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RESEARCH ARTICLE

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

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Abstract

Context 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 is thus crucial for preserving Mediterranean coastal ecosystems.

Objectives We investigated the influence of natural factors, anthropogenic activities and shoreline dynamism on different facets of plant diversity, i.e. species richness and the proportion of typical and ruderal species. Moreover, we examined whether natural and anthropogenic factors act as direct or rather indirect drivers of the loss of dune plant diversity.

Methods 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 dune plant species richness, as well as the proportion of typical and ruderal species, related to the landscape variables and shoreline dynamism. Also, using piecewise structural equation modelling,

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we investigated the complex interplay between landscape variables and shoreline dynamism in shaping coastal plant diversity patterns.

Results 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 were favoured under human-related disturbance, while typical species of the foredune decreased in areas subject to high anthropogenic pressure. Results of the structural equation models highlighted that shoreline dynamism indirectly affected dune plant diversity through its influence on the landscape configuration.

Conclusions Our results indicate 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. Finally, results show that coastal erosion acts as an indirect driver of plant diversity loss.

Keywords Aerial orthophotos · Coastal erosion · Coastal tourism · Dune vegetation · Habitat types · Land cover map · Remote sensing · Species guilds · Typical species

Introduction

Coastal dunes are transitional ecosystems characterised 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 (Jones et al. 2008; Barbier et al. 2011).

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 colonise 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 strongly 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). For example, tourism has altered the structure and plant 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; Vousdoukas et al. 2020). 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, while simultaneously accounting 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.

In this context, 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 (iii) assess whether they directly affect dune vegetation or rather mediate other factors' effect.

Materials and methods

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; Fig. 1a). We focused on 8 sites covering almost the entirety of the sandy coasts of Tuscany (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 characterised by a latitudinal gradient of climate and anthropogenic activity, with the northern sector being overall wetter (higher precipitation) and more densely urbanised (Venturi et al. 2014; Zullo et al. 2015; Fratianni and Acquaotta 2017; Pesaresi et al. 2017). Despite various countermeasures (Pranzini et al. 2018), almost 50% of 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 23.6% 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).

Sampling of vegetation data

Between 2018 and 2021, we sampled 473 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

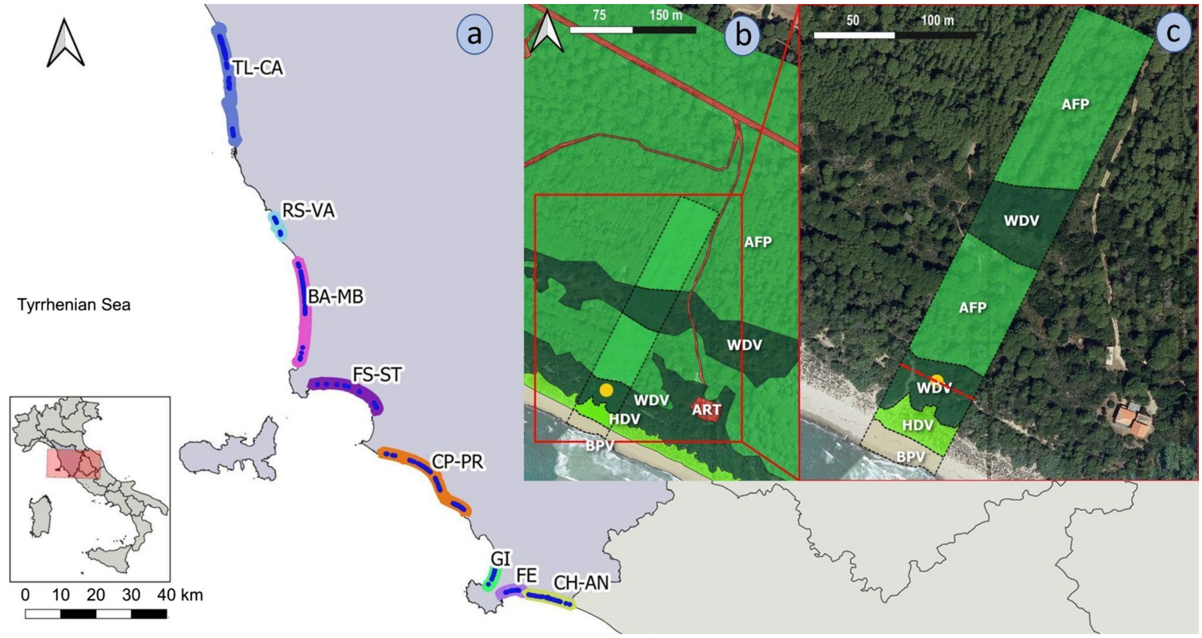

Fig. 1 Study area. Panel **a**: distribution of vegetation plots within the eight analysed coastal sites (highlighted in different colours): TL-CA (from Dune Litoranee di Torre del Lago to Calambrone); RS-VA (Rosignano Solvay and Vada); BA-MB (from Marina di Bibbona to Baratti); FS-ST (from Parco Costiero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

design across an area of approximatively 5.7 km^2. The two sampling strata were 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 135 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 (Supplementary Information, Appendix 1, Table S1). In each plot, we recorded the presence and cover of all plant species. Species cover was visually estimated and expressed on a percentage scale with a 10% interval rank. Nomenclature follows the Portal to the Flora of Italy 2024).

