A complex interplay between natural and anthropogenic factors shapes plant diversity patterns in Mediterranean coastal dunes

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Abstract

A long history of human colonisation has profoundly altered Mediterranean coastal dunes, as well as their capacity of providing ecosystem services important for human well-being. The provisioning of these services depends on the integrity of the dune system, which is formed and maintained by coastal plant communities. Analysing the drivers of plant diversity loss is thus crucial for preserving Mediterranean coastal ecosystems.

Using 20 cm resolution orthophotos, we mapped a wide Mediterranean coastal landscape and obtained a set of variables describing the distribution, abundance and size of natural (coastal dune habitats) and anthropogenic (urban areas and tourism facilities) patches. From the orthophotos, we also quantified the shoreline dynamism (coastal erosion and accretion) occurred in the area over a 10-year period. We then analysed how plant species richness, as well as the proportion of typical and ruderal plant species, related to the landscape variables and shoreline dynamism. Also, using piecewise structural equation modelling, we investigated the complex interplay between landscape variables and shoreline dynamism in shaping coastal plant diversity patterns.

When focusing on plant species richness, we found no evidence of a negative effect of anthropogenic activities (urbanisation and tourism) on the diversity of coastal vegetation. However, analysing typical and ruderal plant species revealed that the latter are favoured under human-related disturbance, while typical species of the foredune decrease in areas subject to high anthropogenic pressure. This indicates that (i) looking only at plant species richness can lead to underestimating the impact of anthropogenic activities on coastal dune vegetation; and (ii) that human-related activities change the composition of dune vegetation, eventually promoting the establishment of ruderal species, which cannot support the functioning of coastal ecosystems and the provisioning of the related ecosystem services. Finally, results of the structural equation models highlighted that coastal erosion is an indirect driver of plant diversity loss, through its influence on the coastal landscape configuration.

Keywords: aerial orthophotos, coastal erosion, coastal tourism, dune vegetation, habitat types, land cover map, remote sensing, species guilds, typical species.

1. Introduction

Coastal dunes are transitional ecosystems characterized by limiting abiotic conditions and strong natural disturbances. Here, a sharp sea-land environmental gradient determined by changes in salinity, water, and nutrient availability, shapes the so-called ‘coastal zonation’. This is a typical mosaic of plant communities coexisting in a short space: from the shoreline towards the inland (Forey et al. 2008; Acosta et al. 2009; Maun 2009; Marcenò et al. 2018). The interaction between sand and coastal plants adapted to burial determines (and maintains) the dune morphology through a process known as *eco-morphodynamism* (Yousefi Lalimi et al. 2017; Malavasi et al. 2021). This, in turn, preserves the integrity of the whole coastal landscape. A well-conserved coastal dune zonation secures the stable provisioning of a wide range of ecosystem services, such as coastal defence (Durán and Moore 2013; Feagin et al. 2015), groundwater storage and purification (Rhymes et al. 2015), nutrient cycling, soil formation and climate regulation (Barbier et al. 2011; Jones et al. 2008).

Maintaining the diversity of plant communities is thus crucial for ensuring the eco-morphodynamism of coastal dunes (Sperandii et al. 2019; Malavasi et al. 2021). In particular, preserving typical (plant) species (defined by Evans and Arvela (2011) as taxa contributing to habitat structuring and functioning and as good indicators of favourable habitat quality; see also Bonari et al. 2021a) is key for dune building and consolidation (Angiolini et al. 2018). The replacement of typical by ruderal species (defined as nitrophilous and synanthropic taxa that colonize areas subject to high disturbance regimes; Pignatti et al. 2005) is especially dangerous, as ruderal species do not fulfil the same functions of typical species (Navarra and Quintana-Ascencio 2012; Biondi et al. 2012a). As a result, ruderal species further exacerbate the negative impact of anthropogenic activities on the dune system (Sarmati et al. 2019). Analysing different species guilds, such as typical and ruderal species, can therefore aid in predicting the consequences of disturbance on coastal plant communities, and, in turn, on the eco-morphodynamism of the dune system (Prisco et al. 2016; Bonari et al. 2021b).

During the last 70 years, European coastal ecosystems have been strongly altered by tourism and urbanisation, which have led to the loss of about three-quarters of the dune systems (Heslenfeld et al. 2004). As a consequence, coastal dunes are currently regarded among the most threatened habitats in Europe (Janssen et al. 2016). Tourism and urbanisation have hit particularly strong in the Mediterranean basin, which is characterised by a long history of human colonisation (Malavasi et al. 2013, 2016; Basnou et al. 2015). Here, human activities have reduced the (natural) heterogeneity of coastal landscapes through fragmentation and habitat loss (Malavasi et al. 2016). As an example, tourism has altered the structure and composition of dune habitats, particularly of the foredune (Tzatzanis et al. 2003; Carboni et al. 2010; Ciccarelli 2014), through both direct (e.g. mechanical beach cleaning, Dugan and Hubbard 2010) and indirect pressures (e.g. trampling and facilitation of invasion by non-native species; Santoro et al. 2012; Dimitrakopoulos et al. 2017).

Along with urbanisation and tourism, coastal erosion is another key driver of plant diversity loss in dune ecosystems (Feagin et al. 2005). Its intensity can be exacerbated by human activities, such as river damming and bed quarrying (Pranzini et al. 2015). The consequences of coastal erosion on dune systems are predicted to be especially severe in the Mediterranean basin due to the simultaneous effect of climate-change related phenomena such as sea-level rise (Antonioli et al. 2017, 2020). However, the impact of coastal erosion on dune vegetation has so far been tested only locally and in isolation, i.e. not accounting for other disturbance types (Ciccarelli et al. 2012; Bertacchi et al. 2016; Bazzichetto et al. 2020). We therefore lack knowledge on whether and how coastal erosion interacts with urbanisation and tourism in affecting coastal communities.

Multiple factors (e.g. integrity of dune habitats, urbanisation, tourism, coastal erosion) can therefore simultaneously affect dune vegetation and its role in the eco-morphodynamism process preserving the coastal ecosystem. In this study, we investigated how these factors determine plant diversity patterns along a wide Mediterranean coast. To this aim, we took a landscape perspective and analysed the association between the configuration (i.e. distribution, size and abundance) of natural and anthropogenic coastal patches (which relate to the conservation status of the dune system and the intensity of anthropogenic pressure insisting on it) and dune vegetation. Importantly, we simultaneously accounted for the effect of coastal erosion. We looked at the whole plant community response to human activities and coastal erosion, as well as at the separate response of typical and ruderal species.

Our aims were to:

i) investigate the response of community species richness, typical species and ruderal species to natural and anthropogenic factors affecting the coastal landscape;

ii) explore the complex interplay among the multiple factors shaping coastal plant diversity, and assess whether they directly affect dune vegetation or rather mediate other factors' effect.

2. Materials and methods

2.1. Study area

Our study area extends across a broad Mediterranean coastal sector of Central Italy (380 km long, of which 215 km comprise sandy beaches), included within the administrative boundary of the Tuscany region (between 43°51′N and 42°22′N; see Fig. 1a). We focused on 8 sites covering almost all Tuscan sandy coasts (Fig. 1a). Here, under natural conditions, the dune vegetation follows the typical coastal zonation of Mediterranean dunes, with annual pioneer species colonising the coastal sector closest to the shoreline, and, moving inland, perennial herbaceous communities occurring on embryonic and shifting dunes. Further inland, species typical of the Mediterranean dune shrubs settle where the dune becomes more stable and less exposed to salt spray, wind, and sand burial (Acosta et al. 2006; Maun 2009; Prisco et al. 2012; Ciccarelli 2015).

The coast of Tuscany is characterized by a latitudinal gradient of climate and anthropogenic activity, with the northern sector being overall wetter (higher precipitation) and more densely urbanized (Venturi et al. 2014; Zullo et al. 2015; Fratianni and Acquaotta 2017; Pesaresi et al. 2017). Despite various countermeasures (Pranzini et al. 2018), the coast has undergone erosion, although with intensity changing across sites. Pranzini et al. (2020) evidenced that between 1985 and 2005: 9.1% of the coast underwent severe erosion, 12.0% low-intensity erosion, 27.0% experienced a slow shoreline retreat, while 21.8% underwent slow accretion. The main causes of this coastal retreat are the drastic reduction of sediment from rivers, riverbed quarrying, and the construction of weirs and dams (Pranzini 2021).

