Three decades later: A resurvey of vegetation biodiversity in Italian coastal dunes

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Abstract

Mediterranean coastal dunes have undergone substantial transformations over the last 70 years due to increasing anthropogenic pressure and environmental change. However, most studies on dune vegetation dynamics have been conducted at local scales, limiting our understanding of long-term plant diversity trends across broader regions. Here, we present the first national-scale assessment of long-term vegetation changes in Italian coastal dunes, based on ReSurveyDunes, a collaborative resurvey initiative. We analysed 519 vegetation plots originally surveyed on average 30 years ago and resampled in 2023-2024 along the entire Italian coastline. We quantified temporal changes in species richness and community composition, with a focus on ecological guilds, and analysed habitat transitions over time across three key dune habitats: upper beach, shifting dunes, and dune grasslands.

Species richness increased across all habitats. However, this trend masked a marked decline of habitat-specialist psammophilous species, particularly in early-successional habitats. Upper beach and shifting dunes showed strong reductions in occurrence and cover of diagnostic species, accompanied by increases in ruderal taxa and species typical of more stabilised or inland habitats. These patterns reflect a redistribution of species along the coastal zonation gradient. Accordingly, nearly one-third of plots changed EUNIS habitat type or disappeared, indicating the coexistence of inland-directed succession and stabilisation with localised degradation and habitat loss, especially in foredune habitats.

Our results show that apparent increases in species richness can conceal profound compositional and habitat-level changes. This highlights the importance of long-term, large-scale resurveys and of complementing richness-based metrics with compositional and habitat-level indicators when evaluating vegetation changes in dynamic coastal dune ecosystems.

Introduction

Coastal dune habitats are currently in a critically poor conservation status, particularly in the Mediterranean (EEA, 2020; Heslenfeld et al., 2008; Janssen et al., 2016). This severe condition, which is consistent across biogeographical regions, is particularly alarming because dune habitats provide essential ecosystem services (Drius et al., 2019; Everard et al., 2010). Major threats arise from increasing human pressures, including overtourism, urban and agricultural expansion, industrial and harbour development (Schlacher et al., 2007), as well as from the spread of non-native and ruderal species (Gao et al., 2020; Géhu & Biondi, 1994. These pressures are widespread along European coasts (EEA, 2020; Janssen et al., 2016), and Italy does not represent an exception. Italian coastal dune habitats are currently reported to be in a critically poor conservation status (Ercole et al., 2021), mirroring the general trends observed across the Mediterranean region. The most important pressures affecting Italian coastal dunes are urban and agricultural expansion (Carranza et al., 2020; Malavasi et al., 2013), tourism (Fantinato, 2019; Farris et al., 2013; Fenu et al., 2013), coastal erosion (Antonioli et al., 2017; Bazzichetto et al., 2020; Ciccarelli 2014), and biological invasions (Carboni et al., 2010).

Temporal changes in Mediterranean coastal dune ecosystems have been investigated using various approaches, including remote-sensing (Bertacchi & Lombardi, 2014; Chelli et al., 2022; Foti et al., 2021; Garcia-Lozano et al., 2018; Šilc et al., 2020), analysis of extensive vegetation data (Prisco et al., 2016a; Sperandii et al., 2018), and vegetation resurveys (Ciccarelli et al., 2025; Del Vecchio et al., 2015; Prisco et al., 2016a; Sarmati et al., 2025b; Sperandii et al., 2021). Among these, the resurveying approach, consisting in the re-sampling of historically surveyed vegetation plots (Kapfer et al., 2017), has proven particularly effective for tracking vegetation change in coastal dunes (Ciccarelli et al., 2025; Del Vecchio et al., 2015; Sperandii et al., 2021). Most resurvey studies conducted so far have consistently highlighted a long-term degradation of coastal dune systems, which has led to the replacement or simplification (homogenisation and loss of diagnostic species) of dune plant communities (Sciandrello et al, 2015; Sperandii et al., 2021), and in the decline of key habitat specialists (Sarmati et al., 2025b; Sperandii et al., 2019, 2021).

So far, studies addressing temporal changes in the vegetation of Italian coastal dunes have predominantly focused on small (Ciccarelli et al., 2025; Cini et al., 2025; Del Vecchio et al., 2015; Prisco et al., 2016b; Sarmati et al., 2025b) to medium-scale (Prisco et al., 2016a; Sperandii et al. 2021) areas. This limitation has hindered national-scale assessments of temporal trends, which are essential for coordinating management and conservation of these threatened ecosystems. In this context, comprehensive and geographically representative resurveying databases, such as ReSurveyEurope (Knollová et al., 2024) and LOTVS (Sperandii et al., 2022), represent a valuable, yet still largely unexplored, resource for evaluating broad-scale vegetation change.

Building on ReSurveyDunes (Acosta et al., 2025), a collaborative database of more than 500 resurveyed vegetation plots spanning the entire Italian sandy coastline, we provide the first national-level overview of long-term vegetation changes in Italian coastal dunes. Focusing on herbaceous coastal dune habitats, we aimed to: (i) analyse temporal trends in species richness and vegetation cover, with particular emphasis on typical, ruderal, and non-native species guilds; (ii) identify the species that most contribute to changes in community composition; and (iii) assess habitat-specific trajectories of change over time.

Materials and methods

Study area

Italian dune systems occur along the Tyrrhenian, Adriatic, and Ionian coasts and display considerable geomorphological variability, driven by differences in sediment supply, wind regimes, coastal dynamics, and human activity (Antonioli et al., 2017). The dune systems included in the ReSurveyDunes database (Acosta et al., 2025) and analysed in the present study cover nearly 10% of the Italian sandy coastline (~360 km) spanning 11 administrative regions and capturing a large share of the geographic and environmental heterogeneity of coastal dune systems in Italy (Fig. 1).

Across the study area, coastal dunes form a continuum of geomorphological and ecological units arranged along a pronounced sea-to-inland environmental gradient (Acosta et al., 2007). Along this gradient, vegetation follows a well-defined zonation pattern from pioneer annual species on the upper beach to perennial communities on fixed dunes, culminating in Mediterranean holm-oak forests (Acosta et al., 2009; Prisco et al., 2012).

Focusing on the herbaceous component of this coastal dune continuum, the upper beach represents the first vegetated zone, dominated by annual nitrophilous pioneer species. This community, largely restricted to Mediterranean coasts (Doing, 1985; Acosta et al., 2009), is highly dynamic and temporally unstable. Further inland, shifting dunes develop as reduced wind intensity promotes sand accumulation, facilitated by perennial rhizomatous dune-forming species (Prisco et al., 2012). Semi-fixed and fixed dunes support the most species-rich and structurally heterogeneous dune grasslands. On stable sands of the inner dune slopes, primary chamaephytic garrigues dominated by *Crucianella maritima* may develop. These communities are absent along the northern Adriatic coast (Prisco et al., 2012; Silan et al., 2017), where perennial grasslands are mainly composed of hemicryptophytes and chamaephytes often associated with mosses and lichens (Silan et al., 2017). Gaps within perennial vegetation are colonised by small annual therophytes, most commonly grasses and forbs (Prisco et al., 2012).

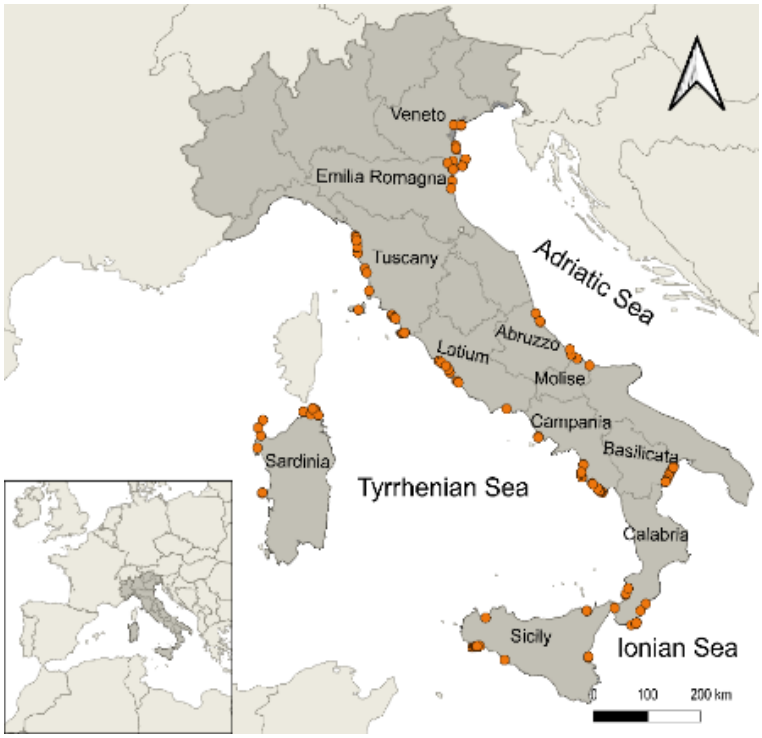

Fig. 1. **Study area**. Distribution of resurveyed historical plots (marked in orange) along the Italian coastal dunes.

Vegetation data

In this study, we relied on ReSurveyDunes (Acosta et al., 2025), an unprecedentedly harmonised database of resurveyed coastal dune vegetation plots compiled by a nationwide network of vegetation scientists. The dataset integrates historical Italian phytosociological relevés resurveyed after about 30 years. Specifically, the dataset consists of 519 vegetation plots, originally recorded between 1974 and 2009 using the phytosociological method and resurveyed in 2023-2024. The maximum time span between the earliest and the most recent survey is 50 years (mean = 30 years; median = 29 years). Analyses were restricted to historical plots that could be accurately relocated based on historical geographic coordinates or detailed topographic and location information (i.e. quasi-permanent vegetation plots; Kapfer et al., 2017). During the resurvey of historical plots, vegetation was recorded within plots having the same size of the corresponding historical relevé. The plot size ranged between 1 and 400 m^2 (median = 25 m^2; mean = 35.4 m^2). Historical as

well as resurveyed plots included a complete list of vascular plant species, with species abundance estimated using the seven-grade Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964). Values were subsequently converted to percentage cover using the mean value of each Braun-Blanquet interval. Metadata associated with each plot included geographic coordinates, location accuracy, sampling year, plot size, and site information.

This study focuses on three herbaceous–chamaephytic coastal dune habitats: upper beach, shifting dunes, and dune grasslands. Historical and resurveyed plots were initially assigned to level-3 EUNIS habitat types using an expert-based approach based on the occurrence and abundance of typical species. To confirm this assignment, we applied an automated, expert-validated classification tool developed for the EUNIS hierarchy (Chytrý et al., 2025), which confirmed that 93.4% of the historical data had been correctly classified (Table 1).

Table 1. **European habitat types of the historical plots**. List of the EUNIS habitat types identified in the historical vegetation plots (Chytrý et al., 2025; Davies et al., 2004). For each habitat type, the corresponding EUNIS code, a brief description, including the associated EU habitat (former Annex I of Directive 92/43/EEC), and a representative set of typical species for the study area are reported, as defined in the Italian Interpretation Manual of the Habitats Directive (Biondi et al., 2009; Biondi & Blasi, 2015). The number of historical plots assigned to each habitat type, together with their proportion of the total dataset is indicated.

Coastal dune habitat	EUNIS code	Description	n (%)	Typical species
Upper beach (UB)	N12	Mediterranean and Black Sea sand beach (EU habitat 1210 - Annual vegetation of drift lines)	78 (15%)	*Atriplex prostrata, Cakile maritima* subsp. *maritima, Euphorbia peplis, Glaucium flavum, Matthiola sinuata, Polygonum maritimum, Salsola kali, Soda inermis*
Shifting dunes (SD)	N14	Mediterranean, Macaronesian and Black Sea shifting coastal dune (including EU habitats: 2110 - Embryonic shifting dunes; 2120 - Shifting dunes along the shoreline with Ammophila arenaria)	332 (64%)	*Achillea maritima* subsp. *maritima*, *Anthemis maritima* subsp. *maritima, Calamagrostis arenaria* subsp. *arundinacea, Centaurea aplolepa* subsp. *subciliata, Convolvulus soldanella, Cyperus capitatus*, *Echinophora spinosa*, *Eryngium maritimum*, *Euphorbia paralias*, *Lotus creticus*, *Medicago marina*, *Pancratium maritimum, Silene succulenta* subsp. c*orsica, Sporobolus pungens, Stachys maritima, Thinopyrum junceum*
Dune grasslands (DG)	N16	Atlantic and Baltic coastal dune grasslands, grey dune (including EU habitats: 2130 - Fixed coastal dunes with herbaceous vegetation) and Mediterranean and Macaronesian coastal dune grasslands, grey dune (including EU habitats: 2210 - Crucianellion maritimae fixed beach dunes, and 2230 - Malcolmietalia dune grasslands)	109 (21%)	*Anchusa crispa* subsp. *crispa, Armeria pungens, Cerastium semidecandrum, Crucianella maritima*, *Cutandia maritima, Daucus pumilus, Ephedra distachya, Festuca fasciculata, Helichrysum italicum, H. stoechas, Lagurus ovatus, Marcus-kochia ramosissima, Maresia nana, Matthiola tricuspidata, Medicago littoralis, Ononis diffusa, O. variegata, Phleum arenarium, Poacynum venetum, Poterium sanguisorba, Rostraria litorea, Seseli tortuosum, Silene colorata, S. gallica, S. niceensis, S. otites* subsp. *otites, S. velutina, Sonchus bulbosus* subsp. *bulbosus*

Taxonomic harmonisation

Taxonomic nomenclature was standardised across both historical and resurveyed plots following Bartolucci et al. (2024). For non-native species, nomenclature followed Galasso et al. (2024).