Plant diversity and proportion of typical and ruderal species

For each plot, we computed the 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 (Supplementary Information, Appendix 1, 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 (Supplementary Information, Appendix 1, 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).

Remote sensing data

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

Land cover map

We produced a detailed land cover map (scale 1:2000, Fig. 1b) by photo interpretation in a QGIS environment (QGIS Development Team 2018). We used both RGB (red–green–blue, i.e. natural colour) and NirGB (near infrared, i.e. modified false colour) orthophotos to enhance the discrimination of conifer taxa (appearing in dark red on the NirGB band) 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 (Supplementary Information, Appendix 1, 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 colonised 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). Land cover types associated with forest vegetation included the evergreen mixed forest and coniferous afforestation found along the innermost and better preserved sandy coasts. 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).

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 (Supplementary Information, Appendix 1, Table S3).

Landscape metrics

Using the land cover map outlined in Sect. Land cover map, we derived a set of metrics describing different characteristics of the coastal landscape.

Specifically, to define the spatial configuration of natural and anthropogenic patches and combine this information with floristic data from the plot, we used the linear buffer approach proposed by Malavasi et al. (2018). In a nutshell, this approach consists in: (1) creating a rectangular buffer around each vegetation plot (Fig. 1b); (2) cropping the portion of the land cover map that intersects the perimeter of the rectangular buffer (Fig. 1c); and (3) computing on the cropped land cover map a set of metrics (see below) characterising the landscape configuration around the vegetation plot. The landscape metrics computed from each rectangular buffer are then assigned (when building the dataset for the analyses) to the corresponding vegetation plot.

In our study, we first 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 adequate 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 within the buffer (e.g. proportion of artificial areas; see Supplementary Information Appendix 1, Table S4).

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; Simpson index: Simpson 1949).

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 in an area that underwent accretion between 2010 and 2019, while a negative value indicates an area that underwent erosion.

Statistical analysis

Response of dune plant communities to natural and anthropogenic factors

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; vif function, car R package, Fox and Weisberg 2019) for each predictor, and excluded those with a VIF value greater than or equal to 5 (Supplementary Information, Appendix 1, Table S4). The final set of predictors included: 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); the proportion of area covered by agricultural and artificial areas (among the anthropogenic land cover classes). Also, we included landscape diversity (Shannon's index), distance to artificial areas and shoreline dynamism. The initial set of predictors also considered the latitude (y-coordinate) of the vegetation plot, as previous studies observed a latitudinal gradient of dune species richness due to the north coast of Tuscany being overall wetter (higher precipitation) and more densely inhabited (Richerson and Lum 1980; Del Vecchio et al. 2018; D'Antraccoli et al. 2019; see also Sect. Study area). However, we subsequently decided to exclude latitude from the analyses as it was found to be highly correlated with the proportion of herbaceous dune vegetation). Finally, we hypothesised that the response of coastal dune plant communities to natural and anthropogenic factors would change along the coastal zonation and, as a result, across habitats. For this reason, we included the statistical interaction between habitat type (included as a categorical variable) and all predictors.

For each GLM, we started with a full model including the previously mentioned statistical interactions. Then, using likelihood ratio tests, we derived a series of reduced models by sequentially dropping terms for which there was no evidence of an interaction with habitat type (type II Anova implemented using the Anova function, car R package; Fox and Weisberg 2019). As a result, we obtained a 'most parsimonious model' including all predictors (main effects for the predictors involved in the statistical interaction), plus the terms associated with statistically significant interactions. Then, we compared the full model against both the most parsimonious and an intercept-only model using the Akaike Information Criterion (AIC; Burnham and Anderson 2004) and selected as best-fitting the one with the lowest AIC.

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.