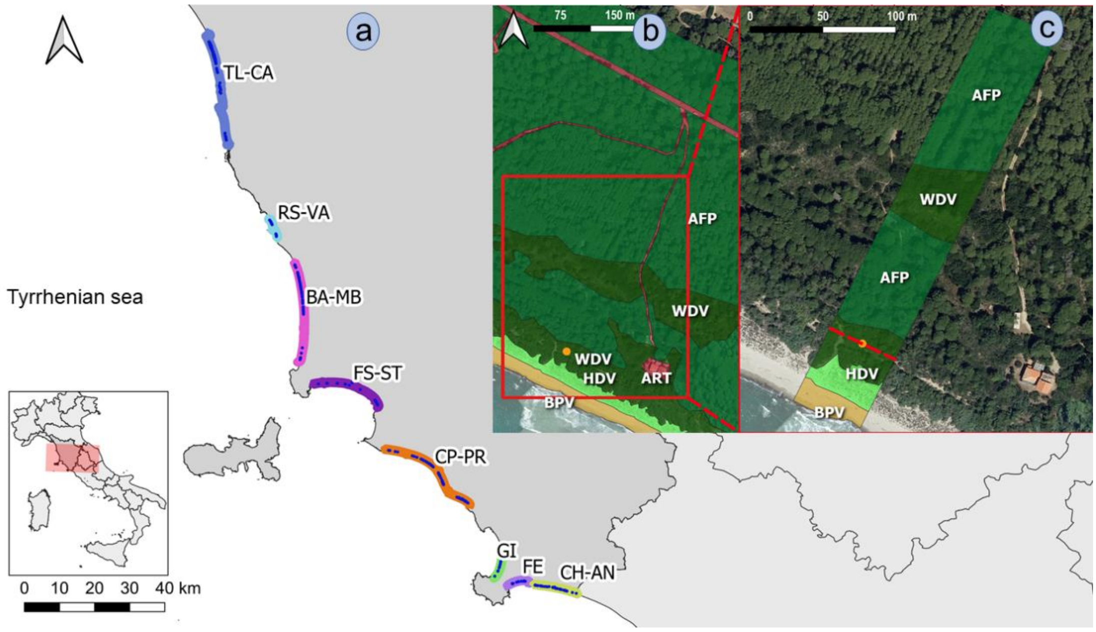

Fig. 1 Study area. a) distribution of vegetation plots within the eight analysed coastal sites (highlighted). TL-CA: from *Dune Litoranee di Torre del Lago* to *Calambrone*; RS-VA: *Rosignano Solvay* and *Vada*; BA-MB: from *Marina di Bibbona to Baratti*; FS-ST: from *Coastal Park of Sterpaia to Tomboli di Follonica e Scarlino*; CP-PR: from *Castiglion della Pescaia* dunes to *Principina a mare*; GI: *Giannella* dunes; FE: *Feniglia* dunes; CH-AN: from *Ansedonia to Chiarone Scalo.* b) an example of the land cover map derived from high-resolution (20 cm) orthophotos. c) an enhanced representation of the land cover map cut by the rectangular buffer (300 m × 50 m), which was built around each vegetation plot (dot in yellow). The dashed red line represents the 50 m width of the buffer. In different colours, an example of mapped land cover categories: coniferous afforestation (AFP); artificial areas (ART); beach pioneer vegetation (BPV); herbaceous dune vegetation (HDV); woody dune vegetation (WDV).

2.2. Sampling of vegetation data

Between 2018 and 2021, we sampled 474 vegetation quadrats of 2 m × 2 m (hereafter referred to as plot), which is considered an adequate number to analyse plant diversity patterns in Mediterranean dune systems (Acosta et al. 2000; Carboni et al. 2009; Maccherini et al. 2020). The sampling was carried out during the vegetative season, i.e. from April to July. Plots were located according to a stratified random design across an area of approximatively 5.7 km^2, with strata being the herbaceous and woody dune sectors. Specifically, 338 plots were located across an area of approximatively 2.88 km^2 from the upper beach to coastal stable dune grassland (herbaceous dune sector), and 136 plots were located across an area of 2.82 km^2 constituted by coastal dune shrubs (woody dune sector). Using the EUNIS habitat classification system (Chytrý et al. 2020), we assigned each plot to the following habitat types: sand beach drift lines (EUNIS code: N12), shifting coastal dunes (N14), coastal stable dune grasslands (N16), and coastal dune shrubs (N1B). Note that these habitat types exhaustively represent all plant communities of Mediterranean coastal dunes (Table S1). In each plot, we recorded the presence and cover of all plant species.

Nomenclature follows Bartolucci et al. (2018) for native species, and Galasso et al. (2018) for non-native species (see also the Portal to the Flora of Italy 2023).

2.3. Plant diversity and proportion of typical and ruderal species

For each plot, we computed species richness (i.e. the total number of species recorded) as a measure of plant diversity. We also calculated the plot-specific proportion of typical and ruderal species. To this aim, we first assigned all species recorded in a plot to the following mutually exclusive guilds: typical, ruderal, and non-native (Table S2). Note that we only considered non-native species to compute the proportion of typical and ruderal species, but we did not analyse them as (1) they occurred sporadically in our plots; and (2) non-native species follow different ecological processes than native species, and a focus on these processes was beyond our scope. Then, we computed the proportion of typical and ruderal species as the ratio between the number of species belonging to each of the two analysed guilds and the total species richness recorded in the plot. Note that species were counted as typical depending on which EUNIS category the plot belonged to. As an example, *Calamagrostis arenaria* subsp. *arundinacea* was considered typical only in plots classified as habitat N14. The list of typical species for our study area was extracted from the Italian Interpretation Manual of the Habitats Directive (Table S1, Biondi et al. 2009; Biondi and Blasi 2015). Species assignment to the ruderal guild followed existing literature (Biondi et al. 2012b; Del Vecchio et al. 2016; Prisco et al. 2017).

2.4. Remote sensing data

From the archive of remote sensing data of Tuscany (GEOscopio 2022), we gathered 20 cm resolution orthophotos acquired in 2019 that we used to produce a land cover map of the coastal landscape (see 2.4.1). From the land cover map, we derived: i) a set of variables related to natural and anthropogenic factors (see 2.4.2) and ii) a measure of shoreline dynamism, i.e. erosion and accretion (see 2.4.3).

2.4.1. Land cover map

We produced a detailed land cover map (scale 1:2000, Fig. 1b) by photo interpretation in a GIS environment (QGIS Development Team 2018). We used both RGB (natural colour) and NirGB (modified false colour) orthophotos to enhance the discrimination of conifer taxa (coloured in dark red) from deciduous species. The final land cover map covered a coastal belt of 300 m width (from the shoreline inwards, hereafter the coastal landscape), which was previously indicated as an adequate extent to analyse coastal dunes in Central Italy (Carranza et al. 2008; Malavasi et al. 2016; Bazzichetto et al. 2018). To allow for interoperability, we classified natural, semi-natural and artificial areas according to the standard European CORINE nomenclature extended to a 4-level detail, which proved to be suitable for describing the vegetation types of coastal dune ecosystems (Acosta et al. 2005; Carboni et al. 2009; Malavasi et al. 2018; Sperandii et al. 2019) and allows comparison among studies.

We mapped a total of 11 land cover types (Table S3): 3 associated with natural psammophilous coastal vegetation, 3 with artificial areas, 2 with forest vegetation belonging to coniferous afforestation and mixed forests, and 3 with non-psammophilous coastal vegetation and semi-natural vegetation. The three land cover vegetation types belonging to psammophilous coastal vegetation are: (1) beach pioneer vegetation, i.e. the upper beach colonized by low pioneer annual vegetation of the drift lines; (2) herbaceous dune vegetation, including the annual and perennial herbaceous psammophilous communities of the foredunes; and (3) woody dune vegetation, corresponding to the shrub vegetation of the fixed dune with *Juniperus* spp. or sclerophyllous shrubs (Acosta et al. 2005). In some cases, a specific land cover class included multiple EUNIS habitat types (e.g. herbaceous dune vegetation included shifting coastal dune communities and coastal stable dune grasslands, corresponding to, respectively, EUNIS N14 and N16). Therefore, it was not possible to perform a 1:1 association between each land cover type and a single habitat type (*sensu* EUNIS class). Land cover types associated with forest vegetation included the evergreen mixed forest and coniferous afforestation found along the innermost and better preserved sandy coasts.

To discriminate between tourism-related and other anthropogenic activities (e.g. urbanisation), we classified tourism (including bath-houses and camping, agriculture fields) and artificial (urban and industrial) areas as separate cover types (Table S3).

2.4.2. Landscape metrics

Using the land cover map described in 2.4.1., we derived a set of metrics describing different characteristics of the coastal landscape.

Specifically, to describe the spatial configuration of natural and anthropogenic patches, we used the linear buffer approach implemented by Malavasi et al. (2018). First, we generated 300 m long (from the shoreline towards the inland) × 50 m wide (along the shoreline) rectangular buffers around each plot (Fig. 1c). The rectangular buffers were oriented so as to perpendicularly cut the coastal landscape. We set the width of the buffers to 50 m (leaving 25 m on each side of the plot). This buffer size was reported as an adequate size to relate the configuration of the coastal landscape with plant diversity (Malavasi et al. 2018). Also, we compared the value of the landscape metrics extracted at 50, 100, and 200 m width and found no differences. Second, for each plot, we computed the proportion (expressed in %) of the area covered by each land cover class (e.g. proportion of artificial areas; see Table S4) in the buffer.

Beyond area-based variables, we computed the shortest distance from each plot to the closest artificial and tourism facility. Also, we computed the Shannon and Simpson's indices to measure landscape diversity and evenness, that is the diversity and evenness of land cover types included within each buffer (Shannon index; Shannon 1948).

2.4.3.Shoreline dynamism

To measure shoreline dynamism (i.e. coastal erosion and accretion), we mapped changes in the shoreline position between 2010 and 2019. To this aim, we gathered a map of the shoreline position for our study area for 2010 from the Tuscan archive of remote sensing data (GEOscopio 2022). Then, we derived the shoreline position for 2019 from our land cover map. Finally, for each plot we first calculated the shortest Euclidean distance from the two shorelines and then subtracted the plot-to-shoreline distance in 2019 from the plot-to-shoreline distance in 2010. A positive value of this metric indicates that the plot was located in an area that underwent accretion between 2010 and 2019, while a negative value indicates an area that underwent erosion.

2.5. Statistical analysis

2.5.1. Effect of anthropogenic factors and coastal erosion on coastal vegetation

We fitted regression models to analyse how species richness, as well as the proportion of typical and ruderal species, related to the landscape variables and shoreline dynamism (i.e. coastal erosion and accretion). Species richness was modelled using a Poisson generalised linear model (GLM) with 'log' link. To model the proportion of typical and ruderal species we used a binomial GLM with 'logit' link.

To reduce the impact of multicollinearity, before fitting the models we computed the variance inflation factor (VIF; ginv function, MASS R package, Venables and Ripley 2002) for each predictor, and excluded those with a VIF value greater than or equal to 5 (Table S4). The final set of predictors included were: the proportion of area covered by beach pioneer vegetation, herbaceous dune vegetation, woody dune vegetation, coniferous afforestation and mixed forest (among the natural land cover classes); agricultural, artificial areas and tourism facilities (among the anthropogenic land cover classes). Other predictors considered were: landscape diversity (Shannon's index), distance to artificial areas and shoreline dynamism. We included latitude of the plot location as an additional predictor, as previous studies observed a latitudinal trend in species richness potentially associated with processes not described by our set of predictors (D'Antraccoli et al. 2019; see also 2.1.). Finally, we hypothesised that the response of coastal dune plant communities to natural and anthropogenic factors would change along the coastal zonation. For this reason, we included the statistical interaction between habitat type (included as a categorical variable) and all predictors except for latitude.