To ensure consistency between historical and resurveyed plot compositions, we systematically checked for potential mismatches between species names, including cases where the same taxon was recorded under different names or where a historical taxon had subsequently been split into multiple entities but referred to the same biological unit. When a taxon was recorded in the historical plots both at the species and subspecies level, we retained the species-level identification for consistency, except in cases where only a single subspecies occurs in the study area, in which case the subspecies name was maintained.

Discrepancies in species nomenclature were resolved for 88 taxa (Supplementary Table S1).

Species-level guilds

Within each habitat, all recorded species were classified into four mutually exclusive ecological guilds: "typical species of the habitat", "typical species of other habitats", "ruderal species" and "non-native species". For example, *Calamagrostis arenaria* subsp. *arundinacea* was classified as a "typical species of the habitat" when occurring in shifting dunes, but as a "typical species of other habitats" when recorded outside shifting dunes.

Typical species were defined as diagnostic and constant taxa associated with their corresponding habitat type, based on the characteristic species combinations provided in the Italian Interpretation Manual of the Habitats Directive (Biondi et al., 2009; Biondi & Blasi, 2015). Typical species of dune habitats are key indicators of habitat integrity, are assumed to contribute substantially to habitat structure and functioning and are widely used as proxies for favourable conservation conditions (Bonari et al., 2021; Del Vecchio et al., 2015; Prisco et al., 2021). In contrast, ruderal and non-native taxa often indicate habitat degradation and disturbance (Biondi et al., 2012; Sarmati et al., 2025a).

Ruderal species were identified according to previous established classifications (Biondi et al., 2012; Del Vecchio et al., 2015; Prisco et al., 2017). For non-native taxa, only neophytes (i.e. species introduced after 1500 AD) were included in the analysis.

Data Analyses

1. Temporal trends in species richness and cover

To assess long-term trends in coastal dune vegetation, we separately analysed temporal change in species richness (i.e., the total number of species recorded in the plot) and total cover (i.e., the sum of the cover of all species in the plot). To this aim, we fitted generalised linear mixed-effects models (GLMMs) using the glmmTMB R package (function *glmmTMB;* Brooks et al., 2017). Specifically, for species richness we assumed a Poisson distribution and used a 'log' link, whereas for cover we assumed a Beta distribution and used a 'logit' link. Furthermore, zero-inflated models were applied to species richness to account for excess zeros in species richness data, primarily due to historical plots that could not be relocated during the resurvey.

Total cover required some transformations to be used in the model. First, since in some cases its value exceeded 100% due to overlapping vegetation layers, we rescaled it to the (0-1) interval. To achieve this, we divided the total cover of each plot by the maximum value observed across the dataset (Prisco et al., 2016a; Sperandii et al., 2018). Second, to accommodate beta-regression requirements, total cover values equal to 0 or 1 were adjusted to a slightly larger and smaller value, respectively, by adding or subtracting a small constant ($\varepsilon = 0.01$; Cribari-Neto & Zeileis, 2010). This was necessary because the Beta probability density function is not defined at 0 and 1. We repeated the same analyses focusing on all species together and separately for each ecological guild.

In the GLMMs, we included sampling time (categorical variable with two levels: historical or revisited), habitat type (categorical variable with three levels: upper beach, shifting dunes, and dune grasslands), and their statistical interaction as fixed effects. Additionally, we included plot size as a covariate to control for the variation in sampling area across plots. We then used the plot identifier nested within the site as random

intercepts to account for the repeated measures design and the fact that multiple plots were sampled in each site.

We assessed model predictive performance using R^2 values computed using the performance R package (Lüdecke et al., 2021). For standard GLMMs, we calculated both marginal and conditional R^2 (function *r2*; Nakagawa & Schielzeth, 2013). For zero-inflated models, we computed likelihood-based Pseudo-R^2 (function *r2_zeroinflated*), as variance-partitioning R^2 measures are not available for these models.

Model diagnostics were visually inspected using simulation-based residuals in the DHARMa R package (function *simulateResiduals*; Hartig, 2024). To compare temporal differences in species richness and total cover within each habitat type, we extracted model-based contrasts between sampling times (i.e., historical vs. revisited) using estimated marginal means (EMMs) and ran post-hoc pairwise comparisons using the emmeans R package (functions *ref_grid* and *contrast*; Lenth, 2025). For each model, the contrast estimates represent the effect of time on species richness or cover and were used to quantify temporal changes within habitats and species guilds. To facilitate interpretation on the response scale, 95% confidence intervals (CIs) were computed (function *confint*; R Core Team, 2022) and their endpoints exponentiated where appropriate (i.e. for species richness models with 'log' link). For species richness models, exponentiated estimates are interpreted as relative changes between historical and resurveyed plots, with values equal to 1 indicating no temporal change (exp(0) = 1). In this case, temporal effects were considered statistically significant when the endpoints of the 95% CIs did not overlap 1.

2. Changes in species composition

To identify the species contributing most to the average dissimilarity between historical and resurveyed plots within each habitat, we performed a SIMPER analysis based on Bray-Curtis dissimilarity (Bray & Curtis, 1957) and implemented with 999 permutations using the vegan R package (function *simper*; Oksanen et al., 2025). The SIMPER analysis decomposes average Bray-Curtis dissimilarity into species-specific contributions, thereby identifying the taxa primarily responsible for differences within and between groups (Oksanen et al., 2025). For each time-period, we calculated the percentage contribution of each species to total dissimilarity and ordered taxa according to their relative contribution. Temporal changes were assessed using permutation tests, and species were grouped by habitat type and ecological guild (i.e., typical species of the habitat, typical species of other habitats, ruderal species, and non-native species) to assess the relative contribution of each guild to community dynamics over time.

3. Habitat transitions

Assigning each vegetation plot at each time step to a level-3 EUNIS habitat type allowed the identification of potential habitat transitions within individual historical-resurvey plot pairs. For each pair, habitat-change trajectories were classified as follows:

i) stable plots, which remained within the same EUNIS habitat type at both time steps;

ii) progressive (successional) plots, which shifted towards more stabilised habitats, characterised by an increase in species typical of more inland habitats;

iii) regressive (retrogressive succession) plots, which shifted towards less stabilised or early-successional habitats, characterised by an increase in species typical of more seaward habitats;

iv) disappeared plots, historical plots that could not be resurveyed because they were completely unvegetated or submerged by the sea, reflecting vegetation loss driven by natural or anthropogenic processes.

Habitat trajectories were visualised using alluvial diagrams generated with ggplot2 (function *ggplot*; Wickham, 2016) and ggalluvial R packages (functions *geom_stratum* and *geom_flow*; Brunson & Read, 2023).

Results

A total of 433 plant species were recorded across both historical and resurveyed plots, of which 20.3% were typical species of dune habitats (n = 88). Of these, 1.8% (n = 8) were associated with the upper beach, 4.4% (n = 19) with shifting dunes, and 14.1% (n = 61) with dune grasslands (Supplementary Table S2). Ruderal species accounted for 22% of the total dataset (n = 95), whereas non-native species represented 7% (n = 30).

1. *Temporal trends in species richness and cover*

Temporal trends in species richness and cover showed complex dynamics, with overall increases of these metrics at the community level masking opposing trends among ecological guilds.

Mixed models revealed an increase in species richness over time in all habitats, with the largest increase observed in the upper beach (Fig. 2a; Supplementary Table S3).

Patterns varied markedly among ecological guilds, especially between ruderal and typical species and were strongly habitat-dependent (Fig. 2b-d; Supplementary Table S3). The number of ruderal species significantly increased over time in the upper beach and shifting dunes, with the largest increase in the upper beach. On the contrary, the richness of typical species of the habitat decreased in the upper beach and shifting dunes, while slightly increasing in dune grasslands. Typical species of other habitats exhibited a pattern similar to that of ruderal species, with their number significantly increasing in both the upper beach and shifting dunes (Fig. 2d). Finally, non-native species showed only minor, non-significant changes over time (Supplementary Table S3).

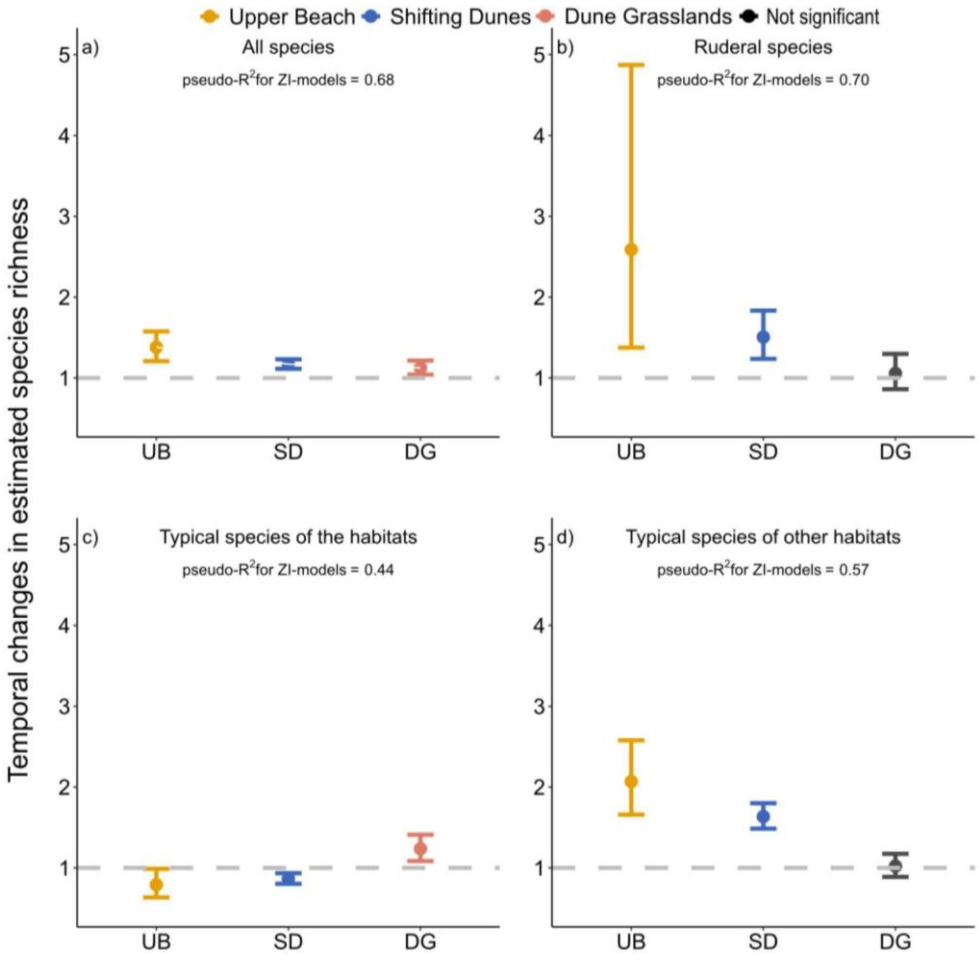

Fig. 2. Results of mixed models assessing temporal changes in species richness. Panels (a–d) show modelled changes in species richness for (a) all species, (b) ruderal species, (c) typical species of the habitat, and (d) typical species of other habitats. These changes are depicted across three habitat types, indicated by different colours (EUNIS N12: upper beach, yellow; N14: shifting dunes, blue; N16: dune grasslands, orange). The y-axis represents the ratio of estimated mean species richness between resurveyed and historical plots. This ratio is obtained by exponentiating the slope parameter from the model, which estimates the effect of time-period on species richness on a log scale. The light grey dotted line at 1 indicates no change in mean species richness over time (exp(0) = 1). Dots represent exponentiated contrasts of estimated marginal means derived from zero-inflated models, while vertical lines indicate 95% confidence intervals (CIs). Coloured symbols denote statistically significant effects ($p < 0.05$; 95% CI does not overlap 1), whereas dark grey symbols indicate non-significant change (95% CI overlaps 1). Pseudo-R^2 values for each model are reported within the corresponding panels.

Concerning total cover, analyses focusing on all species showed that it significantly increased only in dune grasslands (Fig. 3a; Supplementary Table S4). Results for typical species of the habitat were consistent with those obtained for species richness, with a significant decrease in cover in the upper beach and shifting dunes (Fig. 3b). Regarding typical species of other habitats, their cover increased across all habitat types (Fig. 3c). Differences between marginal and conditional R^2 indicate substantial variability among plots and sites, pointing to the role of spatial heterogeneity and local context in mediating temporal dynamics in coastal dune vegetation, beyond the effects captured by the fixed predictors alone. Models for ruderal species cover showed no significant temporal effects and are therefore not shown. Full results are provided in Supplementary Table S4.