Analysis of the interplay between natural and anthropogenic factors through 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 Supplementary Information, Appendix 1, Fig. S1 for a graphical representation of the meta-model). Specifically, we assumed that artificial land cover classes (related to urbanisation and agriculture) affected landscape diversity and shoreline dynamism (e.g. by favouring fragmentation and coastal erosion, respectively). In turn, we expected both the configuration of anthropogenic classes, landscape diversity and shoreline dynamism to affect the area covered by the three land cover classes associated with the dune 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 Sect. "Response of dune plant communities to natural and anthropogenic factors" (species richness, and proportion of typical and ruderal species) 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 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-value > 0.05).

Results

Species richness

The best fitting model for species richness explained 35% (adjusted R-squared) of the overall variability in the response (Fig. 2; Supplementary Information, Appendix 1, Table S5). Species richness increased with the increasing proportion of area covered by beach pioneer dune vegetation (z-value = 4.92, p-value < 0.001) and herbaceous dune vegetation (z-value = 3.17, p-value < 0.01) in all habitat types. The increasing proportion of agricultural areas had a positive effect on the species richness of coastal stable dune grasslands (EUNIS N16), but a negative effect on the species richness of coastal dune shrubs (N1B). In all habitat types, species richness increased with the proportion of artificial areas, with a more marked increment in coastal stable dune grasslands.

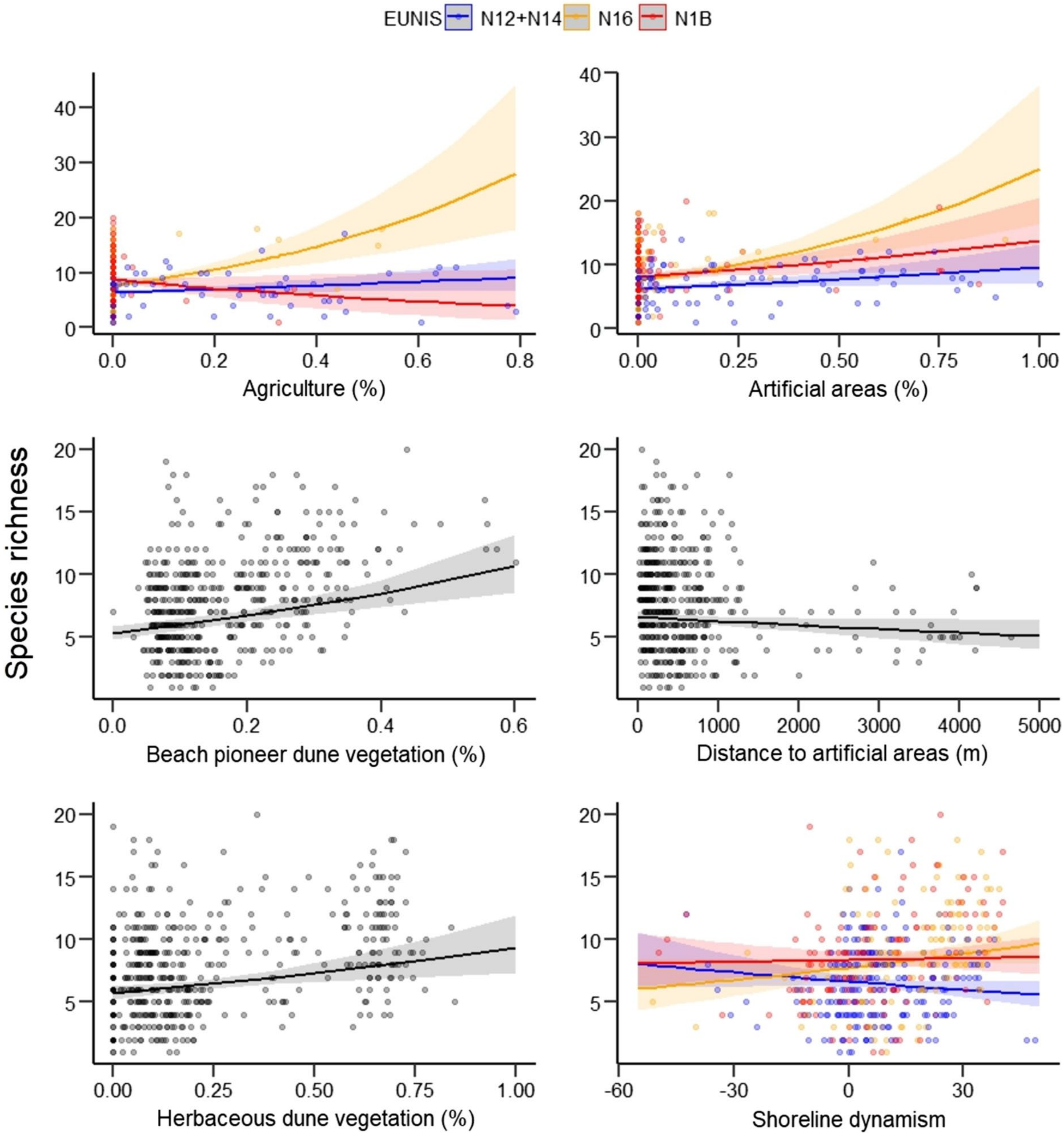

Fig. 2 Prediction plots of the model for species richness. Percentage '%' represents the proportion of area covered by the different land cover classes within the rectangular buffer. Bands represent 95% confidence intervals of the means. EUNIS habitat types codes: shifting dunes (N12+N14), coastal stable dune grasslands (N16), and coastal dune shrubs (N1B). For detailed information, see Supplementary Information, Appendix 1, Table S5