For each GLM, we started with a full model including the previously mentioned interaction. Then, using incremental F-tests, we derived a series of reduced models by sequentially dropping terms for which there was no evidence of an interaction with habitat type (incremental F-tests implemented using the Anova function, car R package; Fox and Weisberg 2019). As a result, the 'most parsimonious model' included all predictors (main effects for the predictors involved in the statistical interaction, plus latitude), plus the terms associated with statistically significant interactions. Then, we compared the full and the most parsimonious and an intercept-only model using the Akaike Information Criterion (AIC, Anderson and Burnham 2004) and selected as best-fitting the one with the lowest AIC. Models' assumptions of linearity, homoscedasticity and normality were visually assessed using the performance R package (Lüdecke et al. 2021).

Given the low number of plots belonging to the sand beach drift lines (EUNIS N12), we aggregated and analysed data of this habitat type together with shifting coastal dunes (N14). This allowed increasing precision in the estimation of regression parameters, as analysing sand beach drift lines alone would have resulted in high variance coefficients associated with this habitat type. By aggregating data for these two habitat types (N12+N14, hereafter referred to as 'shifting dunes'), we assumed they were equally affected by natural and anthropogenic predictors, which is a reasonable assumption given that they are intermingled along the coastal zonation and at a similar distance from the shoreline, and therefore are subject to the same intensity of natural and anthropogenic pressures.

2.5.2. Path analysis

To investigate the complex interplay between natural factors, anthropogenic activities and coastal erosion in determining plant diversity patterns we used piecewise structural equation modelling.

Relying on existing literature on the relationship between anthropogenic and natural factors, shoreline dynamism and coastal vegetation in Mediterranean dunes, we formulated a meta-model representing our assumed network of relationships among the former components (see Fig. S1 for a graphical representation of the meta-model). Specifically, we assumed that artificial land cover classes (related to urbanisation, tourism, and agriculture) affected landscape diversity and shoreline dynamism (e.g. by favouring fragmentation and coastal erosion, respectively). In turn, we expected both the landscape configuration and landscape diversity and shoreline dynamism, to affect the area of the three land cover classes associated with the dune natural habitats (i.e. beach pioneer dune vegetation, herbaceous dune vegetation, and woody dune vegetation). Finally, we assumed that each of the response variables used in 2.5.1. (species richness, and typical and ruderal proportion) was influenced by landscape diversity and shoreline dynamism *via* the area covered by the dune habitats. Piecewise structural equation models (SEMs) were fitted using the R package piecewiseSEM (Lefcheck 2016). To validate the SEMs, missing paths (i.e. paths not originally included in the meta-model) were assessed and included if considered causal, or otherwise left to freely covary. Model fit was evaluated using the Fisher's C statistic. Specifically, the meta-model, updated by the missing paths, was considered as adequately fitting the data if the test associated with Fisher's C statistic was not statistically significant (i.e. $p > 0.05$).

3. **Results**

3.1. Species richness

The best fitting model for species richness explained 35% (adjusted R-squared) of the overall variability in the response (Table S5; Fig. 2). Species richness increased with the increasing proportion of area covered by beach pioneer dune vegetation in all habitat types (z-value = 5.36, p-value < 0.001), while it increased with the proportion of area covered by herbaceous dune vegetation in the inner dune habitats (EUNIS N16 and N1B). A larger proportion of area covered by woody dune vegetation resulted in higher species richness in coastal dune shrub (N1B). On the contrary, it was associated with lower species richness in shifting dunes and coastal stable dune grasslands habitat types (N12+N14 and N16).

The increasing proportion of agricultural areas had a positive effect on the species richness of coastal stable dune grasslands habitat (EUNIS N16), but a negative effect on the species richness of coastal dune shrubs habitat (N1B). In all habitat types, species richness increased with the proportion of artificial areas, with a more marked increment in coastal stable dune grasslands habitat. On the contrary, we observed an overall decrease in species richness at increasing distances from artificial facilities (z-value = -2.11, p-value < 0.05).

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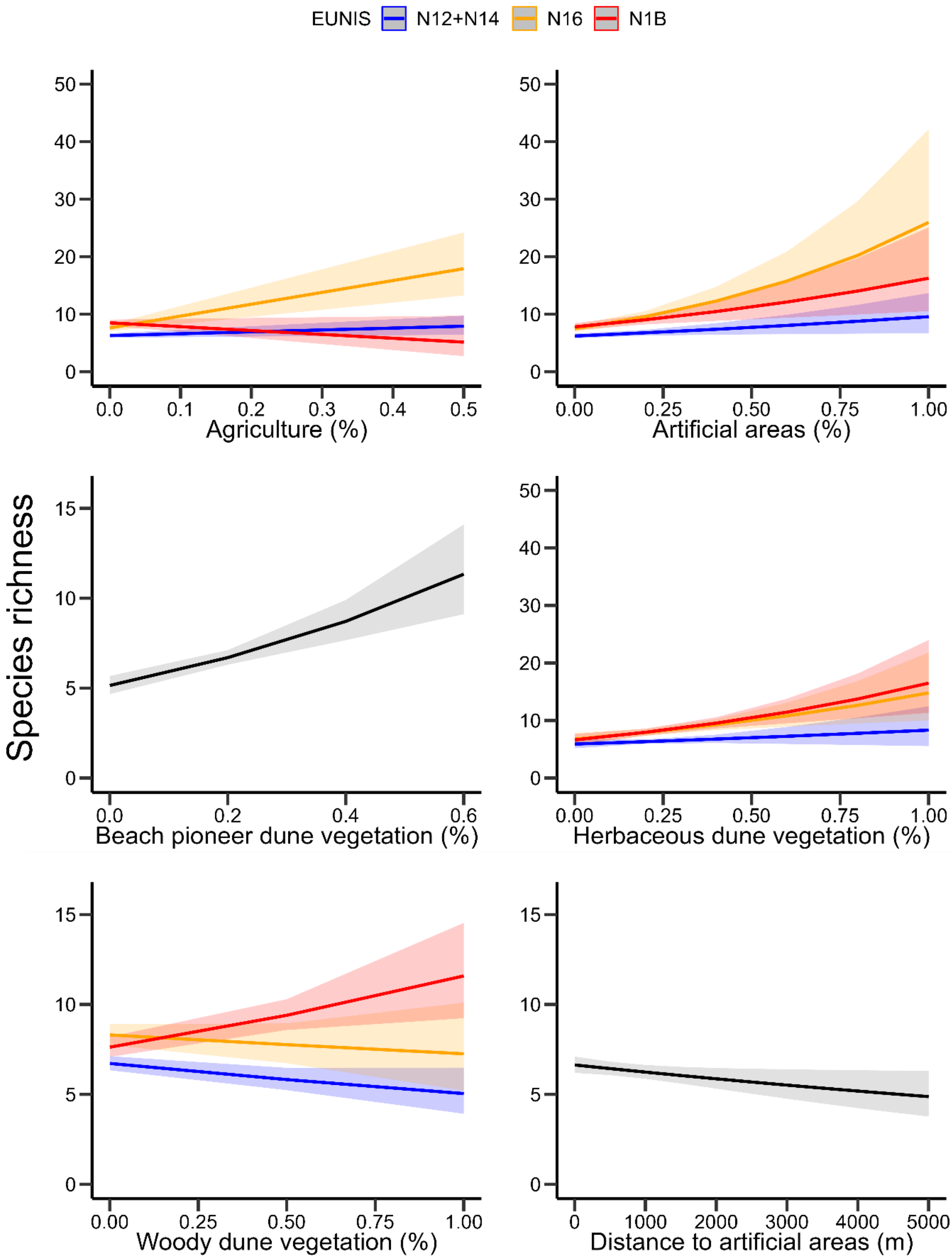

Fig. 2. Prediction plots of the model for species richness.
Percentages '%' represent the proportion of area covered by the different land cover classes. Bands represent 95% confidence intervals of the means. EUNIS habitat types code: sand beach drift lines (N12), shifting coastal dunes (N14), coastal stable dune grasslands (N16), and coastal dune shrubs (N1B).

3.2. Proportion of typical and ruderal species

3.2.1. Typical species

The best fitting model for the proportion of typical species explained 32% (adjusted R-squared) of the total variance (Table S6; Fig. 3).

In areas with high coverage of beach pioneer dune vegetation and herbaceous dune vegetation, the proportion of typical species was lower in shifting dunes and coastal dune shrubs habitats (EUNIS N12+N14, N1B), and higher in coastal stable dune grasslands (N16). Typical species proportion also increased in all habitat types at increasing proportion of area covered by woody dune vegetation. Higher landscape diversity was associated with a lower proportion of typical species of shifting dunes and coastal dune shrubs, but with a higher proportion of typical species of coastal stable dune grasslands.

Results evidenced that the proportion of typical species of all habitat types, except for coastal dune shrub (EUNIS N1B), decreased in areas with large cover of agricultural fields and mixed forests. Also, the proportion of typical species in shifting dunes habitat (N12+N14) was negatively correlated with the proportion of artificial land cover, meaning that the chance of finding typical species typical of these habitats decreased in highly urbanized locations. The proportion of typical species of the foremost habitat types (N12+N14, N16) also decreased at increasing distances from artificial areas. Finally, the proportion of typical species of all habitat types decreased at increasing latitude (i.e. moving towards the North).