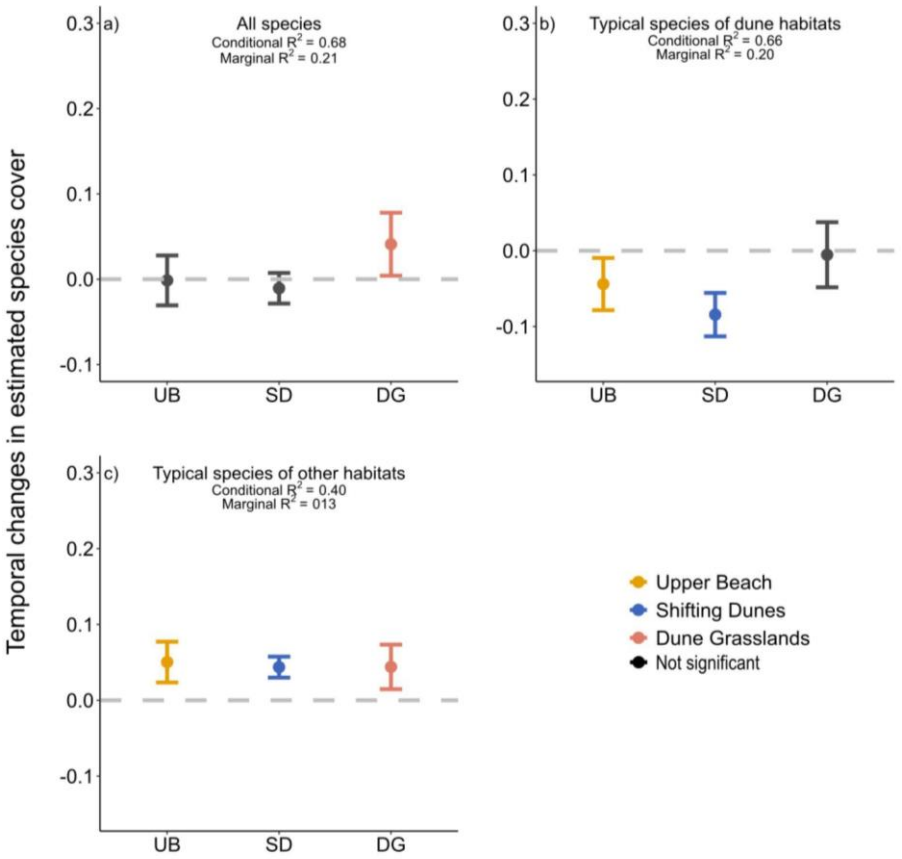

Fig. 3. Results of mixed models assessing temporal changes in species cover. Panels (a–c) display modelled temporal changes in cover for (a) all species, (b) typical species of the habitat, and (c) typical species of other habitats across three habitat types, represented by different colours: (EUNIS N12: upper beach, yellow; N14: shifting dunes, blue; N16: dune grasslands, red). The y-axis represents the relative change in cover between historical and revisited surveys obtained by applying the inverse logit transformation (plogis) to the model

estimates. The light grey dotted line at 0 acts as a threshold indicating no change in cover between the two survey periods. Dots represent the exponentiated contrasts of estimated marginal means from zero-inflated models, with vertical lines indicating the associated 95% confidence intervals (CIs). Coloured symbols represent statistically significant effects ($p < 0.05$, 95% CI does not overlap 0), while dark grey symbols indicate non-significant results (95% CI overlaps 0). Conditional and marginal R^2 values for each model are provided within each panel.

2. Changes in species composition

SIMPER analysis (Fig. 4; Supplementary Table S5 and S6) revealed that the contributions of the different ecological guilds to temporal community dissimilarity varied among habitats. Across habitats, temporal changes in species composition were primarily influenced by typical species of other habitats, while non-native and ruderal species contributed less to overall dissimilarity but showed a steady increase over time, particularly in shifting dunes and dune grasslands. Notably, typical species of the habitat decreased in shifting dunes, while they increased in dune grasslands. Complete species lists and SIMPER outputs are provided in the supplementary materials (Supplementary Table S5 and S6).

In the upper beach, species typical of other habitats (Fig. 4) contributed substantially to community dissimilarity, with a net contribution of +18.05%. Specifically, resurveyed upper beach plots were characterised by an increase in abundance of species typical of shifting dunes (+14.59%) such as *Thinopyrum junceum, Medicago marina*, *Lotus creticus*, *Echinophora spinosa*, and *Calamagrostis arenaria* subsp. *arundinacea,* along with a smaller contribution from dune grasslands species (+2.87%, e.g. *Helichrysum stoechas* subsp. *stoechas*). Although contributing to a lesser extent in dissimilarity, the ingression of taxa from dune shrub and saltmarsh habitats, such as *Juniperus macrocarpa* and *Halimione portulacoides*, is also noteworthy.

While the contributions of non-native and ruderal species to overall dissimilarity were relatively low (+1.30% and +0.42%, respectively), several non-native species not recorded in the historical plots were detected during the resurveys, including *Oenothera* spp., *Oxalis pes-caprae*, *Cenchrus* spp., and *Erigeron* spp. In contrast, typical species of the upper beach did not significantly contribute to temporal dissimilarity.

In shifting dunes, typical species made significant individual contributions to temporal dissimilarity, yet their overall net contribution remained very low. Nevertheless, when examining individual contributions, most typical species of the habitat (e.g. *Calamagrostis arenaria* subsp. *arundinacea, Thinopyrum junceum*, and *Sporobolus pungens*) showed a decrease in abundance in the resurveyed plots, although not significant. A similar decreasing pattern was observed for *Echinophora spinosa* and *Eryngium maritimum,* which both exhibited a significant decline. The increase in abundance observed in shifting dunes was mainly driven by species typical of other habitats. In particular, typical species of dune grasslands contributed most to dissimilarity (+13.44%), including *Festuca fasciculata*, *Helichrysum stoechas* subsp. *stoechas, Ononis variegata*, and *Silene colorata*), all increasing in abundance in the resurveyed plots. A smaller contribution (+4.07%) was associated with the ingression of species typical of upper beach, (e.g. *Cakile maritima* subsp. *maritima*, *Salsola kali*, and *Euphorbia peplis*) as well as typical species of inner-dune woody communities, including *Pistacia lentiscus*, *Pinus pinaster* subsp. *pinaster*, and *Lotus hirsutus*.

In shifting dunes, non-native species (e.g. *Xanthium orientale*, *Oenothera* spp., and *Carpobrotus* sp.pl.) were again the second most important contributors to the increase in abundances over time (+2.69%). The further ingression of invasive taxa, such as *Veronica persica*, *Cenchrus setaceus* and *Opuntia ficus-indica*, is noteworthy. Only one non-native taxon (*Cuscuta* spp.) exhibited a negative trend. Ruderal species (e.g. *Sixalix atropurpurea*, *Hypochaeris radicata*, and *Plantago coronopus*; +2.28%) contributed least to dissimilarity, although their abundance showed an overall increasing trend.

Dune grasslands exhibited the strongest temporal changes in their typical species, which accounted for the largest share of dissimilarity (+18.31%). This pattern was mainly driven by increased abundances of annuals (e.g. *Festuca fasciculata*, *Ononis variegata* and *Medicago littoralis*). The second-largest contribution to dissimilarity (+10.66%) resulted from increasing abundances of species typical of other habitats, in

particular shifting dunes (e.g. *Lotus creticus*, *Calamagrostis arenaria* subsp. *arundinacea*, and *Sporobolus pungens*) and woody fixed-dune communities (e.g. *Juniperus macrocarpa* and *Thymelaea tartonraira* subsp. *tartonraira*). In dune grasslands, ruderal species showed their highest contribution to dissimilarity (e.g. *Plantago coronopus*; +3.61%), exceeding that of non-native species (e.g. *Carpobrotus* sp. pl., +1.47%). Notably, the establishment of the invasive tree *Ailanthus altissima* was also detected.

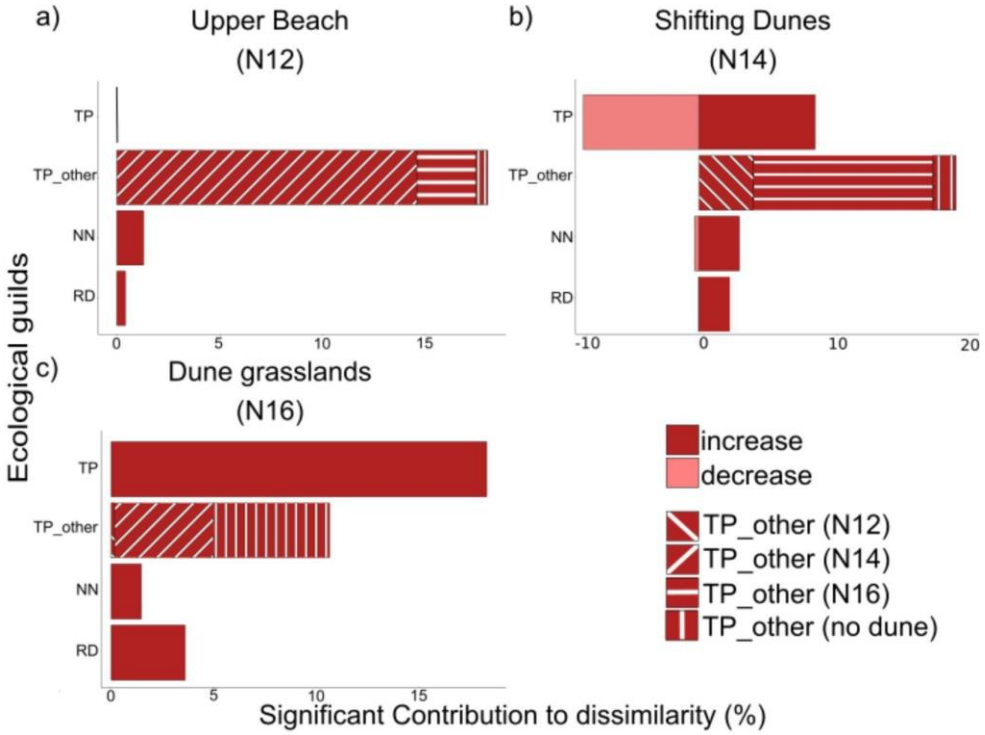

Fig. 4. Significant contributions of ecological guilds to community dissimilarity based on SIMPER analysis. Bars represent the cumulative significant contributions of species within each ecological guild to the total dissimilarity between historical and revisited plots across habitat types (EUNIS N12: upper beach; N14: shifting dunes; N16: dune grasslands). Dark red bars indicate guilds that increased in abundance, while light red bars indicate guilds that decreased. Ecological guilds are broadly classified as follows: NN = non-native; RD = ruderal; TP = typical species of the habitat. Typical species of other habitats are grouped under TP_other, which is further subdivided into TP_other (N12) = typical species of upper beach; TP_other (N14) = typical species of shifting dunes; TP_other (N16) = typical species of dune grasslands; and TP_other (no dune) = typical species of other habitat types not included in the three herbaceous dune habitats investigated.

3. Habitat transitions

Approximately one-third of historical plots (29%) shifted to a different habitat type or could not be relocated during the resurvey (Fig. 5a). The upper beach was the most dynamic habitat, with 43.6% (n = 34) of historical upper-beach plots reclassified during the resurvey. Shifting dunes followed, with 27.1% (n = 90) of their historical plots changing habitat type, closely followed by dune grasslands (23.9%; n = 26).

It's worth to highlight that, among the plots that changed or disappeared (29% of the total), approximately 57% exhibited either disappearance or regressive trajectories, exceeding that of plots showing positive successional advancement (approximately 43%). Within this 57%, 16.7% of plots followed regressive trajectories, shifting towards more seaward or early-successional habitats, while the remainder disappeared. These regressive plots were characterised not only by a decline in typical species of the habitat and an increase in early-successional species, but also by an increase in ruderal, or non-native species (Fig. 5b).

In the upper beach, 41% of shifted plots showed a positive successional shift, 6% displayed regressive trends, and 53% disappeared. In shifting dunes, 44% of plots whose habitat type changed over time underwent positive successional shifts, 17% exhibited regressive trends, and 39% disappeared. Dune grasslands showed a comparable pattern, with 42% of shifted plots showing positive successional shifts, 31% showing regressive trends, and 27% disappeared.