On the contrary, we observed an overall decrease in species richness at increasing distances from artificial facilities (z-value = −2.07, $p\text{-value} < 0.05$). Finally, we observed an increase in species richness of coastal stable dune grasslands and shrubs under coastal accretion, while species richness of shifting dunes (N12 + N14) increased under erosion.

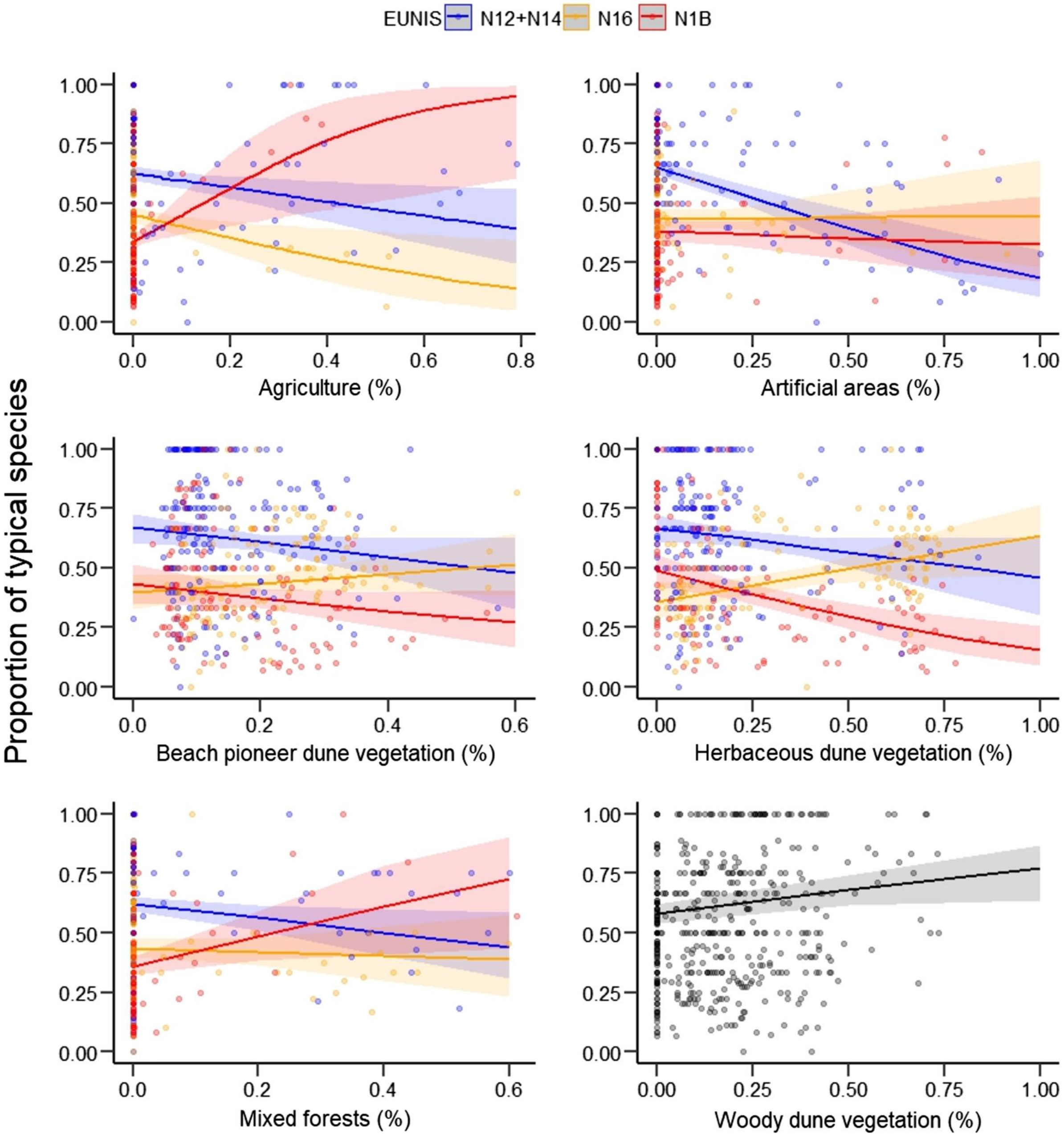

Fig. 3 Prediction plots of the model for the proportion of typical species. Percentage '%' represents the proportion of area covered by different land cover classes within the rectangular buffer. Bands represent 95% confidence intervals for the means. EUNIS habitat types codes: shifting dunes (N12 + N14), coastal stable dune grasslands (N16), and coastal dune shrubs (N1B). For detailed information, see Supplementary Information, Appendix 1, Table S6