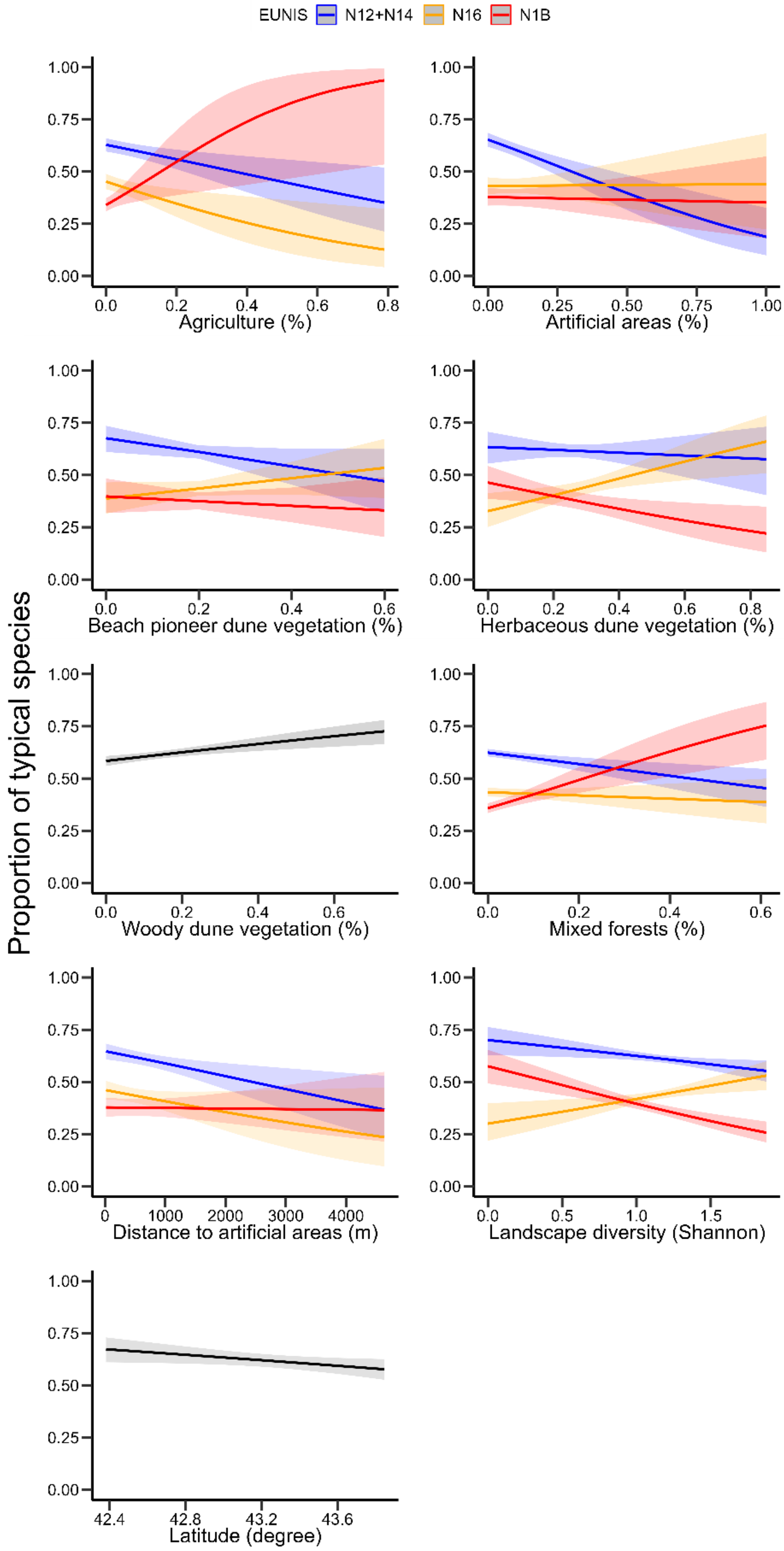

Fig. 3 Prediction plots of the model for the proportion of typical species. Percentages '%' represent the proportion of area covered by different land cover classes. Bands represent 95% confidence intervals for the means. EUNIS habitat types code: sand beach drift lines (N12), shifting coastal dunes (N14), coastal stable dune grasslands (N16), and coastal dune shrubs (N1B).

3.2.2. *Ruderal species*

The best fitting model for the proportion of ruderal species did not include statistical interactions, suggesting that the predictors finally retained in the model equally affected ruderals in all habitat types. The best fitting model explained 21% (adjusted R-squared) of the total variance. The area covered by agriculture and latitude were the only predictors significantly affecting the proportion of ruderal species (Table S6, Fig. 4). Specifically, the increasing area covered by agricultural fields was associated with a higher proportion of ruderal species (z-value = 3.33, p-value < 0.001). Similarly, the proportion of ruderal species increased moving towards the North (i.e. higher latitude; z-value = 5.12, p-value < 0.001).

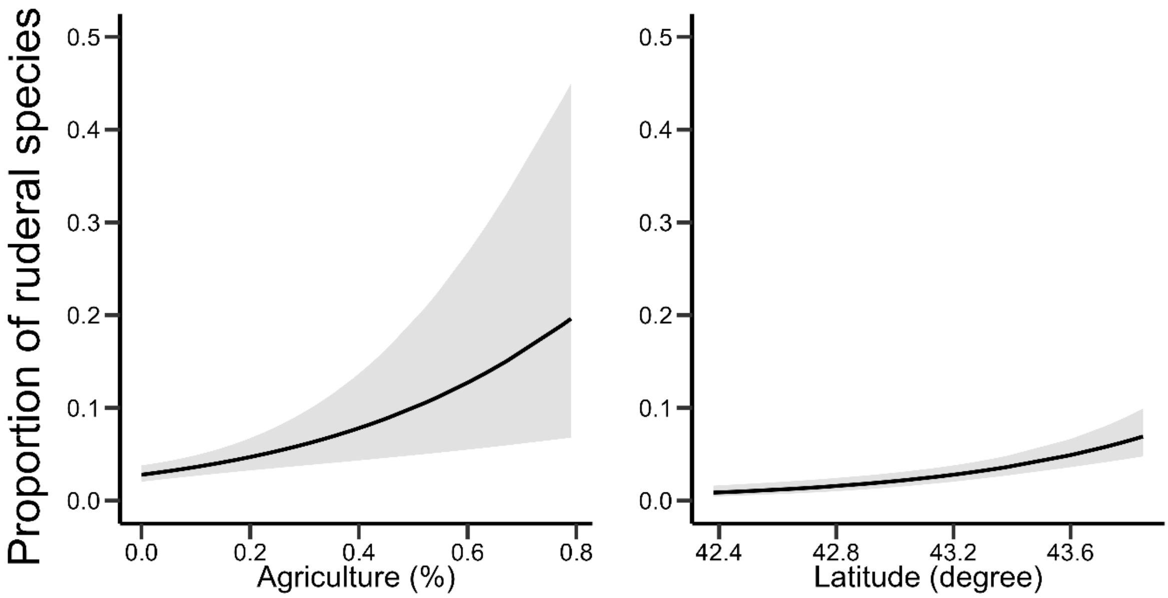

Fig. 4 Prediction plots of the model for the proportion of ruderal species. The proportion of agricultural area (%) in the buffer. Bands represent 95% confidence intervals for the means.

3.3. *Piecewise structural equation models*

Our meta-models (one per response variable), updated with pathways originally excluded, appeared to adequately fit the data (Fig. 5): species richness (Fisher's C = 16.424, p-value = 0.17); proportion of typical species (Fisher's C = 10.832, p-value = 0.37); proportion of ruderal species (C; Fisher's C = 10.832, p-value = 0.37).

In the Northern sites of the study area (i.e. higher latitudes), the coastal landscape appeared characterized by a higher cover of beach pioneer and herbaceous dune vegetation, and of mixed forests (Fig. 5a). High latitudes were also associated with coastal accretion, which overall seemed to favour areas with high cover of beach pioneer and herbaceous dune vegetation, although it also seemed associated with a lower cover of woody dune vegetation, mixed forests and coniferous afforestation. In turn, high cover of both beach pioneer and herbaceous dune vegetation were associated with higher species richness (fig. 5b), thereby suggesting that shoreline dynamism indirectly affected plant diversity through its influence on landscape configuration.

The positive effect of coastal accretion on species richness seemed to be offset by the increasing proportion of area covered by anthropogenic facilities, which not only appeared to promote coastal erosion, but also directly decreased the coverage of almost all coastal natural habitats. Similarly, the area covered by herbaceous dune vegetation and mixed forests was lower in locations close to human facilities. The increasing proportion of agricultural cover, also related to anthropogenic activities, seemed to negatively affect coniferous afforestation, beach pioneer vegetation and woody dune vegetation. These results show that, beyond its direct effect on dune vegetation, human-related disturbance indirectly affected coastal vegetation by reducing the coverage of dune habitats.

Moving southwards (i.e. at low latitudes), the coastal landscape appeared to be characterized by a higher cover of woody dune vegetation and coniferous afforestation, as well as by a higher landscape diversity. However, this area seemed to be also prone to coastal erosion. Furthermore, larger areas of artificial and coniferous afforestation negatively influenced the proportion of typical species, which however showed a negative association with all predictors (for which a significant effect was detected).