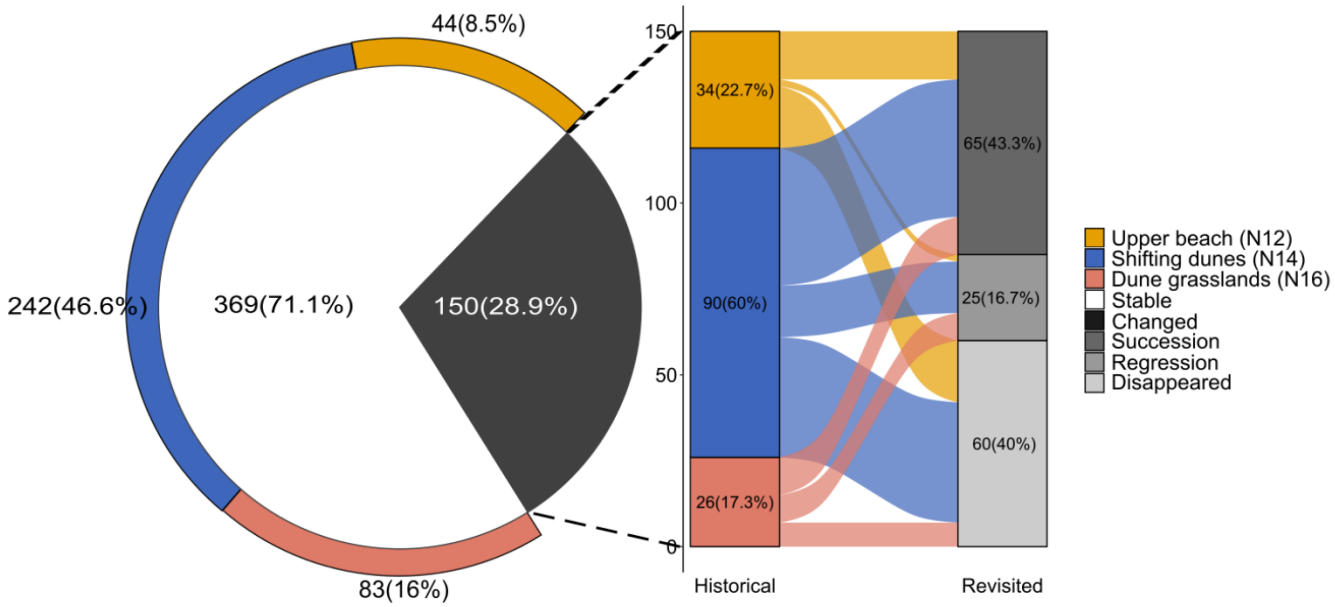

Fig 5. Changes in habitat classification between historical and revisited plots. The left panel shows the proportion of historical plots that remained stable (white area) or changed to a different habitat type (black area). Surrounding the stable plots, coloured semi-circular bands represent the percentage contribution of each habitat type (EUNIS N12: upper beach, yellow; N14: shifting dunes, blue; N16: dune grasslands, red). The right panel provides a detailed breakdown of habitat trajectories over time for the historical plots that changed. It distinguishes plots that underwent positive successional shifts towards more stabilised or inland habitat types (Succession; dark grey), plots that regressed towards earlier successional stages (Regression; light grey), and plots that disappeared (Disappeared; pale grey). See Table 1 for a description of habitat codes.

Discussions

Coastal dune vegetation underwent pronounced changes in species richness, composition, and habitat transitions over the past three decades. Total species richness increased, largely driven by taxa typical of more stabilised or inland habitats, as well as by ruderal species. In contrast, typical species of the habitat declined, particularly in the upper beach and shifting dunes, with only a subtle increase in dune grasslands. Changes in species cover were more limited but broadly mirrored richness patterns. Nearly one-third of plots transitioned to a different habitat type over time, reflecting a combination of localised successional advancement or regressive trends, and habitat loss, especially in the most dynamic early-successional habitats.

1. Temporal trends in species richness and cover

We observed an overall increase in species richness, and, to a lesser extent, in species cover over time. In coastal dunes, which are strongly subjected to anthropogenic pressures (Defeo et al., 2009; Giulio et al., 2020), similar trends have been reported and are best interpreted from a guild-level perspective (Del Vecchio et al., 2015; Makowski & Finkl, 2019; Martínez et al., 2004).

In the upper beach and shifting dunes, typical species of the habitat declined in both richness and cover, whereas ruderal species increased in richness without a corresponding increase in cover. Synanthropic taxa are characterised by high ecological plasticity, rapid reproduction, and resistance to trampling and can quickly colonise disturbed habitats (Biondi et al., 2012; García-Mora et al., 1999; Martínez & García-Franco, 2004; Šilc et al., 2020; Wang et al., 2020). The observed increase in ruderal species richness is consistent with findings reported for other Italian coastal systems (Santoro et al., 2012; Sarmati et al., 2025a; Sperandii et al., 2019). At the same time, typical species of other habitats increased in both richness and cover. Altogether, this pattern indicates substantial shifts in community composition and functionality, likely reflecting modifications in the dune morphology and increased anthropogenic pressures (Del Vecchio et al., 2016; Acosta et al., 2007; Biondi et al., 2012; Hesp et al., 2010; Seer et al., 2015).

In dune grasslands, we observed an increase in the richness of typical species of the habitat, which might suggest well-preserved habitat conditions and a good conservation status. However, this result should be interpreted with caution, as it was largely driven by the greater presence of annual species characteristic of these environments (e.g., *Ononis variegata*, *Festuca fasciculata*, and *Silene colorata*). Such species are known to exhibit stronger spatial and interannual variability than perennial species (Feeley et al., 2020; Poppenwimer et al., 2023) and can take advantage of transient spatial gaps created by the decline or mortality of perennial plants (Biondi et al., 2012; Fischer et al., 2020; Friedman, 2020). This trend occurs alongside an increase in the cover of species from more inland habitats (e.g., *Juniperus macrocarpa*), reflecting concurrent changes towards more stabilized dune habitats, depending on local environmental conditions (Barrett-Mold & Burningham, 2010; Landi et al., 2012).

2. Changes in species composition

In the upper beach, we observed an increasing contribution of species typical of shifting dunes (e.g. *Thinopyrum junceum*, *Medicago marina,* and *Lotus creticus*) to overall compositional dissimilarity over time. These changes likely reflect a natural successional transition from pioneer upper-beach communities to perennial-dominated assemblages of shifting dunes, as previously documented only in a few well-preserved Mediterranean dune systems (Sarmati et al., 2025b). However, this successional trajectory appeared to be accompanied by an increase in species typical of dune grasslands (e.g. *Helichrysum stoechas* subsp. *stoechas,* and *Daucus pumilus*). Collectively, the simultaneous increase of shifting dunes species and the expansion of dune grasslands suggest a progressive homogenisation of plant composition along the natural dune zonation, likely promoted by coastal erosion, trampling and other anthropogenic pressures which compress dune habitats (Defeo et al., 2009; Prisco et al., 2016b; Schlacher et al., 2007, Sperandii et al., 2021). Given the substantial among-plot variability detected by mixed-effects models, the relative importance of these two processes likely varies among sites, depending on local geomorphological context and disturbance type and intensity.

In shifting dunes, compositional change was characterised by the decline of dune-building species, such as *Calamagrostis arenaria* subsp. *arundinacea* and *Thinopyrum junceum*, a pattern consistent with previous findings from Central Italy (Malavasi et al., 2016; Sperandii et al., 2021) and more broadly across the Mediterranean region (Bogdanović et al., 2018; Valcheva at al., 2021). Notably, a reduction in the cover of *Calamagrostis arenaria* subsp. *arundinacea*, a species whose vertical growth is stimulated by sand accretion, may indicate erosional processes (Maun, 2009). This decline coincided with an increase in thermophilic perennial forbs, such as *Lotus creticus* and *Anthemis maritima* subsp. *maritima*, which are known to form replacement communities in disturbed shifting dunes (Acosta et al., 2007; Biondi et al., 2012; Sperandii et al., 2018). Their expansion could also be influenced by climate-driven processes, such as warming or altered precipitation in Mediterranean coastal systems (Del Vecchio et al., 2015; Vesperinas et al., 2001). Additionally, the establishment of species typical of early-successional habitats (e.g. *Cakile maritima* subsp. *maritima*) or of more inland communities, especially dune grasslands (e.g. *Festuca fasciculata* and *Ononis variegata*) contributed strongly to compositional change. Woody and sub-shrub species (e.g. *Juniperus macrocarpa* and *Pinus pinaster* subsp. *pinaster*) also emerged as contributors, suggesting an incipient shift

towards late-successional or woody vegetation types (Álvarez-Molina et al., 2012; Sarmati et al., 2025b; Sperandii et al., 2019). In shifting dunes, changes in species composition over time likely reflect a combination of successional dynamics, with some plots responding to disturbances by reverting to early-successional habitats, while others progress naturally towards later-successional or woody vegetation types (Álvarez-Molina et al., 2012). However, the identification of clear trends in this habitat remains challenging, as the observed patterns are likely shaped by multiple interacting drivers, including land-use change and anthropogenic pressures (Malavasi et al., 2016; Prisco et al., 2016b; Van Der Hagen et al., 2023).

In dune grasslands, consistent with the richness pattern described above, the overall increase in habitat-typical species was mainly driven by annual taxa. The increase in annual species may partially overlap with declines in some perennial species typical of dune grasslands, such as *Helichrysum stoechas* subsp. *stoechas* and *Crucianella maritima*. Although a pronounced decline of *C. maritima* has been reported (Sciandrello et al., 2015; Sperandii et al, 2021), in the present study it was not statistically significant.

Non-native species played a relatively minor role in driving temporal compositional change across coastal dune habitats, but their presence and spread still deserve attention. In the upper beach, non-native taxa contributed only marginally to the compositional dissimilarity over time, likely due to the extreme environmental conditions which make the establishment of new taxa challenging to most species (but see Del Vecchio et al., 2015). An exception is represented by the spread of *Oenothera* spp., not recorded in historical surveys. which reflects a colonisation process (Acosta et al., 2006; de Francesco et al., 2022), likely facilitated both by anthropogenic disturbances (Buffa et al., 2021) and by the high-light conditions typical of this habitat, which may enhance the germination of their seeds (Mihulka et al., 2006; Buffa et al., 2021). Similarly, in dune grasslands, the establishment of invasive woody species is noteworthy. In particular, the expansion of *Ailanthus altissima*, one of the most widespread non-native plants in Italy, may have long-term implications for dune grassland structure and functioning (Lazzaro et al., 2020; Trotta et al., 2020). Taken together, our results suggest that non-native species are not currently the main driver of change, but their increasing presence may represent an emerging pressure on community composition and ecological function over time.

3. Habitat transitions

The spatial distribution of habitat changes showed successional shifts towards more inland stages along the entire gradient, consistent with the natural vegetation zonation sequence towards inland, and particularly pronounced in shifting dunes. While positive successional trends have previously been documented mainly at local scales in highly protected and well-preserved dune systems (Sarmati et al. 2025b), our results suggest that similar trajectories can also be detected across other coastal dune sites at the national scale.

Although a substantial proportion of plots showed transitions consistent with successional advancement, indicating stabilization processes, a similarly high proportion of plots in early-successional dune habitats (upper beach and shifting dunes) disappeared. This pattern indicates that the most pioneer and disturbance-dependent habitats experienced the strongest temporal changes, in line with previous studies reporting pronounced shifts in the seaward and highly dynamic sectors of dune systems (Del Vecchio et al., 2015; Prisco et al., 2016a; Sperandii et al., 2021). Plot disappearance was often associated with shoreline retreat, submergence, or conversion to bare sand driven by tourism-related activities (e.g. construction of bathing facilities or mechanical beach cleaning), trampling, and urban expansion (Hernández-Cordero et al., 2018; Hesp et al., 2010), all widely recognised as major drivers of coastal dune habitat loss worldwide (Feagin et al., 2005; Garzo et al., 2025; Miot da Silva et al., 2008). Plot disappearance was more frequent along the Tyrrhenian and Ionian coasts, in agreement with projections of shoreline retreat and beach surface loss due to sea-level rise (Celata & Gioia, 2024).

Our results further indicated that some plots, particularly in dune grasslands, and a smaller proportion of shifting dune plots, experienced regression to earlier successional stages, often accompanied by increases in the cover of ruderal or non-native species. Taken together with the inland-directed successional shifts

described above, these findings indicate the coexistence of two contrasting and spatially heterogeneous trajectories: inland advancement and regression towards early-successional stages.

Conclusion

While previous local and regional studies have documented temporal vegetation changes in these threatened habitats, our analysis, based on an unprecedentedly comprehensive dataset, shows for the first time that such dynamics are widespread along the entire Italian coastline. Overall, our findings indicate that current coastal dune dynamics are characterised by heterogeneous and locally contrasting processes rather than by a uniform, unidirectional change.

This national-scale assessment provides an overarching view of the dynamics of Italian coastal dune ecosystems, revealing that vegetation change is driven by the interplay between disturbance-related processes and successional dynamics. As a result, inland-directed stabilization coexists with regressive trends and habitat loss along the coastal vegetation gradient. This complexity highlights the need for integrated, long-term monitoring frameworks that combine plot-based resurveys with habitat-level assessments, in order to support coordinated conservation strategies that explicitly account for both stabilisation and degradation processes and enable context-specific, adaptive management responses.