Proportion of typical and ruderal species

Typical species

The best fitting model for the proportion of typical species explained 31% (adjusted R-squared) of the total variance (Fig. 3; Supplementary Information, Appendix 1, Table S6).

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 shrub habitats (EUNIS N12 + N14, N1B), and higher in coastal stable dune grasslands (N16). Large patches of beach pioneer and herbaceous dune vegetation mostly occurred in the northern coastal sectors, which underwent accretion and are usually characterized by strong urbanization and tourism. The proportion of typical species also increased at an increasing proportion of area covered by woody dune vegetation in all habitat types.

The proportion of typical species of all habitat types, except for coastal dune shrubs (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 species typical of these habitats decreased in highly urbanised locations.

Ruderal species

The best fitting model explained 19% (adjusted R-squared) of the total variance. An increase in the proportion of area covered by herbaceous dune vegetation was associated with a weak increase in ruderal species in all habitat types (z-value = 2.20, p-value = < 0.05). Also, we found that the proportion of ruderal species of all habitat types increased at increasing landscape diversity (z-value = 1.98, p-value = < 0.05) and decreased under coastal accretion (z-value = − 2.35, p-value < 0.05). In shifting dunes and coastal stable dune grasslands (EUNIS N12 + N14, N16), the proportion of ruderal species increased with increasing proportion of agricultural and artificial areas (z-value = 3.42, p-value = < 0.001 and z-value = 4.35, p-value = < 0.001, respectively) (Fig. 4; Supplementary Information, Appendix 1, Table S6).

Piecewise structural equation models

Our original meta-model, updated with pathways initially excluded, appeared to adequately fit the data: species richness, proportion of typical species, and proportion of ruderal species (Fisher's C = 10.505, p-value = 0.23).

We observed that a high proportion of artificial areas corresponded with a lower proportion of all land cover classes related to natural vegetation (Fig. 5a). Similarly, an increasing cover of agricultural areas was linked to a decrease in the proportion of beach pioneer vegetation, herbaceous dune vegetation and coniferous afforestation. In addition to reducing the cover of classes associated with coastal natural vegetation, anthropogenic areas seemed to be associated with stronger erosion (Fig. 5a).

More generally, shoreline dynamism indirectly affected species richness and the proportion of typical and ruderal species through its influence on coastal natural vegetation (Fig. 5a, b). In particular, accretion was positively associated with the proportion of beach pioneer vegetation and herbaceous dune vegetation, while erosion correlated with increased woody dune vegetation and coniferous afforestation (Fig. 5a).

Species richness, in turn, was favoured in areas with greater cover of beach pioneer vegetation and herbaceous dune vegetation, whereas typical species were less likely to be found in areas with a larger cover of coniferous afforestation and herbaceous dune vegetation.

On the other hand, ruderal species were favoured by the increasing cover of agricultural and artificial areas, which, on the contrary, had a direct, negative effect on typical species. Although, the proportion of ruderal species decreased at increasing distances from human facilities.