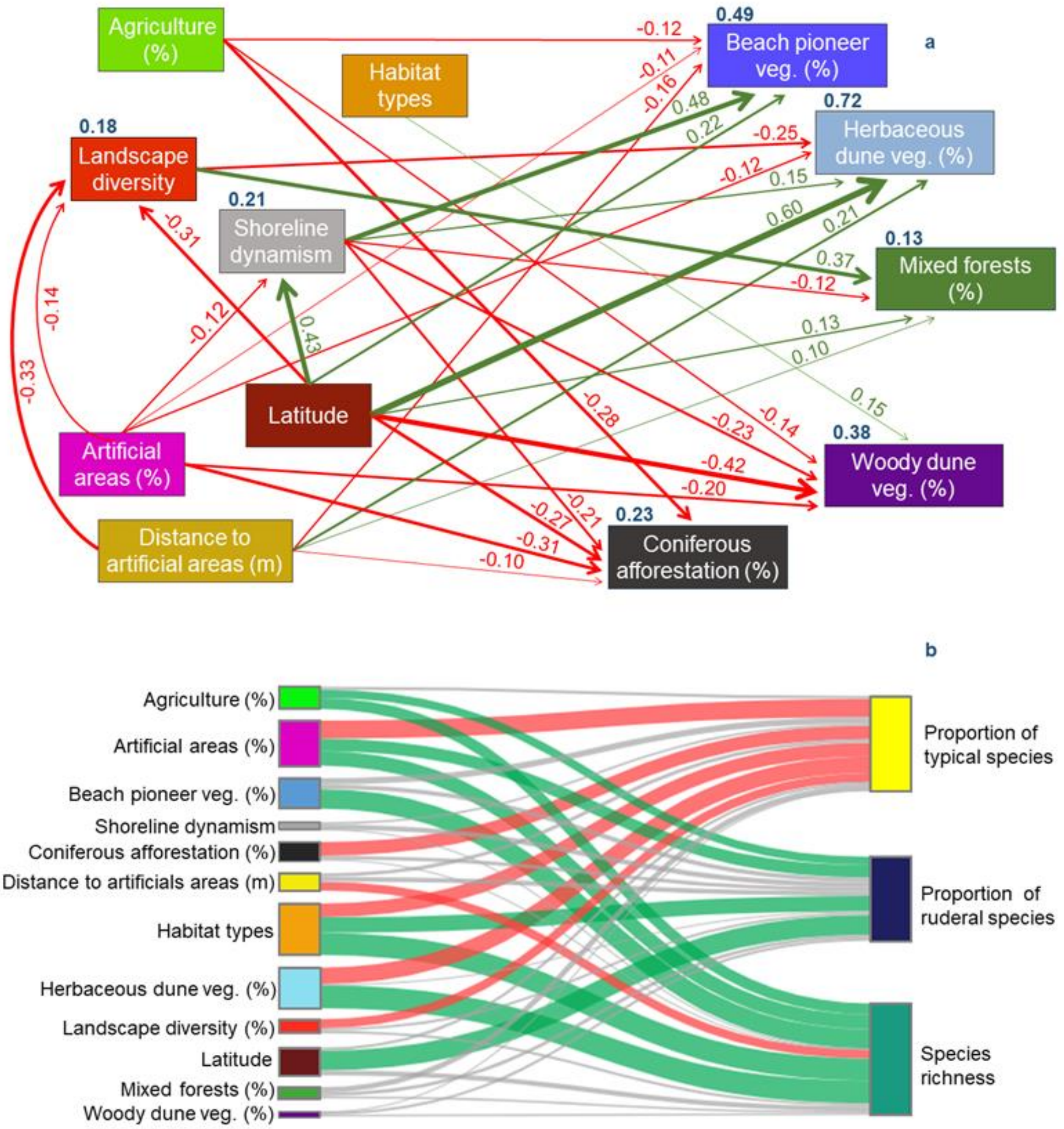

Fig. 5 Output of the piecewise structural equation models.
Piecewise structural equation model representing the interplay (panel a) among different factors affecting species richness, the proportion of typical and of ruderal species (panel b). Note that the network of pathways reported in panel (a) is the same for all piecewise structural equation models (i.e. for species richness, typical and ruderal species). Green arrows (panel a) and flows (panel b) represent (statistically significant) positive relationships, while red arrows and flows represent

(statistically significant) negative relationships. Grey flows in panel (b) indicate statistically non-significant relationships (note that non-significant arrows were removed from panel a due to the already large number of significant arrows). The size of the arrows and flows is proportional to the value of the standardized coefficient (only reported on top of the arrows) of the corresponding predictor. The R^2 (coefficient of determination) associated with each response variable is reported on top of the corresponding variable's label. Veg = vegetation.

4. Discussion

We found that the association between coastal plant communities and natural and anthropogenic factors changed across habitat types. Importantly, analysing typical and ruderal species revealed that these two guilds respond differently to anthropogenic disturbance. In this regard, we observed that agriculture and urbanisation favoured ruderal species at the expenses of typical species in sand beach drift lines and shifting dunes, which are the most important habitats for the eco-morphodynamism of coastal dunes (Malavasi et al. 2021). Interestingly, this pattern did not come out clearly when analysing species richness, which highlights the importance of investigating different plant guilds to get a more comprehensive understanding of how plant diversity responds to natural and anthropogenic factors in coastal dunes. Finally, piecewise structural equation models highlighted shoreline dynamism and, more specifically, coastal erosion as an indirect determinant of plant diversity patterns in coastal dune ecosystems.

4.1. Habitat-specific effect of natural and anthropogenic factors on plant diversity

The response of dune plant communities to natural and anthropogenic factors was habitat-specific, i.e. it varied along the coastal zonation. This is in line with previous studies, which referred to the process by which natural and anthropogenic factors differently affect dune habitats along the zonation as *coastal squeezing*: tourism and coastal erosion have their strongest impact on the foredune communities, while urbanisation and agriculture mostly affect coastal dune shrub habitats (Defeo et al. 2009; Ciccarelli et al. 2012; Malavasi et al. 2013; Mendoza-González et al. 2013; Bertacchi and Lombardi 2013).

4.2. Species richness

Somewhat surprisingly, we found that species richness increased under very different environmental conditions. On the one hand, there was a positive relationship between species richness and the relative area covered by natural coastal habitats (both herbaceous and woody), which is in line with the expectation that species richness is higher in well-preserved coastal dunes (Carboni et al. 2009). On the other hand, regardless of the habitat type, species richness also increased with urbanisation and high cover of agricultural fields. However, analysing separate plant guilds revealed that the proportion of the typical species decreased under high anthropogenic disturbance, while the proportion of ruderal species increased. This suggests that focusing solely on species richness can lead to misleading conclusions on the effect of human-related activities on coastal plant diversity. Indeed, high species richness could be associated with either well-preserved coastal habitats under low anthropogenic disturbance, or communities colonized by ruderal species under strong disturbance. For this reason, we warn against focusing on species richness alone to estimate the influence of anthropogenic disturbance on dune plant diversity.

4.3. Further insights from typical and ruderal species

The proportion of typical species in shifting dunes and coastal stable dune grasslands decreased in densely urbanised areas or areas subject to agricultural activities (Malavasi et al. 2016). On the contrary, typical species of all habitat types were most abundant in areas with a high cover of woody dune vegetation and mixed forests. Previous studies highlighted that well-developed woody dune vegetation sectors and coastal mixed forests are generally associated with an equally well-preserved coastal zonation, and this usually happens under low urbanisation (Malavasi et al. 2013, 2018).

In areas with large patches of beach pioneer and herbaceous dune vegetation we observed a lower proportion of typical species of shifting dunes and a higher proportion of typical species of dune grasslands. In this regard, although we did not detect a direct effect of shoreline dynamism on typical species, we notice that most of large foredune patches occurred in areas that underwent coastal accretion. Typical species of the foredune can cope with sand burial. Yet, an above-average input of sediment may benefit only few of them (e.g. *Thinopyrum junceum* and *Calamagrostis arenaria* subsp. *arundinacea*), and constitute a perturbation from the others (Bazzichetto et al. 2020; see also Maun and Perumal 1999). Concerning typical species of coastal dune grasslands, their proportion may increase in prograding coast due to the lower effect of sea-related environmental stress (Bazzichetto et al. 2020).

The proportion of typical species increased at decreasing landscape diversity in all habitat types but dune grasslands, where we observed the opposite trend. Low landscape diversity usually indicates a well-preserved coastal zonation in terms of structure and functioning (Del Vecchio et al. 2016; Angiolini et al. 2018). In contrast, high landscape diversity is related to habitat fragmentation and loss (Nagendra 2002; Joshi et al. 2006). In this respect, Sperandii et al. (2021) highlighted that both native species richness and plant cover of typical species increase with increasing amount of focal dune habitat. We add that this may not be the case for dune grasslands, which colonise the naturally highly fragmented coastal sector between the foredunes and the fixed dunes, and may thus respond differently to increasing landscape diversity than other habitat types.

Concerning ruderal species, their presence (in all habitat types) seemed to be favoured by agricultural activities. The spread of ruderal species from neighbouring agricultural fields into coastal habitats could explain the greater species richness (and lower proportion of typical species) found in coastal stable dune grasslands in close proximity to large agricultural areas. A larger proportion of ruderal species in coastal habitats is particularly worrying, as it could negatively impact the dune eco-morphodynamism. Ruderals do not have the same functional adaptations to the stressful environmental conditions of coastal dunes (e.g. tolerance to sand burial) that instead characterise typical, psammophilous species. As a result, the replacement of typical species by ruderal species may, in the long-term, compromise the whole process of dune formation and maintenance (Acosta et al. 2007, Hesp 2002).

Focusing on a much broader spatial extent (i.e. the whole study area), we found that the proportion of ruderal species follows a latitudinal gradient i.e. it increases in northern sites. This can be explained by northern sites being more intensively urbanised and more exploited for tourism in our study area, which further highlights the positive association between ruderal species and human presence (Bertacchi 2017; Bonari et al. 2021b).

