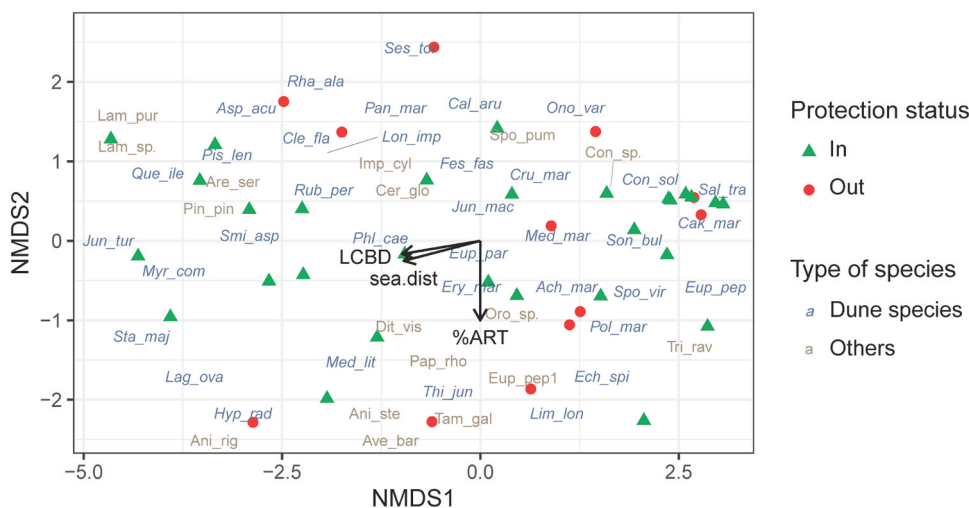


Fig. 5. Output of NMDS ordination, derived from Bray-Curtis similarity matrix based on log-transformed species abundances, for the plots with significant LCBD values (stress = 0.04). Species names (reported in Table S1) were abbreviated as follows: *Achillea maritima* (Ach_mar), *Anisantha rigida* (Ani_rig), *Anisantha sterilis* (Ani_ste), *Arenaria serpyllifolia* (Are_ser), *Asparagus acutifolius* (Asp_acu), *Avena barbata* (Ave_bar), *Cakile maritima* (Cak_mar), *Calamagrostis arenaria* subsp. *arundinacea* (Cal_aru), *Cerastium glomeratum* (Cer_glo), *Clematis flammula* (Cle_fla), *Convolvulus soldanella* (Con_sol), *Convolvulus* sp. (Con_sp.), *Crucianella maritima* (Cru_mar), *Dittrichia viscosa* (Dit_vis), *Echinophora spinosa* (Ech_spi), *Eryngium maritimum* (Ery_mar), *Euphorbia paralias* (Eup_par), *Euphorbia peplis* (Eup_pep), *Euphorbia pepus* (Eup_pep1), *Festuca fasciculata* (Fes_fas), *Hypochaeris radicata* (Hyp_rad), *Imperata cylindrica* (Imp_cyl), *Juniperus macrocarpa* (Jun_mac), *Juniperus turbinata* (Jun_tur), *Lagurus ovatus* (Lag_ova), *Lamium purpureum* (Lam_pur), *Lamium* sp. (Lam_sp.), *Limbarda crithmoides* subsp. *longifolia* (Lim_lon), *Lonicera implexa* (Lon_imp), *Medicago littoralis* (Med_lit), *Medicago marina* (Med_mar), *Myrtus communis* (Myr_com), *Ononis variegata* (Ono_var), *Orobancha* sp. (Oro_sp.), *Pancreatium maritimum* (Pan_mar), *Papaver rhoeas* (Pap_rho), *Phleum arenarium* subsp. *caesium* (Phl_cae), *Pinus pinea* (Pin_pin), *Pistacia lentiscus* (Pis_len), *Polygonum maritimum* (Pol_mar), *Quercus ilex* (Que_ile), *Rhamnus alaternus* (Rha_ala), *Rubia peregrina* (Rub_per), *Salsola tragus* (Sal_tra), *Seseli tortuosum* (Ses_tor), *Smilax aspera* (Smi_asp), *Sonchus bulbosus* (Son_bul), *Sporobolus pumilus* (Spo_pum), *Sporobolus virginicus* (Spo_vir), *Stachys major* (Sta_maj), *Tamarix gallica* (Tam_gal), *Thinopyrum junceum* (Thi_jun), *Trifolium ravennae* (Tri_rav). Landscape variables having a significant correlation with NMDS axes, namely sea distance (sea.dist) and proportion of artificial landcover (%ART), along with LCBD, were overlaid to the ordination plot.