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

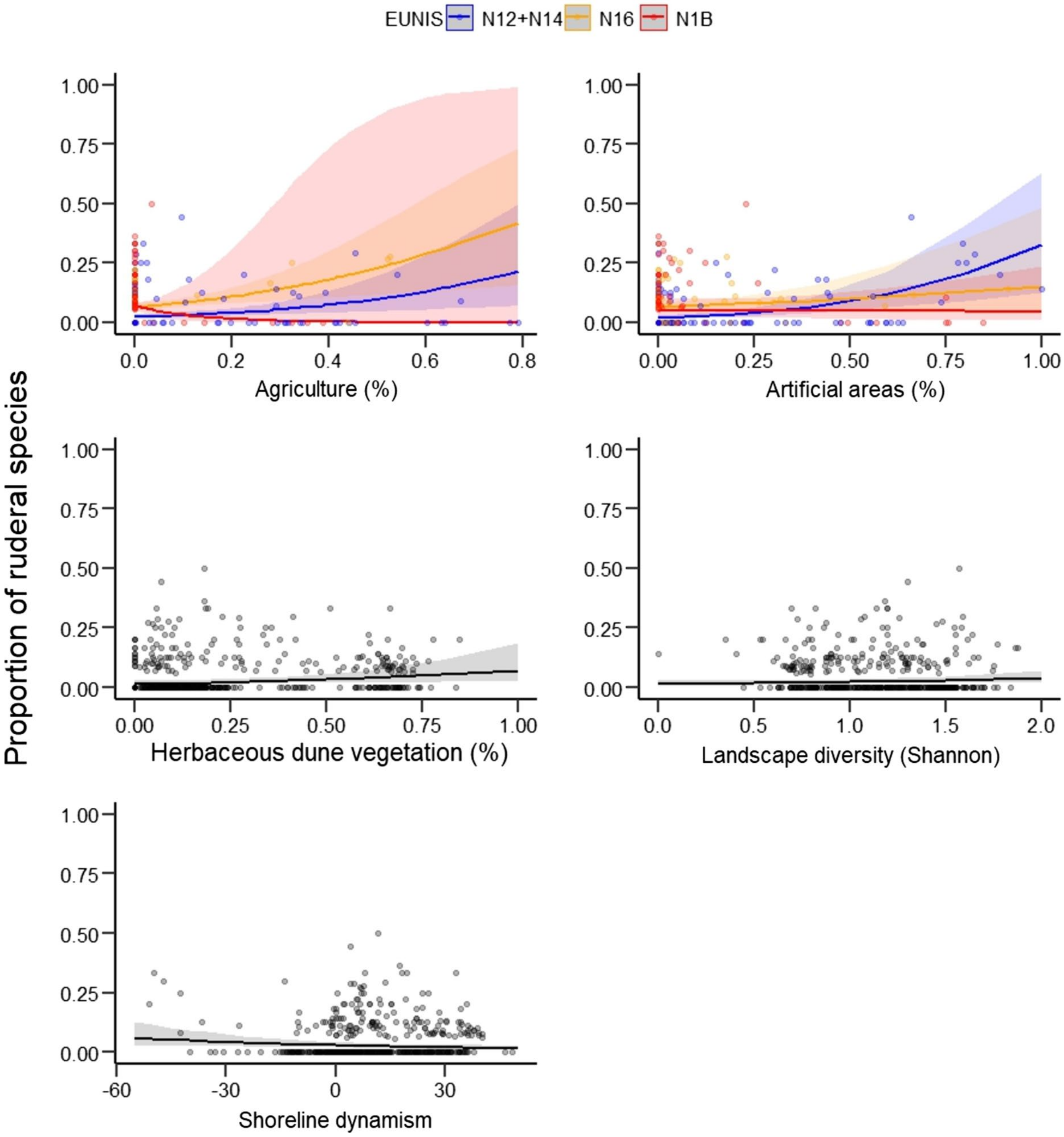

Fig. 4 Prediction plots of the model for the proportion of ruderal species. Percentage '%' represents the proportion of area covered by different land cover classes within the rectangular buffer. Bands represent 95% confidence intervals for the means. EUNIS habitat types codes: shifting dunes (N12 + N14), coastal stable dune grasslands (N16), and coastal dune shrubs (N1B). For detailed information, see Supplementary Information, Appendix1, Table S6

drift lines and shifting dunes, which are the most important habitats for the eco-morphodynamism of coastal dunes (Duarte et al. 2013; 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