4.4. Complex interplay among the factors affecting dune vegetation

Structural equation models confirmed that shoreline dynamism and anthropogenic activities are important drivers of plant diversity patterns, through their influence on the configuration of the coastal landscape. As expected, we found that coastal erosion was stronger in areas with high cover of artificial areas, confirming that human activities can exacerbate erosion. However, highly urbanised areas seemed to host higher species richness. As discussed above, this result should be interpreted cautiously, since the high proportion of artificial areas was also associated with a decrease of typical species and an increase of ruderal species. Once again, in species-poor habitats with limiting environmental conditions (such as coastal dunes), species richness alone may be a misleading measure of the impact of anthropogenic activities on dune plant diversity

Structural equation models also indicated coniferous afforestation as a direct factor decreasing the proportion of typical species in coastal habitats. In the last decades, conifer afforestation has gained high ecological, recreational, and landscape value (Mazza et al 2011), but this has promoted tourism and its impact on dune habitats (Bonari et al 2017). Among the direct impacts of tourism, trampling can lead to soil compaction, thereby creating an unfavourable environment for plant species of the embryonic and mobile dunes, which are favoured by loose sandy substrates (Maun 2009). The naturalistic valorisation of conifer afforestation has thus possibly turned to a further threat for the preservation of the dune system.

In conclusion, our results highlight that, in ecosystems characterised by strong environmental filters and to high anthropogenic disturbance such as coastal dunes, species richness *per se* may not be a valid measure of the impact of human-related activities on plant community composition. In this regard, we stress the importance of considering different facets of plant diversity (i.e. the proportion of typical and ruderal species) to avoid achieving misleading conclusions when focusing solely on species richness.

Another key aspect emerging from our study is that anthropogenic activities favour ruderal over typical species. We warn that this will have negative consequences on the maintenance of the coastal eco-morphodynamism, which underpins the multiple services provided by coastal ecosystems.

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Conflict of 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.

Contributions

Manuele Bazzichetto, Simona Sarmati, Claudia Angiolini and Simona Maccherini contributed to the study conception and design. Simona Sarmati, Claudia Angiolini, Andrea Bertacchi, Matilde Gennai,.

Bruno Foggi, Simona Maccherini, Daniele Viciani collected the vegetation data. Simona Sarmati analyzed the data with Manuele Bazzichetto, Marta Gaia Sperandii,Vojtěch Barták, Matilde Gennai, Gianmaria Bonari, Claudia Angiolini, and Daniele Viciani. Simona Sarmati, Manuele Bazzichetto, Marta Gaia Sperandii and Claudia Angiolini wrote the first draft of the manuscript. All authors commented on previous manuscript versions, and read and approved the final version.

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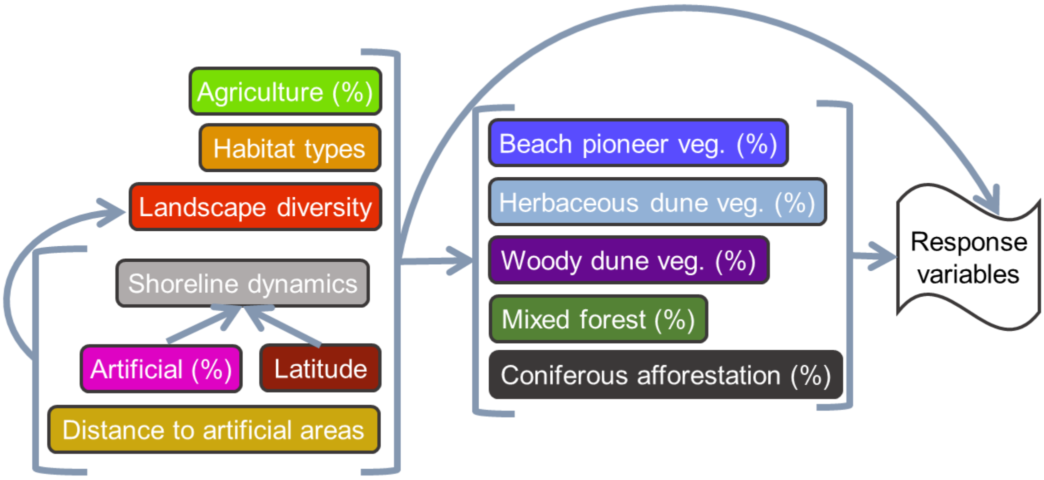

Fig. S1 Hypothesized meta-model used to analyse the complex interplay between landscape configuration and shoreline dynamism, and their effect on coastal dune plant diversity. Response variables included: species richness, proportion of typical species and proportion of ruderal species. Veg = vegetation.

Table S1. List of EUNIS habitat types

List of EUNIS codes along with the corresponding habitat type(s) included in the Annex I of the Habitats Directive (92/43/EEC) and their related typical species (nomenclature follows Bartolucci et al. 2018). N = number of vegetation plots assigned to each EUNIS habitat types.

3-level EUNIS	Description	EU Habitats Directive (Annex I 92/43/EEC)	Typical species
N12 - Sand beach driftlines (N = 23)	Annual pioneer herbaceous formations typically found near the shoreline	1210 - Annual vegetation of drift lines (upper beach)	*Atriplex prostrata*, *Cakile maritima* subsp. *maritima, Euphorbia peplis*, *Convolvulus soldanella*, *Matthiola sinuata*, *Polygonum maritimum, Salsola kali*
N14 - Shifting coastal dunes (N = 185)	Mobile and semi-permanent dune systems including embryonic and shifting dunes	2110 - Embryonic shifting dunes (embryo dune) characterized by *Thinopyrum junceum* (= *Elymus farctus*)	*Achillea maritima* subsp. *maritima, Anthemis maritima* subsp. *maritima, Calamagrostis arenaria* subsp. *arundinacea*, *Centaurea aplolepa*, *Cyperus capitatus*, *Echinophora spinosa*, *Thinopyrum junceum*, *Eryngium maritimum*,

		2120 - Shifting dunes along the shoreline with *Ammophila arenaria* (white dune)	*Euphorbia paralias*, *Medicago marina*, *Ononis variegata*, *Solidago virgaurea* subsp. *litoralis*, *Sporobolus virginicus*, *Stachys maritima*
N16 - Coastal stable dune grasslands (N = 130)	Perennial grasslands of the fixed and semifixed dunes and annual species-rich communities that colonize grasslands clearings	2210 - *Crucianellion maritimae* fixed and semifixed dunes dominated by *Crucianella maritima* 2230 - *Malcolmietalia* dune grasslands 2240 - *Brachypodietalia* dune grasslands with annuals	*Crucianella maritima*, *Cutandia maritima*, *Daucus pumilus*, *Festuca fasciculata* (= *Vulpia fasciculata*), *Helichrysum stoechas*, *Lagurus ovatus*, *Lomelosia rutifolia*, *Marcus-kochia ramosissima*, *Medicago littoralis*, *Pancratium maritimum*, *Phleum arenarium* subsp. *caesium*, *Seseli tortuosum*, *Silene canescens*, *Sonchus bulbosus* subsp. *bulbosus, Tuberaria guttata*
N1B - Coastal dune shrubs (N = 136)	Stable dunes with *Juniperus* spp. communities or sclerophyllous shrubs	2250 - Coastal dunes with *Juniperus* spp. 2260 - *Cisto-Lavanduletalia* dune sclerophyllous shrubs	*Arbutus unedo*, *Asparagus acutifolius*, *Cistus creticus eriocephalus*, *Clematis flammula*, *Daphne gnidium*, *Erica multiflora*, *Juniperus oxycedrus*, *J. phoenicea*, *Lonicera implexa* subsp. *implexa, Myrtus communis*, *Osyris alba*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rhamnus alaternus* subsp. *alaternus, Rubia peregrina*, *Ruscus aculeatus*, *Salvia rosmarinus*, *Smilax aspera*, *Stachys major*

Table S2. List of all sampled plant species

List of all sampled species. Species are classified in typical (T), ruderal (R), alien (A). All species not included in these three categories were classified as other species (O). Species nomenclature and families follows Bartolucci et al. (2018) and Galasso et al. (2018). Species are sorted alphabetically by type, family and specie's name.

Family	Species	Type
AIZOACEAE	*Carpobrotus acinaciformis*	A
ASPARAGACEAE	*Yucca gloriosa*	A
ASPHODELACEAE	*Aloë maculata*	A
ASTERACEAE	*Ambrosia psilostachya*	A
ASTERACEAE	*Erigeron canadensis*	A
ASTERACEAE	*Erigeron sumatrensis*	A
ASTERACEAE	*Symphyotrichum squamatum*	A
ASTERACEAE	*Xanthium italicum*	A
FABACEAE	*Amorpha fruticosa*	A
FABACEAE	*Robinia pseudacacia*	A
PITTOSPORACEAE	*Pittosporum tobira*	A
POACEAE	*Arundo donax*	A

POACEAE	*Avena sterilis*	A
POACEAE	*Paspalum vaginatum*	A
POACEAE	*Phalaris canariensis*	A
POACEAE	*Sporobolus pumilus*	A
ROSACEAE	*Prunus armeniaca*	A
AMARYLLIDACEAE	*Pancratium maritimum*	T
ANACARDIACEAE	*Pistacia lentiscus*	T
APIACEAE	*Daucus pumilus*	T
APIACEAE	*Echinophora spinosa*	T
APIACEAE	*Eryngium maritimum*	T
APIACEAE	*Seseli tortuosum* subsp. *tortuosum*	T
ASPARAGACEAE	*Asparagus acutifolius*	T
ASPARAGACEAE	*Ruscus aculeatus*	T
ASTERACEAE	*Achillea maritima* subsp. *maritima*	T
ASTERACEAE	*Anthemis maritima* subsp. *maritima*	T
ASTERACEAE	*Centaurea aplolepa* subsp. *subciliata*	T
ASTERACEAE	*Helichrysum stoechas* subsp. *stoechas*	T
ASTERACEAE	*Solidago litoralis*	T
ASTERACEAE	*Sonchus bulbosus* subsp. *bulbosus*	T
BRASSICACEAE	*Cakile maritima* subsp. *maritima*	T
BRASSICACEAE	*Marcus-kochia ramosissima*	T
BRASSICACEAE	*Matthiola sinuata*	T
CAPRIFOLIACEAE	*Lomelosia rutifolia*	T
CAPRIFOLIACEAE	*Lonicera implexa* subsp. *implexa*	T
CARYOPHYLLACEAE	*Silene canescens*	T
CHENOPODIACEAE	*Atriplex prostrata*	T
CHENOPODIACEAE	*Salsola kali*	T
CISTACEAE	*Cistus creticus* subsp. *eriocephalus*	T
CISTACEAE	*Tuberaria guttata*	T
CONVOLVULACEAE	*Convolvulus soldanella*	T
CUPRESSACEAE	*Juniperus oxycedrus*	T
CUPRESSACEAE	*Juniperus phoenicea*	T
CYPERACEAE	*Cyperus capitatus*	T
ERICACEAE	*Arbutus unedo*	T
ERICACEAE	*Erica multiflora* subsp. *multiflora*	T
EUPHORBIACEA	*Euphorbia paralias*	T
EUPHORBIACEA	*Euphorbia peplis*	T
FABACEAE	*Medicago littoralis*	T
FABACEAE	*Medicago marina*	T
FABACEAE	*Ononis variegata*	T
LAMIACEAE	*Salvia rosmarinus*	T
LAMIACEAE	*Stachys major*	T
LAMIACEAE	*Stachys maritima*	T
MYRTACEAE	*Myrtus communis*	T
OLEACEAE	*Phillyrea angustifolia*	T
POACEAE	*Calamagrostis arenaria* subsp. *arundinacea*	T