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Supplementary Material

Table S1. **Taxonomic standardisation of species nomenclature in the historical plots**. List of species with inconsistent nomenclature in historical plots, standardised for consistent comparison across time steps. The table shown the corresponding resolved names, along with the rationale for each taxonomic resolution (resolved action).

Original name	Resolved name	Resolved action
Anthemis maritima	Anthemis maritima maritima	only a single subspecies was recorded
Anthemis maritima maritima	Anthemis maritima maritima	only a single subspecies was recorded
Artemisia campestris	Artemisia campestris variabilis	only subspecies present, is endemic also
Artemisia campestris variabilis	Artemisia campestris variabilis	only subspecies present, is endemic also
Bromus hordeaceus	Bromus hordeaceus	at species level
Bromus hordeaceus divaricatus	Bromus hordeaceus	at species level
Cakile maritima	Cakile maritima maritima	only a single subspecies was recorded
Cakile maritima maritima	Cakile maritima maritima	only a single subspecies was recorded
Carpobrotus	Carpobrotus	ibridation problems
Carpobrotus acinaciformis	Carpobrotus	ibridation problems
Carpobrotus edulis	Carpobrotus	ibridation problems
Cenchrus longispinus	Cenchrus sp.pl.	complex or unclear nomenclatural history
Cenchrus spinifex	Cenchrus sp.pl.	complex or unclear nomenclatural history
Cistus creticus	Cistus creticus	complex or unclear nomenclatural history
Cistus creticus eriocephalus	Cistus creticus	complex or unclear nomenclatural history
Corynephorus articulatus	Corynephorus	complex or unclear nomenclatural history
Corynephorus divaricatus	Corynephorus	complex or unclear nomenclatural history
Cuscuta	Cuscuta	complex or unclear nomenclatural history
Cuscuta campestris	Cuscuta	complex or unclear nomenclatural history
Cuscuta cesattiana	Cuscuta	complex or unclear nomenclatural history
Dactylis glomerata	Dactylis glomerata	at species level
Dactylis glomerata hispanica	Dactylis glomerata	at species level
Daucus carota	Daucus carota	at species level
Daucus carota carota	Daucus carota	at species level
Daucus carota hispanicus	Daucus carota	at species level
Daucus carota maritimus	Daucus carota	at species level
Dittrichia viscosa	Dittrichia viscosa viscosa	only a single subspecies was recorded
Dittrichia viscosa viscosa	Dittrichia viscosa viscosa	only a single subspecies was recorded
Erigeron bonariensis	Erigeron	complex or unclear nomenclatural history
Erigeron canadensis	Erigeron	complex or unclear nomenclatural history
Erigeron sumatrensis	Erigeron	complex or unclear nomenclatural history
Festuca fasciculata	Festuca fasciculata	complex or unclear nomenclatural history

Festuca pyramidata	Festuca fasciculata	complex or unclear nomenclatural history
Galatella tripolium	Galatella tripolium pannonica	only a single subspecies was recorded
Galatella tripolium pannonica	Galatella tripolium pannonica	only a single subspecies was recorded
Helichrysum stoechas	Helichrysum stoechas stoechas	only a single subspecies was recorded
Helichrysum stoechas stoechas	Helichrysum stoechas stoechas	only a single subspecies was recorded
Hordeum murinum	Hordeum murinum leporinum	only a single subspecies was recorded
Hordeum murinum leporinum	Hordeum murinum leporinum	only a single subspecies was recorded
Limonium articulatum	Limonium contortirameum	according with the new nomenclature
Limonium contortirameum	Limonium contortirameum	according with the new nomenclature
Linum usitatissimum	Linum usitatissimum angustifolium	only a single subspecies was recorded
Linum usitatissimum angustifolium	Linum usitatissimum angustifolium	only a single subspecies was recorded
Lotus creticus	Lotus creticus	complex or unclear nomenclatural history
Lotus cytisoides	Lotus creticus	complex or unclear nomenclatural history
Odontites luteus	Odontites luteus luteus	only a single subspecies was recorded
Odontites luteus luteus	Odontites luteus luteus	only a single subspecies was recorded
Oenothera biennis	Oenothera sp.pl.	complex or unclear nomenclatural history
Oenothera parviflora	Oenothera sp.pl.	complex or unclear nomenclatural history
Oenothera stucchii	Oenothera sp.pl.	complex or unclear nomenclatural history
Oenothera suaveolens	Oenothera sp.pl.	complex or unclear nomenclatural history
Picris hieracioides	Picris hieracioides hieracioides	only a single subspecies was recorded
Picris hieracioides hieracioides	Picris hieracioides hieracioides	only a single subspecies was recorded
Pinus pinaster	Pinus pinaster pinaster	only a single subspecies was recorded
Pinus pinaster pinaster	Pinus pinaster pinaster	only a single subspecies was recorded
Plantago coronopus	Plantago coronopus	complex or unclear nomenclatural history
Plantago macrorhiza	Plantago coronopus	complex or unclear nomenclatural history
Plantago weldenii	Plantago coronopus	complex or unclear nomenclatural history
Polycarpon tetraphyllum	Polycarpon tetraphyllum	at species level
Polycarpon tetraphyllum alsinifolium	Polycarpon tetraphyllum	at species level
Polycarpon tetraphyllum diphyllum	Polycarpon tetraphyllum	at species level
Raphanus raphanistrum	Raphanus raphanistrum	at species level
Raphanus raphanistrum landra	Raphanus raphanistrum	at species level
Raphanus raphanistrum raphanistrum	Raphanus raphanistrum	at species level
Reseda alba	Reseda alba alba	only a single subspecies was recorded
Reseda alba alba	Reseda alba alba	only a single subspecies was recorded
Rumex acetosella	Rumex acetosella	at species level
Rumex acetosella pyrenaicus	Rumex acetosella	at species level
Rumex bucephalophorus	Rumex bucephalophorus	at species level
Rumex bucephalophorus bucephalophorus	Rumex bucephalophorus	at species level
Salsola kali	Salsola kali	complex or unclear nomenclatural history
Salsola squarrosa controversa	Salsola kali	complex or unclear nomenclatural history

Salsola tragus	Salsola kali	complex or unclear nomenclatural history
Scolymus grandiflorus	Scolymus hispanicus	at species level
Scolymus hispanicus	Scolymus hispanicus	at species level
Scolymus hispanicus hispanicus	Scolymus hispanicus	at species level
Seseli tortuosum	Seseli tortuosum tortuosum	only a single subspecies was recorded
Seseli tortuosum tortuosum	Seseli tortuosum tortuosum	only a single subspecies was recorded
Silene otites	Silene otites otites	only a single subspecies was recorded
Silene otites otites	Silene otites otites	only a single subspecies was recorded
Silene canescens	Silene colorata	complex or unclear nomenclatural history
Silene colorata	Silene colorata	complex or unclear nomenclatural history
Sonchus asper	Sonchus asper	at species level
Sonchus asper asper	Sonchus asper	at species level
Sonchus bulbosus	Sonchus bulbosus bulbosus	only a single subspecies was recorded
Sonchus bulbosus bulbosus	Sonchus bulbosus bulbosus	only a single subspecies was recorded
Teucrium capitatum capitatum	Teucrium capitatum capitatum	complex or unclear nomenclatural history
Teucrium polium	Teucrium capitatum capitatum	complex or unclear nomenclatural history

Table S2. **Number (plain text) and percentage (in italic) of species observed across each ecological guild for different habitat types, comparing historical and revisited plots**. The table reports the total occurrence of species as well as the breakdown by guilds: non-native species (neophytes), ruderal species, typical species of the habitat, and typical species of other habitats.

Ecological guilds	Upper beach (N12)				Shifting Dunes (N14)				Dune Grasslands (N16)			
	historical		revisited		historical		revisited		historical		revisited	
	n	*%*	n	*%*	n	%	n	%	n	%	n	%
all species	61	*14.1*	96	*22.2*	188	*43.4*	217	*50.1*	246	*56.8*	260	*60*
non-native	8	*1.8*	11	*2.5*	18	*4.2*	21	*4.8*	9	*2.1*	18	*4.2*
ruderal	13	*3*	19	*4.4*	42	*9.7*	51	*11.8*	55	*12.7*	51	*11.8*
typical species of the habitat	7	*1.6*	7	*1.6*	17	*3.9*	19	*4.4*	51	*11.8*	47	*10.9*
typical species of other habitats	24	*5.5*	44	*10.2*	66	*15.2*	74	*17.1*	51	*11.8*	58	*13.4*

Table S3. Changes in the species richness over time across selected habitat types and ecological guilds. Mixed models result for temporal changes in species richness across the three coastal habitat types: upper beach (EUNIS N12), shifting dunes (N14) and dune grasslands (N16). For each ecological guild analysed, the estimate change in species richness, the standard error (SE), z-value, and p-value are provided. Significant trends are indicated by coloured arrows, green when positive, red for negative. Non-significant trends are denoted by a dashed line.

Ecological guilds	Habitat types (EUNIS)	trend	estimate	SE	z-value	p-value
All Species	Upper Beach (N12)	↑	1.38	0.07	4.76	< 0.001
All Species	Shifting dunes (N14)	↑	1.17	0.03	6.16	< 0.001
All Species	Dune Grasslands (N16)	↑	1.13	0.04	3.05	0.002
Non-native Species	Upper Beach (N12)	--	1.27	0.18	1.34	0.18
Non-native Species	Shifting dunes (N14)	--	1.10	0.09	0.98	0.33
Non-native Species	Dune Grasslands (N16)	--	1.49	0.21	1.86	0.06
Typical Species of the Habitat	Upper Beach (N12)	↓	0.79	0.11	-2.07	0.039
Typical Species of the Habitat	Shifting dunes (N14)	↓	0.87	0.04	-3.74	0.002
Typical Species of the Habitat	Dune Grasslands (N16)	↑	1.24	0.07	3.17	0.002
Typical Species of Other Habitats	Upper Beach (N12)	↑	2.07	0.11	6.46	< 0.001
Typical Species of Other Habitats	Shifting dunes (N14)	↑	1.64	0.05	10.03	< 0.001
Typical Species of Other Habitats	Dune Grasslands (N16)	--	1.02	0.07	0.30	0.762
Ruderal Species	Upper Beach (N12)	↑	2.59	0.32	2.95	0.003
Ruderal Species	Shifting dunes (N14)	↑	1.51	0.10	4.08	< 0.001
Ruderal Species	Dune Grasslands (N16)	--	1.06	0.11	0.53	0.595

Table S4. Temporal changes in the species abundances across selected habitat types and ecological guilds. Mixed models result for temporal changes in species cover across the three coastal habitat types: upper beach (EUNIS N12), shifting dunes (N14) and dune grasslands (N16). For each species guild analysed, the estimate change in species richness, the standard error (SE), z-value, and p-value are provided. Significant trends are indicated by coloured arrows, green when positive, red for negative. Non-significant trends are denoted by a dashed line.

Ecological guilds	Habitat types (EUNIS)	trend	estimate	SE	z-value	p-value
All species	Upper Beach (N12)	--	0.50	0.14	-0.10	0.921
All species	Shifting dunes (N14)	--	0.48	0.06	-1.17	0.241
All species	Dune Grasslands (N16)	↑	0.55	0.09	2.20	0.028
Non-native Species	Upper Beach (N12)	--	0.51	0.33	0.16	0.873
Non-native Species	Shifting dunes (N14)	--	0.56	0.16	1.40	0.161
Non-native Species	Dune Grasslands (N16)	--	0.59	0.27	1.42	0.156
Typical Species of the Habitat	Upper Beach (N12)	↓	0.32	0.16	-2.74	0.006
Typical Species of the Habitat	Shifting dunes (N14)	↓	0.34	0.07	-7.39	< 0.0001
Typical Species of the Habitat	Dune Grasslands (N16)	--	0.44	0.11	-0.24	0.809
Typical Species of Other Species	Upper Beach (N12)	↑	0.67	0.18	4.10	< 0.0001
Typical Species of Other Species	Shifting dunes (N14)	↑	0.64	0.08	7.15	< 0.0001
Typical Species of Other Species	Dune Grasslands (N16)	↑	0.61	0.13	3.05	0.002
Ruderal Species	Upper Beach (N12)	--	0.50	0.17	0.10	0.923
Ruderal Species	Shifting dunes (N14)	--	0.54	0.08	1.77	0.076
Ruderal Species	Dune Grasslands (N16)	--	0.55	0.14	1.35	0.176

Table S5. **SIMPER contributions of species guilds**. For each habitat type (EUNIS N12: upper beach; N14: shifting dunes; N16: dune grasslands), species were classified into ecological guilds and assessed for significant increases or decreases in abundance between historical and revisited surveys. The reported contribution values represent each guild's share of the average dissimilarity between survey periods, along with the number of species contributing to decreases or increases in abundance and the resulting net contribution. Species guilds: NN = non-native species, RD = ruderal species, TP = species typical of the habitat, TP_other = species typical of other habitats. For example, TP_other (N14) = refers to species typical of the shifting dunes habitat (N14), while TP_other (no dune) = refers to species typical of other habitats than those investigated.