In terms of species richness, in the North of the region protected sites are richer in dune species than non-protected ones, while in the South the two areas show similar data. Touristic and recreational activities, indeed, are particularly intense in the North, and are known to cause a reduction of species richness in coastal dunes, especially where there is no protection (Santoro et al., 2012b; Prisco et al., 2021).

Remarkably, the richness of synanthropic and alien species inside and outside protected areas is similar. The synanthropic species tend to be more resistant to human-induced alterations than dune plants, and in some cases they increase in altered sites occupying gaps unexploited by dune species (Del Vecchio et al., 2015). The absence of a positive effect of anthropic disturbance on the species richness of synanthropic and alien species could be due to the extreme abiotic conditions of the coastal environment that limit non-specialized species, as observed in other studies (Carboni et al., 2010; Malavasi et al., 2016). Moreover, this result suggests that protection measures do not stop the entrance of species related to anthropic disturbance in protected areas. Protected areas, indeed, are connected to their surroundings by multiple ecological processes (Hansen and DeFries, 2007; Holenstein et al., 2021). In coastal dunes, the surroundings can act as an introduction source for synanthropic species (Carboni et al., 2011; Bazzichetto et al., 2018), and coastal dunes are indeed particularly prone to invasions (Lozano et al., 2023). Thus, for conservation it is crucial to manage these ecosystems as a whole, paying attention also to the surrounding landscape (Cox and Underwood, 2011).

Nonetheless, the total number of alien species found in Tuscany is low, in line with other studies (Ciccarelli et al., 2014), and notably, some of the most widespread and harmful invasive species, as *Carpobrotus* spp. (Carboni et al., 2010), were not found in the surveyed plots.

The analysis of β -diversity can provide deeper information on the processes structuring plant communities (Legendre and Cáceres, 2013). In this study, different patterns emerge according to the group of species under investigation, independently of the protection status of the areas. For dune species, the most important component of β -diversity is the replacement. This result can be explained as the gain and loss of species occurring among the different habitats of dune ecosystems (Legendre, 2014). Dune species generally have narrow ecological ranges and particular ecophysiological adaptations (Angiolini et al., 2018). On the contrary, the dominant component of β -diversity of synanthropic and alien species is richness difference, suggesting that there is a limited pool of these species and that the differences among sites are mainly determined by the loss of species, as was found also in other studies (e.g. Tordoni et al., 2018).

The spatially hierarchical partitioning of γ -diversity points out a similar situation: the diversity of dune species is significant at all levels, indicating that there are ecological processes shaping this community at different scales. On the other hand, for synanthropic and alien species, only the plot level is significant, suggesting that their species pool is limited, and β -diversity can be captured just by

Table 4

Species Contributions to Beta Diversity (SCBD) and species frequencies (%) in the Tuscany dataset, and SCBD values computed separately for the Northern and Southern parts of the region. The species are ordered according to decreasing SCBD values and only the species with SCBD values higher than the mean are reported.