POACEAE	*Cutandia maritima*	T
POACEAE	*Elymus farctus*	T
POACEAE	*Festuca fasciculata*	T
POACEAE	*Lagurus ovatus*	T
POACEAE	*Phleum arenarium* subsp. *caesium*	T
POACEAE	*Sporobolus virginicus*	T
POLYGONACEAE	*Polygonum maritimum*	T
RANUNCULACEAE	*Clematis flammula*	T
RHAMNACEAE	*Rhamnus alaternus* subsp. *alaternus*	T
RUBIACEAE	*Crucianella maritima*	T
RUBIACEAE	*Rubia peregrina*	T
SANTALACEAE	*Osyris alba*	T
SMILACACEAE	*Smilax aspera*	T
THYMELAEACEAE	*Daphne gnidium*	T
APIACEAE	*Crithmum maritimum*	O
ARALIACEAE	*Hedera helix* subsp. *helix*	O
ARECACEAE	*Chamaerops humilis*	O
ASTERACEAE	*Chondrilla juncea*	O
ASTERACEAE	*Cichorium intybus*	O
ASTERACEAE	*Cota tinctoria*	O
ASTERACEAE	*Hedypnois rhagadioloides*	O
ASTERACEAE	*Hypochaeris achyrophorus*	O
ASTERACEAE	*Hypochaeris glabra*	O
ASTERACEAE	*Hypochaeris radicata*	O
ASTERACEAE	*Jacobaea maritima* subsp. *maritima*	O
ASTERACEAE	*Limbarda crithmoides* subsp. *longifolia*	O
ASTERACEAE	*Reichardia picroides*	O
ASTERACEAE	*Urospermum dalechampii*	O
BRASSICACEAE	*Maresia nana*	O
BRASSICACEAE	*Raphanus raphanistrum* subsp. *landra*	O
CAMPANULACEAE	*Campanula rapunculus*	O
CAPRIFOLIACEAE	*Sixalix atropurpurea*	O
CARYOPHYLLACEAE	*Arenaria leptoclados* subsp. *leptoclados*	O
CARYOPHYLLACEAE	*Arenaria serpyllifolia* subsp. *serpyllifolia*	O
CARYOPHYLLACEAE	*Cerastium diffusum* subsp. *diffusum*	O
CARYOPHYLLACEAE	*Petrorhagia prolifera*	O
CARYOPHYLLACEAE	*Silene otites*	O
CHENOPODIACEAE	*Atriplex halimus*	O
CHENOPODIACEAE	*Halimione portulacoides*	O
CISTACEAE	*Cistus creticus* subsp. *creticus*	O
CONVOLVULACEAE	*Convolvulus* sp.	O
CONVOLVULACEAE	*Cuscuta* sp.	O
CYPERACEAE	*Carex flacca* s.l.	O
CYPERACEAE	*Cyperus rotundus*	O
CYPERACEAE	*Schoenus nigricans*	O
EQUISETACEAE	*Equisetum ramosissimum*	O

EUPHORBIACEA	*Euphorbia barrelieri*	O
EUPHORBIACEA	*Euphorbia peplus*	O
FABACEAE	*Lotus hirsutus*	O
FABACEAE	*Medicago lupulina*	O
FABACEAE	*Medicago rigidula*	O
FABACEAE	*Onobrychis caput-galli*	O
FABACEAE	*Ononis reclinata*	O
FABACEAE	*Trifolium angustifolium* subsp. *angustifolium*	O
FABACEAE	*Trifolium dubium*	O
FABACEAE	*Trifolium squamosum*	O
FABACEAE	*Trifolium striatum* subsp. *striatum*	O
FAGACEAE	*Quercus ilex* subsp. *ilex*	O
GENTIANACEAE	*Blackstonia perfoliata*	O
GENTIANACEAE	*Centaurium erythraea*	O
GERANIACEAE	*Geranium pusillum*	O
JUNCACEA	*Juncus acutus* subsp. *acutus*	O
JUNCACEA	*Juncus inflexus* subsp. *inflexus*	O
LAMIACEAE	*Clinopodium nepeta*	O
LAMIACEAE	*Mentha suaveolens* subsp. *suaveolens*	O
LAMIACEAE	*Stachys arvensis*	O
LAMIACEAE	*Teucrium capitatum* subsp. *capitatum*	O
LAMIACEAE	*Teucrium flavum* subsp. *flavum*	O
LAMIACEAE	*Teucrium polium* subsp. *polium*	O
LINACEAE	*Linum corymbulosum*	O
LINACEAE	*Linum maritimum*	O
LINACEAE	*Linum strictum*	O
LINACEAE	*Linum tenuifolium*	O
OLEACEAE	*Phillyrea latifolia*	O
ONAGRACEAE	*Oenothera* sp.	O
OROBANCHACEAE	*Odontites luteus* subsp. *luteus*	O
OROBANCHACEAE	*Orobanche minor*	O
PAPAVERACEAE	*Fumaria bicolor*	O
PAPAVERACEAE	*Glaucium flavum*	O
PINACEAE	*Pinus pinaster* subsp. *pinaster*	O
PINACEAE	*Pinus pinea*	O
PLANTAGINACEAE	*Plantago coronopus*	O
PLUMBAGINACEAE	*Limonium multiforme*	O
POACEAE	*Alopecurus myosuroides* subsp. *myosuroides*	O
POACEAE	*Ampelodesmos mauritanicus*	O
POACEAE	*Anisantha rubens*	O
POACEAE	*Avena barbata*	O
POACEAE	*Avena fatua*	O
POACEAE	*Brachypodium rupestre*	O
POACEAE	*Brachypodium* sp.	O
POACEAE	*Brachypodium sylvaticum*	O
POACEAE	*Imperata cylindrica*	O

POACEAE	*Parapholis incurva*	O
POACEAE	*Phleum hirsutum* subsp. *ambiguum*	O
POACEAE	*Phragmites australis*	O
POACEAE	*Rostraria pubescens*	O
POACEAE	*Tripidium ravennae* subsp. *ravennae*	O
POLYGONACEAE	*Rumex bucephalophorus*	O
RESEDACEAE	*Reseda alba*	O
ROSACEAE	*Rubus hirtus*	O
RUBIACEAE	*Asperula cynanchica* subsp. *cynanchica*	O
RUBIACEAE	*Galium murale*	O
RUBIACEAE	*Sherardia arvensis*	O
SOLANACEAE	*Solanum* sp.	O
TAMARICACEAE	*Tamarix africana*	O
TAMARICACEAE	*Tamarix gallica*	O
THYMELAEACEAE	*Daphne sericea*	O
ULMACEAE	*Ulmus minor*	O
APIACEAE	*Daucus carota*	R
APIACEAE	*Torilis arvensis* subsp. *arvensis*	R
ASTERACEAE	*Centaurea sphaerocephala* subsp. *sphaerocephala*	R
ASTERACEAE	*Crepis foetida* subsp. *foetida*	R
ASTERACEAE	*Dittrichia viscosa* subsp. *viscosa*	R
ASTERACEAE	*Scolymus hispanicus*	R
ASTERACEAE	*Sonchus asper*	R
ASTERACEAE	*Sonchus oleraceus*	R
BORAGINACEAE	*Myosotis arvensis*	R
BRASSICACEAE	*Raphanus raphanistrum*	R
CARYOPHYLLACEAE	*Cerastium glomeratum*	R
CHENOPODIACEAE	*Chenopodium album* subsp. *album*	R
CONVOLVULACEAE	*Convolvulus arvensis*	R
FABACEAE	*Medicago minima*	R
FABACEAE	*Trifolium campestre*	R
FABACEAE	*Vicia bithynica*	R
GERANIACEAE	*Geranium purpureum*	R
OROBANCHACEAE	*Orobanche artemisiae-campestris*	R
PAPAVERACEAE	*Papaver rhoeas* subsp. *rhoeas*	R
POACEAE	*Anisantha madritensis* subsp. *madritensis*	R
POACEAE	*Anisantha rigida*	R
POACEAE	*Anisantha sterilis*	R
POACEAE	*Anisantha tectorum*	R
POACEAE	*Catapodium balearicum*	R
POACEAE	*Catapodium hemipoa*	R
POACEAE	*Cynodon dactylon*	R
POACEAE	*Dactylis glomerata*	R
POACEAE	*Elymus repens* subsp. *repens*	R
POACEAE	*Poa bulbosa*	R

POLYGONACEAE	*Polygonum aviculare* subsp. *aviculare*	R
PRIMULACEAE	*Lysimachia arvensis*	R
RANUNCULACEAE	*Clematis vitalba*	R
ROSACEAE	*Rubus ulmifolius*	R
SCROPHULARIACEAE	*Verbascum sinuatum*	R

Table S3. List of mapped land cover classes

List of mapped land cover classes expanded up to the fourth level of detail of the CORINE code (and description). A detailed description of each class is also reported. In bold was indicated the reference to each specific coverage class in this paper.