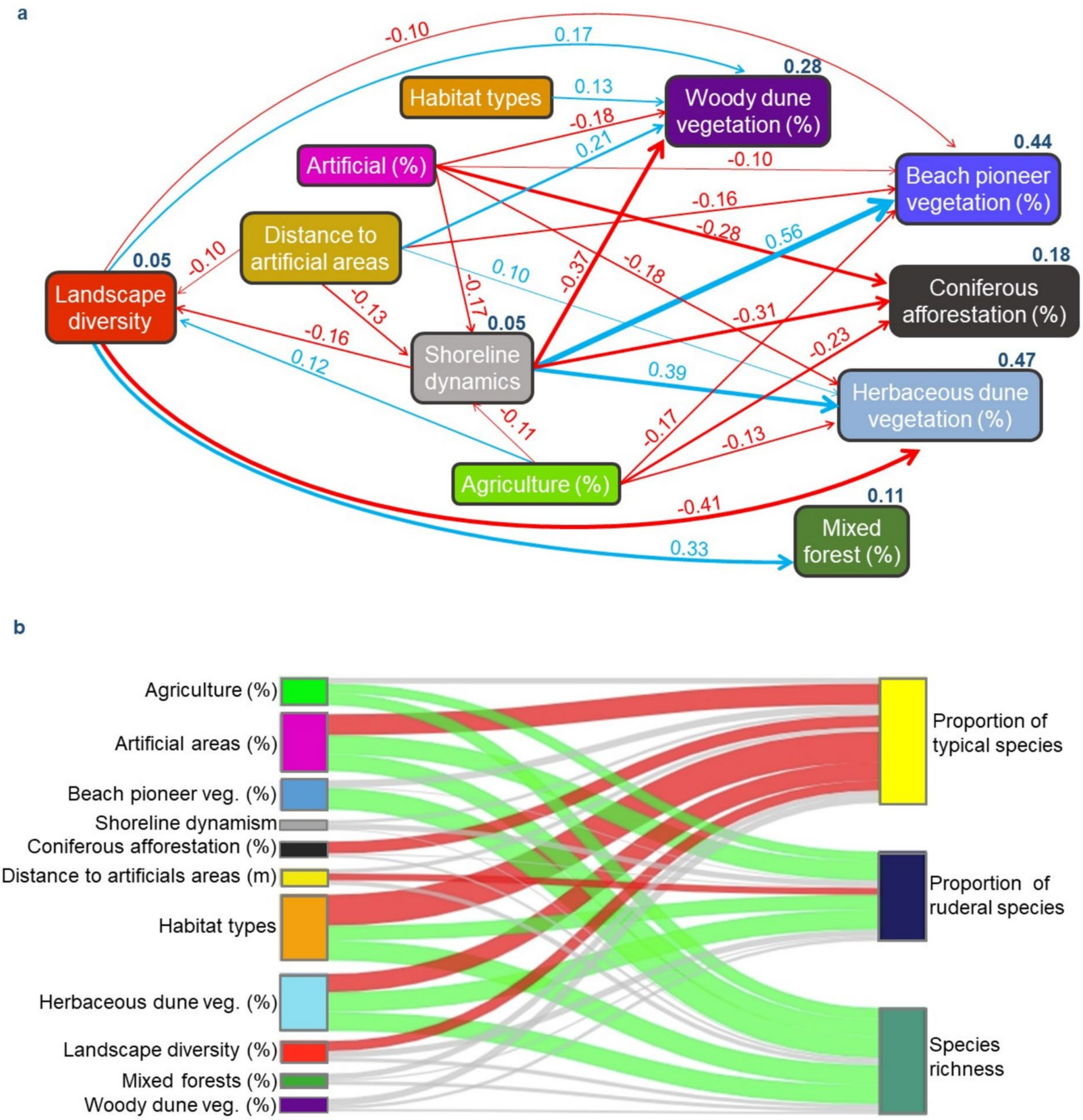

Fig. 5 Results of the piecewise structural equation models. Panel **a**: piecewise structural equation model representing the interplay among natural and anthropogenic factors affecting species richness, the proportion of typical and ruderal species. Note that the network of pathways reported in panel a is the same for all response variables (i.e. for species richness, typical and ruderal species), and it is therefore reported only once. Blue and red arrows represent positive and negative associations, respectively. Standardised coefficients are reported on top of arrows, while *R*-squared values are reported on top of boxes for endogenous variables. Panel **b**: associations between variables displayed in panel a and the three response variables. Green and red flows represent (statistically significant) positive and negative associations, respectively. Grey flows indicate non statistically significant relationships. The size of arrows (panel a) and flows (panel b) is proportional to the value of the corresponding standardised coefficients. Veg.: vegetation

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.

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 aligns with the phenomenon of coastal squeezing, which has been described and reported in previous studies on dune systems worldwide (Lithgow et al. 2009; Lansu et al. 2024).

Tourism (Keirbiriou et al. 2008; Calvão et al. 2013) and coastal erosion (Keijsers et al. 2015; Bazzichetto et al. 2020) exert their strongest impact on the foredune communities, through dune reshaping, flattening (Nordstrom 2021), and heavy trampling (Farris et al. 2013; Šilc et al. 2017). Further inland, urbanisation and agriculture encroach on coastal dune shrubs habitats, gradually reducing their extent (Kemper et al. 1999; Defeo et al. 2009; Malavasi et al. 2013).

The multiple facets of species richness

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, which is in line with the expectation that species richness is higher in well-preserved coastal dunes (García-Mora et al. 2000; Carboni et al. 2009; Sperandii et al. 2021). On the other hand, regardless of the habitat type, species richness also increased with urbanisation and high cover of agricultural fields, as also found by Aguilera et al. (2022) and Amorim et al. (2023) in, respectively, Chilean and Brazilian dune systems. However, analysing separate plant guilds revealed that the proportion of typical species (such as *Calamagrostis arenaria* subsp. *arundinacea* and *Thinopyrum junceum*) decreased under high anthropogenic disturbance, while the proportion of ruderal species (such as *Anisantha sterilis*, *Centaurea sphaerocephala* subsp. *sphaerocephala* and *Dittrichia viscosa* subsp. *viscosa*) 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 colonised 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. In this regard, our findings align with recent macroecology studies highlighting that, although human activities negatively impact biodiversity, species richness often fails to capture these effects, and may provide a sub-optimal measure of biodiversity change under anthropogenic pressure (Vellend 2017; Blowes et al 2019).