Habitat	Type	Contribution Decrease	Contribution Increase	N. species ↓	N. species ↑	Net contribution
Upper Beach	NN	11.18	1.74	7	7	-9.44
Upper Beach	RD	1.24	3.27	9	16	2.03
Upper Beach	TP	40.87	4.4	5	2	-36.47
Upper Beach	TP_other (N14)	1.16	20.4	1	13	19.23
Upper Beach	TP_other (N16)	0.20	8.27	3	16	8.06
Upper Beach	TP_other (no dune)	0.77	2.65	6	11	1.88
Shifting Dunes	NN	3.97	3.08	8	17	-0.89
Shifting Dunes	RD	0.82	3.09	21	40	2.27
Shifting Dunes	TP	54.26	8.71	12	7	-45.55
Shifting Dunes	TP_other (N12)	0.46	4.2	1	7	3.73
Shifting Dunes	TP_other (N16)	1.59	14.1	14	33	12.51
Shifting Dunes	TP_other (no dune)	1.02	2.31	12	22	1.28
Dune Grasslands	NN	1.25	1.64	4	14	0.4
Dune Grasslands	RD	2.60	6.22	37	36	3.61
Dune Grasslands	TP	27.74	24.61	26	26	-3.12
Dune Grasslands	TP_other (N12)	0.24	0.46	3	3	0.23
Dune Grasslands	TP_other (N14)	3.71	15.25	4	13	11.54
Dune Grasslands	TP_other (no dune)	1.15	5.8	16	30	4.66

Table S6. **Species that contributed to dissimilarity (SIMPER) between historical and resurveyed plots for each habitat type**. Output of SIMPER analysis showing the contribution of each species to the average dissimilarity between historical and revisited plots, grouped by habitat type (EUNIS N12: upper beach; N14: shifting dunes; N16: dune grasslands). sd = standard deviation; ratio = ratio of average dissimilarity to standard deviation. Statistically significant contributions to dissimilarity (p-value) are listed at the top of the table and highlighted in bold. Species guilds: AR = Archeophytes; NN = non-native species; NT = refers to all native species not included in the other guilds analysed; RD = ruderal species; TP = species typical of the habitat; TP_other = species typical of other habitats. For example, TP_other (N14) refers to species typical of the shifting dunes habitat (N14), whereas TP_other (no dune) indicates species typical of other habitats not belonging to the three habitat types investigated.

Upper Beach Species	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Thinopyrum junceum	**0.03**	**0.05**	**0.67**	**0.85**	**2.87**	**0.04**	**0.52**	**0.001**	**TP_other (N14)**
Medicago marina	**0.02**	**0.05**	**0.4**	**0.23**	**2.75**	**0.03**	**0.65**	**0.002**	**TP_other (N14)**
Lotus creticus	**0.02**	**0.07**	**0.3**	**0.03**	**2.4**	**0.03**	**0.68**	**0.007**	**TP_other (N14)**
Echinophora spinosa	**0.02**	**0.04**	**0.4**	**0.2**	**1.6**	**0.02**	**0.7**	**0.023**	**TP_other (N14)**
Calamagrostis arenaria arundinacea	**0.02**	**0.04**	**0.37**	**0.12**	**1.13**	**0.02**	**0.72**	**0.014**	**TP_other (N14)**
Helichrysum stoechas stoechas	**0.01**	**0.04**	**0.23**	**0**	**1.12**	**0.01**	**0.82**	**0.024**	**TP_other (N16)**
Juniperus macrocarpa	**0**	**0.03**	**0.18**	**0**	**0.38**	**0.01**	**0.87**	**0.028**	**TP_other (no dune)**
Anthemis maritima maritima	**0**	**0.02**	**0.23**	**0**	**0.35**	**0**	**0.88**	**0.012**	**TP_other (N14)**
Oenothera sp.pl.	**0**	**0.01**	**0.36**	**0**	**0.3**	**0**	**0.89**	**0.004**	**NN**
Daucus pumilus	**0**	**0.02**	**0.19**	**0**	**0.28**	**0**	**0.9**	**0.034**	**TP_other (N16)**
Oxalis pes-caprae	**0**	**0.01**	**0.45**	**0**	**0.37**	**0**	**0.91**	**0.002**	**NN**
Cenchrus sp.pl.	**0**	**0.01**	**0.23**	**0**	**0.13**	**0**	**0.91**	**0.024**	**NN**
Cyperus capitatus	**0**	**0.01**	**0.25**	**0.05**	**0.12**	**0**	**0.92**	**0.046**	**TP_other (N14)**
Festuca fasciculata raggr.	**0**	**0.01**	**0.26**	**0**	**0.22**	**0**	**0.92**	**0.008**	**TP_other (N16)**
Marcus-kochia ramosissima	**0**	**0.01**	**0.28**	**0**	**0.18**	**0**	**0.93**	**0.011**	**TP_other (N16)**
Silene colorata compl.	**0**	**0.01**	**0.24**	**0**	**0.15**	**0**	**0.94**	**0.016**	**TP_other (N16)**
Avena barbata	**0**	**0**	**0.29**	**0**	**0.17**	**0**	**0.95**	**0.009**	**RD**

Upper Beach Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Senecio leucanthemifolius	**0**	**0.01**	**0.19**	**0**	**0.12**	**0**	**0.95**	**0.037**	**NT**
Reichardia picroides	**0**	**0**	**0.29**	**0**	**0.17**	**0**	**0.95**	**0.01**	**NT**
Hypochaeris glabra	**0**	**0.01**	**0.22**	**0**	**0.13**	**0**	**0.95**	**0.027**	**NT**
Erigeron sp.pl.	**0**	**0.01**	**0.18**	**0**	**0.08**	**0**	**0.96**	**0.049**	**NN**
Seseli tortuosum tortuosum	**0**	**0**	**0.24**	**0**	**0.13**	**0**	**0.96**	**0.015**	**TP_other (N16)**
Mercurialis annua	**0**	**0.01**	**0.21**	**0**	**0.1**	**0**	**0.96**	**0.038**	**RD**
Lomelosia rutifolia	**0**	**0**	**0.21**	**0**	**0.12**	**0**	**0.97**	**0.029**	**TP_other (N16)**
Lagurus ovatus	**0**	**0**	**0.22**	**0**	**0.13**	**0**	**0.97**	**0.032**	**TP_other (N16)**
Orobanche minor	**0**	**0**	**0.21**	**0**	**0.1**	**0**	**0.97**	**0.031**	**NT**
Phleum arenarium	**0**	**0**	**0.21**	**0**	**0.1**	**0**	**0.97**	**0.036**	**TP_other (N16)**
Hypochaeris radicata	**0**	**0**	**0.22**	**0**	**0.12**	**0**	**0.97**	**0.032**	**RD**
Stachys maritima	**0**	**0**	**0.18**	**0**	**0.07**	**0**	**0.99**	**0.05**	**TP_other (N14)**
Cakile maritima maritima	0.17	0.17	1.01	13.33	11.08	0.22	0.22	0.191	TP
Salsola kali aggr	0.09	0.12	0.77	7.05	5.02	0.12	0.33	0.535	TP
Xanthium orientale	0.08	0.12	0.65	5.1	3.32	0.1	0.44	0.372	NN
Matthiola tricuspidata	0.04	0.07	0.5	2.07	3.15	0.05	0.48	0.237	TP_other (N16)
Glaucium flavum	0.03	0.11	0.29	1.52	1.82	0.04	0.56	0.882	TP
Euphorbia peplis	0.03	0.05	0.6	1.82	1.02	0.04	0.6	0.28	TP
Polygonum maritimum	0.02	0.08	0.3	1.85	0.63	0.03	0.63	0.785	TP
Eryngium maritimum	0.02	0.03	0.47	0.38	0.95	0.02	0.74	0.106	TP_other (N14)
Sporobolus pungens	0.01	0.04	0.39	0.33	0.92	0.02	0.76	0.054	TP_other (N14)
Phragmites australis	0.01	0.05	0.26	0.57	0.63	0.02	0.78	0.878	NT
Limbarda crithmoides longifolia	0.01	0.03	0.42	0.2	0.9	0.02	0.79	0.061	TP_other (no dune)
Cynodon dactylon	0.01	0.04	0.26	0.2	0.62	0.01	0.81	0.213	RD
Convolvulus soldanella	0.01	0.02	0.49	0.43	0.17	0.01	0.83	0.118	TP_other (N14)

Upper Beach Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Pancratium maritimum	0.01	0.03	0.25	0.12	0.37	0.01	0.84	0.159	TP_other (N14)
Atriplex prostrata	0.01	0.02	0.41	0.25	0.2	0.01	0.85	0.872	TP
Raphanus raphanistrum	0.01	0.03	0.18	0.22	0.23	0.01	0.85	0.705	RD
Rumex bucephalophorus	0.01	0.04	0.13	0	0.63	0.01	0.86	0.097	NT
Euphorbia paralias	0	0.02	0.32	0.1	0.4	0.01	0.87	0.285	TP_other (N14)
Soda inermis	0	0.02	0.29	0.12	0.13	0.01	0.88	0.198	TP
Dittrichia viscosa viscosa	0	0.02	0.18	0.22	0.08	0	0.89	0.797	RD
Cutandia maritima	0	0.01	0.28	0.03	0.15	0	0.9	0.06	TP_other (N16)
Paspalum vaginatum	0	0.01	0.26	0.15	0	0	0.9	0.502	NN
Achillea maritima maritima	0	0.01	0.19	0.03	0.3	0	0.91	0.086	TP_other (N14)
Ambrosia psilostachya	0	0.01	0.23	0.07	0.07	0	0.92	0.407	NN
Elymus repens repens	0	0.01	0.15	0.03	0.1	0	0.93	0.191	RD
Amorpha fruticosa	0	0	0.12	0.03	0	0.06	0.99	0.887	NN
Cuscuta sp.pl.	0	0	0.12	0.03	0	0	0.99	0.899	NN
Thinopyrum acutum	0	0.01	0.21	0.12	0	-0.06	0.93	0.948	NT
Arundo donax	0	0.01	0.17	0.03	0.03	0	0.94	0.384	AR
Beta vulgaris maritima	0	0	0.31	0.15	0.03	0	0.94	0.95	RD
Silene niceensis	0	0.01	0.13	0	0.22	0	0.94	0.095	TP_other (N16)
Halimione portulacoides	0	0.01	0.23	0.12	0.03	0	0.94	0.964	TP_other (no dune)
Sporobolus pumilus	0	0.01	0.21	0.03	0.08	0	0.95	0.325	NN
Convolvulus sepium	0	0.01	0.16	0.07	0	0	0.95	0.882	NT
Senecio inaequidens	0	0.01	0.17	0	0.07	0	0.96	0.06	NN
Medicago rigidula	0	0.01	0.12	0.03	0	0.02	0.98	0.847	NT
Ambrosia tenuifolia	0	0.01	0.17	0.03	0.03	-0.02	0.96	0.738	NN
Lysimachia arvensis	0	0	0.26	0.03	0.1	0	0.96	0.109	RD

Upper Beach Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Lobularia maritima	0	0.01	0.16	0.03	0.03	0	0.97	0.785	TP_other (no dune)
Poacynum venetum	0	0.01	0.17	0.03	0.03	0	0.97	0.825	TP_other (N16)
Sonchus oleraceus	0	0.01	0.16	0	0.05	0	0.97	0.077	RD
Pinus pinaster pinaster	0	0.01	0.14	0	0.03	0	0.98	0.086	TP_other (no dune)
Cyperus esculentus	0	0.01	0.12	0	0.03	0	0.98	0.127	AR
Pistacia lentiscus	0	0.01	0.12	0	0.05	0	0.98	0.117	TP_other (no dune)
Sonchus asper	0	0	0.18	0	0.08	0	0.98	0.058	RD
Medicago littoralis	0	0	0.13	0	0.05	0	0.98	0.104	TP_other (N16)
Sonchus maritimus	0	0	0.13	0.05	0	0.01	0.99	0.94	NT
Hordeum marinum	0	0	0.12	0.03	0	0	0.99	0.929	NT
Glycyrrhiza glabra	0	0	0.13	0.03	0	0	1	0.93	NT
Mentha aquatica aquatica	0	0	0.13	0.03	0	0	1	0.93	NT
Scirpoides holoschoenus	0	0	0.12	0	0.03	-0.01	0.98	0.115	TP_other (no dune)
Centaurium pulchellum pulchellum	0	0	0.13	0.03	0	0.01	1	0.94	NT
Hypochaeris achyrophorus	0	0	0.16	0.03	0.02	-0.01	0.98	0.873	RD
Galactites tomentosus	0	0	0.18	0	0.07	0	0.98	0.058	RD
Equisetum ramosissimum	0	0.02	0.13	0.22	0	-0.05	0.93	0.931	RD
Tamarix gallica	0	0	0.11	0	0.02	0.06	0.99	0.172	TP_other (no dune)
Sonchus bulbosus bulbosus	0	0	0.18	0	0.05	0	0.99	0.061	TP_other (N16)
Anisantha madritensis	0	0.01	0.12	0.03	0	-0.01	0.98	0.847	RD
Mesembryanthemum nodiflorum	0	0	0.13	0	0.05	0.01	0.99	0.097	TP_other (no dune)
Odontites luteus luteus	0	0	0.13	0	0.05	0	0.99	0.084	TP_other (no dune)