CORINE Code	CORINE Description	Detailed description
1.1.1.2.	Artificial areas	**Artificial facilities**, including urban fabrics, and industrial and commercial units
1.4	Artificial, non-agricultural vegetated areas	**Tourism facilities**, including bathing houses and camping
2	Agricultural areas	**Agricultural areas**, including arable land, permanent crops, pastures, and heterogeneous agricultural areas.
3.1.2.1	Afforestation	**Coniferous afforestation** on coastal dunes with *Pinus* spp.
3.1.3.1	Mixed forests	**Mixed forests**: vegetation formation composed principally of trees, including shrub and bush understorey, where neither broad-leaved nor coniferous species predominate
3.2.3.1.	Mediterranean maquis	**Woody dune vegetation** growing on fixed dune. Includes shrub and sclerophyll communities dominated by *Juniperus* spp. and *Cistus-Lavenduletalia* typical of the EUNIS habitat: N1B
3.2.4.1.	Semi-natural Woody Vegetation	Bushy vegetation with scattered trees represented by foredune woodland degradation or forest regeneration/recolonization
3.2.4.2.	Semi-natural Herbaceous Vegetation	Abandoned meadows and pastures with different degree of degradation or recolonization
3.3.1.1.	Open sand	**Beach pioneer vegetation**: upper beach characterised by open sand colonised by pioneer annual vegetation. Includes the EUNIS habitat N12

3.3.1.2.	Herbaceous Dune Vegetation	**Herbaceous Dune Vegetation**: foredunes colonised by herbaceous vegetation intermingled to open sectors. Includes the EUNIS habitat N14 and N16
4	Wetlands	Inland and coastal wetlands and marshes

Table S4. List of predictors used in the linear and generalized linear models, and in structural equation models.

All variables below were calculated within each linear buffer. Exceptions are: distance to artificial areas, distance to tourism facilities, and shoreline dynamism, which were measured in term of minimum distance from each vegetation plot. Variables in bold were not correlated in the variance inflation factors (VIF; ginv function, MASS R package, Venables and Ripley 2002), and therefore were included in the statistical analyses.

Name	Description
Beach pioneer vegetation (%)	Proportion (%) of areas covered by beach pioneer vegetation land cover class
Herbaceous dune vegetation (%)	Proportion (%) of areas covered by herbaceous dune vegetation land cover class
Woody Dune Vegetation (%)	Proportion (%) of areas covered by woody dune vegetation land cover class
Mixed forests (%)	Proportion (%) of areas covered by mixed forests land cover class
Coniferous afforestation (%)	Proportion (%) of areas covered by coniferous afforestation with *Pinus* spp. land cover class
Agricultural (%)	Proportion (%) of areas covered by agricultural land cover class
Artificial areas (%)	Proportion (%) of areas covered by artificial land cover class
Tourism facilities (%)	Proportion (%) of areas covered by tourism facilities land cover class
Landscape diversity (Shannon's index)	Shannon's diversity Index of land cover class
Landscape diversity (Simpson's index)	Simpson's diversity index of land cover class
Number of classes	Number of land cover classes
Distance to artificial areas	Minimum distance from each vegetation plot to the centroid of artificial patches

Distance to tourism facilities	Minimum distance from each vegetation plot to the centroid of touristic patches
Shoreline dynamism	Shoreline erosion (negative values) and accretion (positive values) between 2010 - 2019
Latitude	Latitude (Y coordinate) of each vegetation plot

Table S5. Summary of the model for species richness. Statistically significant relationships are highlighted in bold. Adjusted R^2: 35%

	Richness			
Predictors	***Estimate***	***Std. Error***	***z-value***	***p-Value***
(Intercept)	4.10	2.71	1.51	0.131
EUNIS N16	0.01	0.12	0.07	0.942
EUNIS N1B	0.03	0.11	0.25	0.803
Beach Pioneer Veg. (%)	**1.32**	**0.25**	**5.36**	**<0.001**
Herbaceous Dune Veg. (%)	0.34	0.26	1.30	0.193
Woody Dune Veg. (%)	-0.29	0.26	-1.11	0.265
Agriculture (%)	**0.46**	**0.22**	**2.07**	**<0.05**
Artificial areas (%)	**0.43**	**0.20**	**2.21**	**<0.05**
Tourism facilities (%)	0.09	0.25	0.36	0.718
Mixed forests	-0.29	0.22	-1.35	0.176
Coniferous afforestation	0.01	0.16	0.08	0.935
Distance to artificial areas	**-0.00**	**0.00**	**-2.11**	**<0.05**
Shoreline dynamism	-0.00	0.00	-0.06	0.949
Landscape diversity (Shannon's index)	0.12	0.07	1.66	0.097
Latitude	-0.06	0.06	-0.94	0.346
EUNIS N16:Herbaceous dune vegetation (%)	**0.44**	**0.22**	**1.96**	**<0.05**
EUNIS N1B:Herbaceous dune vegetation (%)	**0.57**	**0.22**	**2.64**	**<0.01**
EUNIS N16:Woody dune vegetation (%)	0.15	0.38	0.40	0.686
EUNIS N1B:Woody dune vegetation (%)	**0.71**	**0.30**	**2.36**	**<0.05**
EUNIS N16:Agriculture (%)	**1.25**	**0.35**	**3.60**	**<0.001**
EUNIS N1B:Agriculture (%)	**-1.47**	**0.67**	**-2.18**	**<0.05**
EUNIS N16:Artificial areas (%)	**0.81**	**0.27**	**3.03**	**<0.01**
EUNIS N1B:Artificial areas (%)	0.30	0.24	1.27	0.204

Table S6 Summary of the model for proportion of typical and ruderal species. Statistically significant relationships are highlighted in bold. Adjusted R^2: 32% (proportion of typical species); 21% (proportion of ruderal species).

	Proportion of typical species				***Proportion of ruderal species***			
Predictors	***Estimate***	***Std. Error***	***z-value***	***p-Value***	***Estimate***	***Std. Error***	***z-value***	***p-Value***
(Intercept)	**13.57**	**5.78**	**2.35**	**<0.05**	**-66.59**	**12.13**	**-5.49**	**<0.001**
EUNIS N16	**-2.84**	**0.61**	**-4.70**	**<0.001**	**0.78**	**0.19**	**4.06**	**<0.001**
EUNIS N1B	**-1.05**	**0.48**	**-2.19**	**<0.05**	**0.92**	**0.20**	**4.64**	**<0.001**
Beach pioneer vegetation (%)	-1.43	0.74	-1.93	0.054	-1.05	1.12	-0.94	0.349
Herbaceous dune vegetation (%)	-0.29	0.59	-0.48	0.628	-1.05	0.95	-1.11	0.268
Woody dune vegetation (%)	**0.87**	**0.41**	**2.12**	**<0.05**	-1.03	0.84	-1.23	0.219
Agriculture (%)	**-1.44**	**0.47**	**-3.10**	**<0.01**	**2.71**	**0.81**	**3.33**	**<0.001**
Artificial areas (%)	**-2.01**	**0.41**	**-5.14**	**<0.001**	1.10	0.73	1.51	0.132
Tourism facilities (%)	-0.71	0.53	-1.35	0.177	0.55	1.08	0.50	0.614
Mixed forests	**-1.13**	**0.54**	**-2.11**	**<0.05**	-0.33	0.92	-0.36	0.716
Coniferous afforestation	-0.23	0.33	-0.71	0.478	-0.62	0.77	-0.80	0.424
Distance to artificial areas	**-0.00**	**0.00**	**-2.98**	**<0.01**	0.00	0.00	0.36	0.718
Shoreline dynamism	0.00	0.00	1.15	0.250	-0.01	0.01	-1.91	0.056
Landscape diversity (Shannon's index)	-0.34	0.23	-1.46	0.146	0.19	0.30	0.64	0.520
Latitude	**-0.28**	**0.14**	**-2.04**	**<0.05**	**1.47**	**0.29**	**5.12**	**<0.001**

EUNIS N16:Beach pioneer vegetation (%)	**2.42**	**0.93**	**2.61**	**<0.01**	-	-	-	-
EUNIS N1B:Beach pioneer vegetation (%)	0.95	0.96	0.98	0.326	-	-	-	-
EUNIS N16:Herbaceous dune vegetation (%)	**1.92**	**0.56**	**3.43**	**<0.001**	-	-	-	-
EUNIS N1B:Herbaceous dune vegetation (%)	**-1.03**	**0.53**	**-1.98**	**<0.05**	-	-	-	-
EUNIS N16:Agriculture (%)	-0.76	0.84	-1.00	0.364	-	-	-	-
EUNIS N1B:Agriculture (%)	**5.70**	**1.70**	**3.36**	**<0.001**	-	-	-	-
EUNIS N16:Artificial areas (%)	**2.14**	**0.57**	**3.76**	**<0.001**	-	-	-	-
EUNIS N1B:Artificial areas (%)	**1.98**	**0.49**	**4.06**	**<0.001**	-	-	-	-
EUNIS N16:Mixed forests (%)	0.82	0.80	1.01	0.311	-	-	-	-
EUNIS N1B:Mixed forests (%)	**3.92**	**1.16**	**3.39**	**0.001**	-	-	-	-
EUNIS N16: Distance to artificial areas	-0.00	0.00	0.18	**0.855**	-	-	-	-
EUNIS N1B: Distance to artificial areas	**0.00**	**0.00**	**2.10**	**<0.05**	-	-	-	-
EUNIS N16:Landscape diversity (Shannon's index)	**0.86**	**0.39**	**2.21**	**<0.05**	-	-	-	-
EUNIS N1B:Landscape diversity (Shannon's index)	-0.38	0.34	-1.13	0.259	-	-	-	-

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