Species	SCBD	Frequency (%)	SCBD (North)	SCBD (South)
<i>Juniperus macrocarpa</i>	0.14	34.78	0.16	0.14
<i>Calamagrostis arenaria</i> subsp. <i>arundinacea</i>	0.09	22.33	0.10	0.08
<i>Thinopyrum junceum</i>	0.06	42.69	0.06	0.07
<i>Helichrysum stoechas</i>	0.05	34.39	0.05	0.06
<i>Pancratium maritimum</i>	0.05	25.30	0.06	0.02
<i>Cakile maritima</i>	0.04	16.80	0.01	0.07
<i>Eryngium maritimum</i>	0.04	18.18	0.05	0.02
<i>Anthemis maritima</i>	0.03	15.02	0.01	0.06
<i>Euphorbia paralias</i>	0.03	20.55	0.04	0.01
<i>Festuca fasciculata</i>	0.03	32.21	0.03	0.01
<i>Echinophora spinosa</i>	0.03	19.96	0.03	0.02
<i>Medicago marina</i>	0.02	10.87	0.01	0.04
<i>Achillea maritima</i>	0.02	4.74	0.01	0.03
<i>Medicago littoralis</i>	0.02	32.41	0.03	0.01
<i>Seseli tortuosum</i>	0.02	18.97	0.03	0.00
<i>Lomelosia rutifolia</i>	0.02	11.26	0.03	0.00
<i>Crucianella maritima</i>	0.02	7.71	0.02	0.02
<i>Ononis variegata</i>	0.02	10.08	0.02	0.01
<i>Pistacia lentiscus</i>	0.02	9.09	0.00	0.03
<i>Salsola tragus</i>	0.02	16.01	0.01	0.03
<i>Smilax aspera</i>	0.01	16.80	0.01	0.02
<i>Pinus pinaster</i>	0.01	5.53	0.00	0.02
<i>Sporobolus virginicus</i>	0.01	12.06	0.00	0.02
<i>Phillyrea angustifolia</i>	0.01	8.10	0.00	0.02
<i>Phleum arenarium</i> subsp. <i>caesium</i>	0.01	13.44	0.01	0.00
<i>Lagurus ovatus</i>	0.01	18.18	0.01	0.01
<i>Convolvulus soldanella</i>	0.01	10.08	0.01	0.00
<i>Erica multiflora</i>	0.01	4.15	0.00	0.02
<i>Salvia rosmarinus</i>	0.01	2.77	0.00	0.01
<i>Silene canescens</i>	0.01	15.22	0.01	0.00
<i>Cerastium glomeratum</i>	0.01	12.25	0.01	0.00
<i>Hypochaeris radicata</i>	0.01	6.92	0.01	0.00
<i>Euphorbia pepilis</i>	0.01	7.31	0.01	0.00
<i>Sporobolus pumilus</i>	0.01	2.37	0.01	0.00
<i>Silene otites</i>	0.01	11.46	0.01	0.00

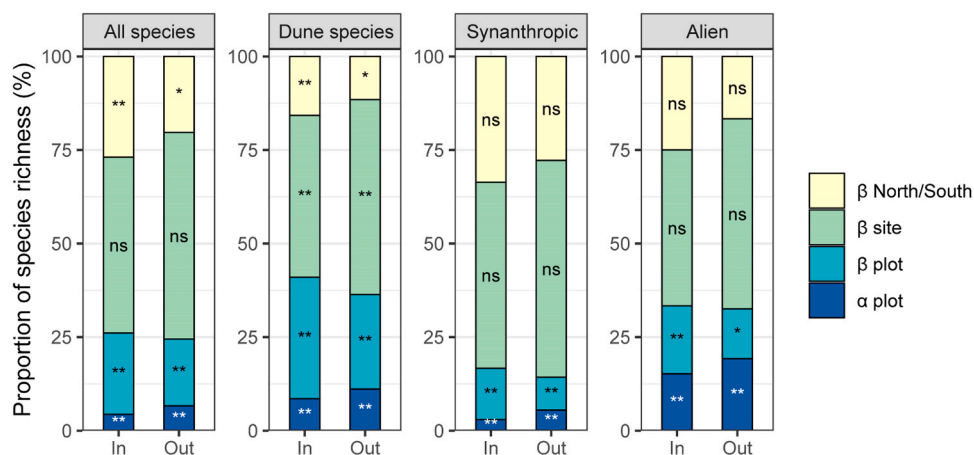


Fig. 6. Contributions (%) of the α and β -diversity components to the total species richness of the study area, for each protection status (inside/outside protected areas) and each species group. Contributions were determined through the additive partitioning approach (** $p < 0.01$; * $p < 0.05$; ns = non-significant).

the variability between plots.

The prevalence of replacement for focal species has a consequence for conservation: it means that for the conservation of this group of species it is preferable to protect multiple areas, preferring the ones with the most unique sites, rather than to protect only the sites

with the highest species richness (Socolar et al., 2016; Carlos-Júnior et al., 2019; Hill et al., 2021). High LCBD values generically indicate sites with a high uniqueness with respect to the overall status of the study area (Legendre and De Cáceres, 2013), and therefore can indicate also sites subjected to disturbance or characterized by peculiar ecological conditions (Dubois et al., 2020; Perez Rocha et al., 2023).

In our study, high contributions to β -diversity were given by sites with low species richness, as observed in many other studies (Heino and Grönroos, 2017; Dubois et al., 2020; Hill et al., 2021; Perez Rocha et al., 2023). Moreover, LCBD had a complex relation with environmental factors: it increased with increasing proximity to the shoreline, indicating that sites closer to the sea are highly unique, but it also increased with decreasing slopes, which are generally characteristic of the communities located at both extremes of the coastal zonation (Acosta et al., 2007). Also, the positive relation between LCBD and distance to artificial surfaces suggests that ecological uniqueness can be reduced by anthropic disturbance, as observed also in other works (García-Navas et al., 2022). The low proportion of variation of LCBD explained by local environmental variables is consistent with findings for stream insect assemblages (Heino and Grönroos, 2017) and agricultural landscapes (García-Navas et al., 2022), and could be due to the fact that ecological uniqueness is linked to multiple communities across the coastal zonation rather than specific environmental conditions. However, it is necessary to take into account the species composition of the unique sites before drawing conclusions on their conservation value.