Further insights from typical and ruderal species

We found that 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). Specifically for shifting dunes, typical species are most commonly constituted by perennial rhizomatous geophytes characterised by relatively conservative strategies (e.g. slow-growing rates), such as *Calamagrostis arenaria* subsp. *arundinacea*, *Sporobolous pungens* and *Thinopyrum junceum*. These species are penalised under low sand burial and high landscape fragmentation, both conditions favoured by human activities (Maun 2009; Farris et al. 2013). Moving inland, we found that typical species of coastal dune shrubs were most abundant in areas with a high cover of mixed forests. These species (e.g. *Juniperus oxycedrus* and *J. phoenicea*) can only resist moderate disturbance, and therefore colonise the inner sectors of the coastal zonation, with milder environmental conditions. 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; Salgado et al. 2022).

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*), while constituting a perturbation for 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).

Concerning ruderal species, their presence (in all habitat types) seemed to be favoured by anthropogenic activities. Among the most common ruderal species, we found synanthropic plants such as *Anisantha sterilis*, *Cerastium glomeratum* and *Lysimachia arvensis.* Ruderal species usually colonise agricultural fields and areas subject to high anthropogenic disturbance (Malavasi et al. 2016; Rendeková and Mičieta 2017). Their potential spread from agricultural fields into neighbouring coastal habitats could explain the greater species richness (and lower proportion of typical species) which we found in stable dune grasslands in close proximity to large agricultural areas. A similar phenomenon was observed in plant invasion: agricultural fields (abandoned or still in use) serve as pools of alien species, which spread into adjacent natural habitats (Vilà and Ibáñez 2011). A larger proportion of ruderal species in coastal habitats is particularly worrying, as they do not have the same functional adaptations of typical species to the stressful environmental conditions of coastal dunes (e.g. succulent leaves, leaf rolling, and hairy leaves to respond to the high salt concentration; growth stimulation by sand burial). As a result, the replacement of typical species by ruderal species may, in the long-term, compromise the eco-morphodynamism process underpinning dune formation and maintenance (Hesp 2002; Acosta et al. 2007). Finally, we observed that the proportion of ruderal species also increased under high landscape diversity, which is related to habitat fragmentation and loss (Nagendra 2002; Joshi et al. 2006).

Complex interplay among the factors affecting dune vegetation

Structural equation models evidenced that shoreline dynamism and anthropogenic activities are important drivers of plant diversity patterns in coastal dunes (Nordstrom 2021; Lansu et al. 2024). As expected, we found that coastal erosion was stronger in areas with high cover of artificial areas, confirming that human activities can exacerbate erosion. Interestingly, shoreline dynamism affected dune vegetation only indirectly by influencing the extent of land cover classes linked to natural habitats. On one hand, coastal accretion corresponded to larger patches of foredune classes (beach pioneer and herbaceous dune vegetation), which in turn promoted species richness and ruderal plants. On the other hand, coastal sectors undergoing erosion were linked to larger patches of coniferous afforestation and a smaller proportion of typical species. At the same time, typical species were more likely to be found in areas with low herbaceous dune vegetation, which also occurred under erosion. Our findings thus suggest that shoreline dynamism is part of an intricate network of relationships, and its mediating effect on dune vegetation cannot be fully understood without accounting for the simultaneous effect of anthropogenic activities. We note, however, that the complexity of the pathways assumed by our meta-model makes it difficult to extend our results to coastal sectors that differ significantly from our study system (i.e. non-Mediterranean dunes).

In the last decades, conifer afforestation has gained high ecological, recreational, and landscape value (Mazza et al. 2011), but this has promoted an increase in anthropogenic pressure and its impact on dune habitats (Bonari et al. 2017). The strengthening in 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.

Author contributions M.B., S.S., C.A., and S.M. contributed to the study conception and design. S.S., C.A., A.B., M.G., B.F., S.M., and D.V. collected the vegetation data. S.S. analyzed the data with M.B., M.G.S., and V.B. S.S., M.B., M.G.S., and C.A. 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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Data Availability Data will be released upon request. An extract of the land cover map is available as a supplementary file.

Declarations

Conflict of interest The authors declare no competing interests.

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