Upper Beach Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Cerastium ligusticum	0	0	0.13	0	0.03	0	0.99	0.104	NT
Hordeum murinum leporinum	0	0.01	0.12	0.03	0	-0.01	0.98	0.847	RD
Tribulus terrestris	0	0.01	0.12	0.03	0	0	0.98	0.847	RD
Ephedra distachya	0	0	0.18	0	0.07	0.01	0.99	0.058	TP_other (N16)
Frankenia laevis laevis	0	0	0.13	0	0.05	0	0.99	0.095	TP_other (no dune)
Senecio vulgaris	0	0	0.13	0	0.03	0	0.99	0.103	NT
Stipellula capensis	0	0	0.13	0	0.03	0	0.99	0.103	NT
Urospermum picroides	0	0	0.13	0	0.03	0	0.99	0.103	NT
Vicia dasycarpa	0	0	0.13	0	0.03	0	0.99	0.103	NT
Rumex acetosella	0	0	0.12	0.03	0	-0.01	0.98	0.87	RD
Daucus carota	0	0	0.12	0.03	0	0.01	0.99	0.929	RD
Maresia nana	0	0	0.13	0.05	0	0	0.99	0.94	TP_other (N16)
Artemisia campestris variabilis	0	0	0.13	0.03	0	0	0.99	0.93	TP_other (N16)
Artemisia caerulescens caerulescens	0	0.02	0.13	0.22	0	-0.07	0.93	0.931	TP_other (no dune)
Euphorbia pithyusa cupanii	0	0.01	0.21	0.12	0	0.03	0.96	0.963	TP_other (no dune)
Anisantha rigida	0	0	0.13	0	0.03	0.03	1	0.084	RD
Malva parviflora	0	0	0.13	0	0.03	0	1	0.097	RD
Crithmum maritimum	0	0	0.12	0.03	0	0	0.99	0.929	TP_other (no dune)
Juncus maritimus	0	0	0.13	0.03	0	0	1	0.94	TP_other (no dune)
Echium plantagineum	0	0	0.13	0	0.03	0	1	0.094	RD
Narcissus tazetta	0	0	0.13	0	0.03	0	1	0.094	NT
Solanum nigrum	0	0	0.13	0	0.03	0	1	0.094	RD
Urtica dioica	0	0	0.13	0	0.03	0	1	0.094	RD
Brassica fruticulosa fruticulosa	0	0	0.13	0	0.03	0	1	0.092	NT

Upper Beach Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Solidago virgaurea litoralis	0	0	0.13	0	0.03	0	1	0.084	NT
Smilax aspera	0	0	0.12	0	0.02	0	1	0.117	TP_other (no dune)
Glebionis coronaria	0	0	0.13	0	0.03	0	1	0.095	RD
Quercus ilex	0	0	0.13	0	0.02	0	1	0.104	TP_other (no dune)
Silene otites otites	0	0	0.13	0	0.03	0	1	0.077	TP_other (N16)
Coleostephus myconis	0	0	0.13	0	0.02	0	1	0.084	NT

Shifting Dunes Species	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Echinophora spinosa	**0.04**	**0.06**	**0.66**	**4.51**	**2.64**	**0.04**	**0.33**	**0.001**	**TP**
Eryngium maritimum	**0.03**	**0.06**	**0.61**	**3.7**	**2.96**	**0.04**	**0.41**	**0.001**	**TP**
Pancratium maritimum	**0.03**	**0.06**	**0.46**	**1.34**	**3.28**	**0.04**	**0.49**	**0.001**	**TP**
Lotus creticus	**0.03**	**0.06**	**0.39**	**0.99**	**3.51**	**0.03**	**0.58**	**0.001**	**TP**
Cakile maritima maritima	**0.02**	**0.05**	**0.37**	**1.07**	**2.03**	**0.02**	**0.6**	**0.001**	**TP_other (N12)**
Festuca fasciculata raggr.	**0.02**	**0.05**	**0.37**	**0.37**	**2.83**	**0.03**	**0.65**	**0.001**	**TP_other (N16)**
Anthemis maritima maritima	**0.02**	**0.05**	**0.32**	**0.47**	**2.21**	**0.02**	**0.69**	**0.001**	**TP**
Helichrysum stoechas stoechas	**0.01**	**0.05**	**0.3**	**0.49**	**1.51**	**0.01**	**0.7**	**0.008**	**TP_other (N16)**
Ononis variegata	**0.01**	**0.04**	**0.34**	**0.53**	**1.72**	**0.02**	**0.72**	**0.001**	**TP_other (N16)**
Xanthium orientale	**0.01**	**0.03**	**0.41**	**0.55**	**0.97**	**0.01**	**0.73**	**0.002**	**NN**
Silene colorata compl.	**0.01**	**0.02**	**0.58**	**0.4**	**1.24**	**0.01**	**0.76**	**0.001**	**TP_other (N16)**
Silene niceensis	**0.01**	**0.02**	**0.39**	**0.57**	**0.75**	**0.01**	**0.77**	**0.016**	**TP_other (N16)**
Lomelosia rutifolia	**0.01**	**0.04**	**0.21**	**0.17**	**1.18**	**0.01**	**0.78**	**0.001**	**TP_other (N16)**
Salsola kali aggr	**0.01**	**0.01**	**0.52**	**0.35**	**0.75**	**0.01**	**0.79**	**0.002**	**TP_other (N12)**

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Cutandia maritima	0.01	0.02	0.42	0.51	0.68	0.01	0.8	0.032	TP_other (N16)
Juniperus macrocarpa	0.01	0.02	0.31	0.07	0.89	0.01	0.81	0.001	TP_other (no dune)
Phleum arenarium	0.01	0.02	0.27	0.25	0.7	0.01	0.82	0.001	TP_other (N16)
Medicago littoralis	0.01	0.02	0.41	0.07	0.91	0.01	0.83	0.001	TP_other (N16)
Matthiola tricuspidata	0.01	0.03	0.19	0.13	0.78	0.01	0.84	0.001	TP_other (N16)
Oenothera sp.pl.	0	0.01	0.28	0.26	0.36	0.01	0.85	0.036	NN
Sixalix atropurpurea	0	0.02	0.19	0.28	0.32	0	0.86	0.035	RD
Crucianella maritima	0	0.02	0.17	0.24	0.3	0.01	0.87	0.013	TP_other (N16)
Euphorbia peplis	0	0.01	0.32	0.18	0.25	0	0.87	0.031	TP_other (N12)
Carpobrotus sp.pl.	0	0.03	0.14	0.01	0.43	0	0.87	0.002	NN
Hypochaeris radicata	0	0.01	0.33	0.14	0.39	0	0.88	0.011	RD
Reichardia picroides	0	0.01	0.41	0.16	0.3	0.01	0.89	0.006	NT
Cuscuta sp.pl.	0	0.01	0.34	0.25	0.03	0	0.9	0.003	NN
Euphorbia terracina	0	0.01	0.3	0.11	0.26	0	0.9	0.001	TP
Plantago coronopus aggr	0	0.02	0.15	0.02	0.43	0.01	0.91	0.002	RD
Pistacia lentiscus	0	0.03	0.08	0.03	0.33	0	0.91	0.024	TP_other
Daucus pumilus	0	0.01	0.25	0.08	0.24	0.01	0.92	0.043	TP_other (N16)
Polygonum maritimum	0	0.01	0.29	0.07	0.17	0	0.92	0.045	TP_other (N12)
Erigeron sp.pl.	0	0.01	0.26	0.07	0.23	0	0.92	0.002	NN
Helichrysum italicum tyrrhenicum	0	0.02	0.07	0.09	0.13	0	0.93	0.048	TP_other (N16)
Anisantha rigida	0	0.01	0.17	0.11	0.27	0	0.93	0.013	RD
Solidago virgaurea virgaurea	0	0.01	0.19	0.05	0.2	0	0.93	0.022	NT
Pinus pinaster pinaster	0	0.02	0.08	0	0.18	0	0.94	0.005	TP_other (no dune)
Lysimachia arvensis	0	0.01	0.26	0.01	0.17	0	0.94	0.001	RD

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Lotus hirsutus	0	0.01	0.16	0.03	0.19	0	0.94	0.004	TP_other (no dune)
Silene otites otites	0	0.01	0.18	0.04	0.18	0	0.94	0.037	TP_other (N16)
Anthemis arvensis	0	0.02	0.09	0	0.27	0.01	0.95	0.003	RD
Seseli tortuosum tortuosum	0	0	0.28	0.05	0.14	0	0.95	0.008	TP_other (N16)
Ambrosia tenuifolia	0	0.01	0.12	0.03	0.12	0	0.95	0.01	NN
Cenchrus sp.pl.	0	0.01	0.13	0.03	0.11	0	0.95	0.005	NN
Raphanus raphanistrum	0	0	0.2	0.05	0.08	0	0.95	0.032	RD
Marcus-kochia ramosissima	0	0	0.23	0.02	0.11	0.01	0.96	0.008	TP_other (N16)
Salvia rosmarinus	0	0.01	0.08	0.01	0.06	0	0.96	0.035	TP_other (no dune)
Hypochaeris glabra	0	0	0.22	0.01	0.1	0	0.96	0.001	NT
Senecio inaequidens	0	0	0.17	0.03	0.05	0	0.96	0.003	NN
Anisantha tectorum	0	0.01	0.11	0.02	0.08	0	0.96	0.003	RD
Andryala integrifolia	0	0	0.23	0.02	0.11	0	0.96	0.004	TP_other (N16)
Medicago minima	0	0	0.19	0.02	0.06	0	0.96	0.008	TP_other (N16)
Polycarpon tetraphyllum	0	0	0.17	0.01	0.08	0	0.96	0.001	TP_other (N16)
Rumex bucephalophorus	0	0	0.15	0.01	0.06	0.01	0.97	0.005	NT
Trifolium arvense	0	0.01	0.06	0	0.13	0	0.97	0.012	NT
Polypogon maritimus maritimus	0	0	0.19	0.04	0.05	0	0.97	0.048	TP
Avena barbata	0	0	0.15	0.02	0.05	0	0.97	0.005	RD
Odontites luteus luteus	0	0	0.19	0.01	0.09	0	0.97	0.001	TP_other (no dune)
Cerastium ligusticum	0	0.01	0.11	0	0.09	0	0.97	0.001	NT
Urospermum dalechampii	0	0	0.16	0.01	0.05	0	0.97	0.001	RD
Linum strictum	0	0	0.12	0	0.1	0	0.97	0.002	NT
Soda inermis	0	0.01	0.1	0	0.06	0	0.97	0.002	TP_other (N12)

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Arundo donax	0	0	0.16	0.01	0.05	0	0.97	0.012	AR
Glycyrrhiza glabra	0	0.01	0.08	0.01	0.06	0.01	0.98	0.008	NT
Erodium laciniatum laciniatum	0	0.01	0.08	0.02	0.06	0	0.98	0.04	NT
Orobanche minor	0	0	0.18	0	0.07	0	0.98	0.001	NT
Periploca graeca	0	0	0.08	0	0.06	0	0.98	0.002	NT
Anisantha diandra	0	0	0.15	0	0.06	0	0.98	0.001	TP_other (N16)
Catapodium rigidum	0	0	0.14	0.01	0.04	0	0.98	0.014	RD
Echium plantagineum	0	0	0.13	0.02	0.02	0	0.98	0.031	RD
Cerastium semidecandrum	0	0	0.14	0.01	0.03	0	0.98	0.006	TP_other (N16)
Lysimachia foemina	0	0	0.15	0	0.05	0	0.98	0.001	NT
Allium sphaerocephalon sphaerocephalon	0	0	0.11	0.01	0.02	0	0.99	0.04	RD
Scirpoides holoschoenus	0	0	0.08	0	0.06	0	0.99	0.006	TP_other (no dune)
Anisantha rubens	0	0	0.07	0	0.02	0	0.99	0.004	NT
Papaver rhoeas rhoeas	0	0	0.07	0	0.05	0	0.99	0.006	RD
Sonchus oleraceus	0	0	0.12	0.01	0.02	0	0.99	0.012	RD
Sonchus asper	0	0	0.07	0	0.02	0	0.99	0.01	RD
Vicia pseudocracca	0	0	0.09	0	0.02	0	0.99	0.003	NT
Asparagus acutifolius	0	0	0.11	0	0.02	0	0.99	0.026	TP_other (no dune)
Rhagadiolus stellatus	0	0	0.09	0	0.02	0	0.99	0.005	NT
Avellinia festucoides	0	0	0.08	0	0.02	0	0.99	0.006	TP_other (N16)
Atriplex prostrata	0	0	0.09	0	0.02	0	0.99	0.004	TP_other (N12)
Limonium contortirameum	0	0	0.05	0	0.01	0	0.99	0.012	TP_other (no dune)
Avena sterilis	0	0	0.06	0	0.04	0	0.99	0.013	AR
Cota tinctoria	0	0	0.06	0	0.04	0	0.99	0.013	NT
Lactuca sativa serriola	0	0	0.06	0	0.04	0	0.99	0.013	RD