In this study, the ordination of the sites with significant LCBD showed that their uniqueness is due to various reasons. Most of the unique sites are well-preserved aspects of coastal dune vegetation, corresponding to different habitats along the sea-inland zonation. As these sites are exceptions, the overall status of coastal dunes in Tuscany appears to be degraded, and synanthropic species are indeed widespread throughout our study area. Interestingly, several unique sites are covered by the pioneer vegetation of drift lines, a naturally species-poor habitat characterized by highly specialized species like *Cakile maritima*, *Salsola tragus*, *Convolvulus soldanella* (Prisco et al., 2012). As emerged from other works, this habitat is often in an unfavourable conservation status (Bertacchi, 2017; Sperandii et al., 2019; Sarmati et al., 2019), because it is highly vulnerable to tourism and mechanical cleaning (Attorre et al., 2013), while being also sensitive to erosion (Bazzichetto et al., 2020). Nonetheless, our analysis also revealed the presence of unique sites characterized by *Calamagrostis arenaria* subsp. *arundinacea*, by *Crucianella maritima*, by dune grasslands, and by dune scrubs, suggesting that there is not a single habitat to give priority to, and stressing the importance of conserving the complete coastal vegetation mosaic (Acosta et al., 2009).

A similar indication emerges from the analysis of the SCBD. Indeed, the species contributing the most to the regional β -diversity are *Juniperus macrocarpa*, *Calamagrostis arenaria* subsp. *arundinacea*, *Thinopyrum junceum*, and *Cakile maritima*, which are the most representative and the structural species of the main communities occurring in the coastal zonation (Acosta et al., 2007). In addition, many of these species have high frequency in our dataset, and thus are the ones varying the most in occurrence and abundance, as observed in previous studies (Heino and Grönroos, 2017; Fanfarillo et al., 2023). Such results underline the importance of conserving the whole dune zonation (Acosta et al., 2009).

Notably, some of the unique sites are not protected and thus particularly vulnerable, so these results can serve as a base to choose what areas should be included in the network of protection (Dubois et al., 2020). The expansion of the network, however, would also require assessing the current and future distribution of threats like urbanization, as was done recently by Doxa et al. (2017). At the same time, our results also highlighted the importance of considering species composition alongside LCBD analysis, separating dune species from synanthropic and alien species. Indeed, high value of LCBD may indicate also sites rich in synanthropic species and surrounded by a high proportion of artificial land, or altered in other ways, as two sites particularly rich in *Achillea maritima*, a sub-nitrophilous species that is an indicator of dune degradation when present with high coverage (Acosta et al., 2007). Remarkably, when these sites are located inside protected areas, high value of LCBD can be also an indication on where to address restoration efforts (Legendre and De Cáceres, 2013).

5. Conclusions

Our approach proved to be effective for prioritizing coastal dune sites based on their ecological uniqueness. The analysis of β -diversity allowed to identify new sites for conservation on a regional scale and to assess the effectiveness of the existing network of protected areas by analyzing their distribution. We observed some differences between protected and non-protected areas, but these differences changed according to which type of diversity metric was considered and which group of species was analyzed, suggesting that it is essential to consider different groups of species separately and indicating the dune species group as the most interesting to explore.

In the North of Tuscany, protected areas appear to be richer in dune species, while in the South the overall situation seems more homogeneous. Definitive conclusions on the effectiveness of protected areas for the conservation of coastal dune diversity cannot be drawn, also because much depends on the initial state of the protected area (Sperandii et al., 2020), however our results suggest that there are some unique sites with high conservation value which are not protected and some protected sites with low level of conservation, raising the question of whether the existing network of protected areas should be better assessed.

Potential future steps include extending the analysis to other aspects of diversity, such as functional, phylogenetic or spectral diversity, to assess how appropriate the current network is for the protection of them. Moreover, the scale of analysis could be expanded to include larger areas, and, finally, the outputs of these analyses can be gathered to suggest new relevant sites to prioritize for protection giving an important contribution to the 2030 Conservation Strategy of European Commission (2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03085](https://doi.org/10.1016/j.gecco.2024.e03085).

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