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Trifolium campestre	0	0	0.06	0	0.04	0	0.99	0.013	RD
Phillyrea angustifolia	0	0	0.09	0	0.02	0	0.99	0.005	TP_other (no dune)
Ononis natrix ramosissima	0	0	0.08	0	0.02	0	0.99	0.005	TP_other (N16)
Allium polyanthum	0	0	0.05	0	0.01	0	0.99	0.006	TP_other (no dune)
Calendula arvensis	0	0	0.05	0	0.01	0	0.99	0.006	RD
Veronica persica	0	0	0.09	0	0.02	0	0.99	0.002	NN
Imperata cylindrica	0	0	0.08	0	0.01	0	0.99	0.004	TP_other (no dune)
Herniaria glabra	0	0	0.08	0	0.01	0	0.99	0.006	NT
Plantago albicans	0	0	0.06	0	0.01	0	0.99	0.011	TP_other (N16)
Allium commutatum	0	0	0.08	0	0.01	0	0.99	0.005	TP_other (no dune)
Festuca incurva	0	0	0.06	0	0.01	0	0.99	0.011	NT
Cenchrus setaceus	0	0	0.08	0	0.01	0	0.99	0.006	NN
Cyperus esculentus	0	0	0.05	0	0.01	0	1	0.012	AR
Robinia pseudoacacia	0	0	0.05	0	0.01	0	1	0.011	NN
Medicago orbicularis	0	0	0.08	0	0.01	0	1	0.004	NT
Silene gallica	0	0	0.08	0	0.01	0	1	0.004	TP_other (N16)
Clematis flammula	0	0	0.06	0	0.01	0	1	0.011	TP_other (no dune)
Cachrys pungens	0	0	0.05	0	0.01	0	1	0.009	NT
Armeria pungens	0	0	0.06	0	0.01	0	1	0.011	TP_other (N16)
Scrophularia canina	0	0	0.06	0	0.01	0	1	0.009	NT
Erysimum crassistylum	0	0	0.06	0	0.01	0	1	0.011	NT
Senecio vulgaris	0	0	0.06	0	0.01	0	1	0.01	NT
Helichrysum litoreum	0	0	0.06	0	0.01	0	1	0.011	TP_other (N16)
Festuca geniculata geniculata	0	0	0.06	0	0.01	0	1	0.008	NT

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Seseli tortuosum maritimum	0	0	0.06	0	0.01	0	1	0.01	TP_other (N16)
Juniperus phoenicea	0	0	0.06	0	0.01	0	1	0.01	TP_other (no dune)
Lolium rigidum	0	0	0.06	0	0.01	0	1	0.006	RD
Citrullus lanatus	0	0	0.05	0	0	0	1	0.015	AR
Clinopodium nepeta	0	0	0.06	0	0.01	0	1	0.012	RD
Trifolium scabrum	0	0	0.06	0	0.01	0	1	0.008	NT
Myrtus communis	0	0	0.06	0	0.01	0	1	0.012	TP_other (no dune)
Helichrysum italicum siculum	0	0	0.06	0	0.01	0	1	0.008	TP_other (N16)
Mercurialis annua	0	0	0.06	0	0.01	0	1	0.01	RD
Solanum nigrum	0	0	0.06	0	0.01	0	1	0.005	RD
Trifolium striatum	0	0	0.06	0	0.01	0	1	0.005	NT
Vicia dasycarpa	0	0	0.06	0	0.01	0	1	0.007	NT
Squilla pancration	0	0	0.06	0	0.01	0	1	0.01	TP_other (no dune)
Crepis neglecta corymbosa	0	0	0.06	0	0.01	0	1	0.008	RD
Ononis reclinata	0	0	0.06	0	0.01	0	1	0.008	NT
Saxifraga tridactylites	0	0	0.06	0	0.01	0	1	0.008	RD
Trifolium nigrescens	0	0	0.06	0	0.01	0	1	0.008	NT
Centaurea aplolepa subciliata	0	0	0.06	0	0.01	0	1	0.011	TP
Macrobriza maxima	0	0	0.06	0	0.01	0	1	0.007	RD
Rostraria cristata	0	0	0.06	0	0.01	0	1	0.011	NT
Carlina gummifera	0	0	0.06	0	0.01	0	1	0.011	NT
Jasione montana	0	0	0.06	0	0.01	0	1	0.009	NT
Anthemis peregrina	0	0	0.06	0	0.01	0	1	0.006	TP
Clematis vitalba	0	0	0.05	0	0	0	1	0.012	RD
Lonicera caprifolium	0	0	0.05	0	0	0	1	0.012	NT
Silene bellidifolia	0	0	0.06	0	0.01	0	1	0.009	NT
Thapsia garganica	0	0	0.06	0	0.01	0	1	0.009	NT

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Geranium purpureum	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.012**	**RD**
Petrorhagia prolifera	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.012**	**NT**
Cladanthus mixtus	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.007**	**TP_other (N16)**
Opuntia ficus-indica	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.01**	**NN**
Anisantha fasciculata	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.007**	**NT**
Chenopodium album	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.009**	**RD**
Galium aparine	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.009**	**RD**
Lamium amplexicaule	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.009**	**RD**
Geranium molle	**0**	**0**	**0.06**	**0**	**0.01**	**0**	**1**	**0.009**	**NT**
Medicago lupulina	**0**	**0**	**0.06**	**0**	**0**	**0**	**1**	**0.007**	**RD**
Calamagrostis arenaria arundinacea	0.13	0.17	0.78	13.8	10.16	0.15	0.15	0.959	TP
Thinopyrum junceum	0.11	0.13	0.85	12.43	10.72	0.14	0.29	0.999	TP
Sporobolus pungens	0.03	0.09	0.38	3.76	1.67	0.04	0.37	0.999	TP
Medicago marina	0.03	0.06	0.54	3.06	2.84	0.04	0.45	0.939	TP
Sporobolus pumilus	0.03	0.1	0.26	2.64	1.49	0.03	0.52	0.999	NN
Achillea maritima maritima	0.03	0.07	0.37	3.22	1.07	0.03	0.55	0.977	TP
Convolvulus soldanella	0.02	0.05	0.44	1.81	1.63	0.02	0.62	0.865	TP
Cyperus capitatus	0.02	0.04	0.4	1.35	1.35	0.02	0.67	0.874	TP
Euphorbia paralias	0.01	0.03	0.37	1.01	0.62	0.02	0.75	0.332	TP
Crithmum maritimum	0.01	0.05	0.17	0.61	0.36	0	0.8	0.866	TP_other (no dune)
Centaurea sphaerocephala sphaerocephala	0.01	0.03	0.2	0.58	0.24	0	0.84	0.999	TP_other (N16)
Lagurus ovatus	0	0.01	0.39	0.22	0.45	0	0.85	0.058	TP_other (N16)
Matthiola sinuata	0	0.01	0.37	0.38	0.28	0.01	0.86	0.947	TP_other (N12)
Poacynum venetum	0	0.04	0.09	0.3	0.27	0.01	0.88	0.284	TP_other (N16)

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Ambrosia psilostachya	0	0.02	0.18	0.29	0.16	0	0.89	0.858	NN
Limbarda crithmoides longifolia	0	0.01	0.25	0.14	0.43	0	0.89	0.051	TP_other (no dune)
Cynodon dactylon	0	0.01	0.27	0.15	0.29	0.01	0.9	0.402	RD
Scolymus hispanicus	0	0.01	0.26	0.26	0.17	0	0.91	0.145	RD
Rostraria litorea	0	0.02	0.12	0.16	0.15	0	0.92	0.252	TP_other (N16)
Silene succulenta corsica	0	0.02	0.12	0.13	0.09	0.01	0.93	0.941	TP
Launaea fragilis	0	0.01	0.29	0.15	0.09	0	0.93	0.417	NT
Dittrichia viscosa viscosa	0	0.01	0.12	0.19	0.05	0.01	0.94	0.997	RD
Daucus carota	0	0.01	0.17	0.1	0.11	0	0.94	0.984	RD
Sonchus bulbosus bulbosus	0	0.01	0.17	0.06	0.1	0	0.95	0.887	TP_other (N16)
Glaucium flavum	0	0	0.23	0.06	0.09	0	0.95	0.125	TP_other (N12)
Solidago virgaurea litoralis	0	0	0.2	0.1	0	0	0.95	0.993	NT
Verbascum sinuatum	0	0	0.16	0.06	0.07	0	0.96	0.057	RD
Thinopyrum acutum	0	0	0.19	0.09	0.01	0	0.96	0.994	NT
Phragmites australis	0	0	0.18	0.06	0.04	0	0.96	0.595	NT
Hedypnois rhagadioloides	0	0	0.21	0.03	0.07	0	0.97	0.316	NT
Silene velutina	0	0.01	0.06	0.14	0	0	0.97	0.995	TP_other (N16)
Smilax aspera	0	0	0.17	0.02	0.05	0	0.97	0.088	TP_other (no dune)
Ononis diffusa	0	0	0.13	0.07	0.03	0	0.97	0.867	TP_other (N16)
Diplotaxis tenuifolia	0	0.01	0.09	0.07	0	0	0.97	0.992	RD
Artemisia campestris variabilis	0	0	0.09	0.07	0	0	0.98	0.997	TP_other (N16)
Senecio leucanthemifolius	0	0	0.14	0.02	0.04	0	0.98	0.187	NT
Anisantha madritensis	0	0	0.14	0.03	0.03	0	0.98	0.989	RD
Reseda alba alba	0	0	0.15	0.02	0.03	0	0.98	0.111	RD

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Lobularia maritima	0	0	0.11	0.02	0.02	0	0.98	0.34	TP_other (no dune)
Rubia peregrina	0	0	0.13	0.03	0.02	0	0.98	0.972	TP_other (no dune)
Anisantha sterilis	0	0	0.13	0.01	0.03	0	0.98	0.068	RD
Parapholis incurva	0	0	0.12	0.01	0.03	0	0.98	0.067	NT
Oxalis pes-caprae	0	0	0.14	0.01	0.04	0	0.98	0.11	NN
Amorpha fruticosa	0	0	0.14	0.03	0.01	0	0.98	1	NN
Pinus pinea	0	0	0.1	0.01	0.02	0	0.98	0.479	TP_other (no dune)
Asphodelus tenuifolius	0	0	0.12	0.01	0.02	0	0.98	0.086	NT
Chondrilla juncea	0	0	0.1	0.02	0.01	0	0.98	0.992	RD
Convolvulus sepium	0	0	0.06	0.04	0	0	0.98	0.994	NT
Sonchus tenerrimus	0	0	0.13	0.03	0.01	0	0.98	0.997	RD
Echium sabulicola sabulicola	0	0	0.14	0.03	0.02	0	0.98	0.991	TP_other (N16)
Picris hieracioides hieracioides	0	0	0.09	0.02	0.01	0.01	0.99	0.163	RD
Ephedra distachya	0	0	0.11	0.01	0.03	0	0.99	0.164	TP_other (N16)
Silene vulgaris	0	0	0.13	0.03	0.01	0	0.99	0.998	RD
Plantago lanceolata	0	0	0.11	0.01	0.01	0	0.99	0.272	RD
Catapodium balearicum	0	0	0.09	0.01	0.01	0	0.99	0.976	RD
Bituminaria bituminosa	0	0	0.09	0.01	0.01	0	0.99	0.089	RD
Daphne gnidium	0	0	0.08	0	0.01	0	0.99	0.097	TP_other (no dune)
Ambrosia maritima	0	0	0.09	0.02	0	0	0.99	0.998	TP_other (N16)
Senecio transiens	0	0	0.07	0.02	0	0	0.99	0.996	TP_other (N16)
Agave americana americana	0	0	0.09	0.01	0.02	0	0.99	0.598	NN
Bromopsis ramosa ramosa	0	0	0.11	0.02	0.01	0	0.99	0.616	NT
Medicago rigidula	0	0	0.07	0.01	0	0	0.99	0.994	NT

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Pinus halepensis halepensis	0	0	0.07	0.01	0.01	0	0.99	0.15	TP_other (no dune)
Dactylis glomerata	0	0	0.1	0.02	0	0	0.99	0.997	RD
Verbascum niveum garganicum	0	0	0.1	0.01	0.02	0	0.99	0.393	NT
Vitex agnus-castus	0	0	0.05	0.01	0	0	0.99	0.986	TP_other (no dune)
Beta vulgaris maritima	0	0	0.08	0.01	0.01	0	0.99	0.176	RD
Euphorbia peplus	0	0	0.09	0	0.01	0	0.99	0.084	RD
Onobrychis caput-galli	0	0	0.07	0.01	0.01	0	0.99	0.948	NT
Juncus acutus acutus	0	0	0.08	0.01	0.01	0	0.99	0.197	TP_other (no dune)
Triticum vagans	0	0	0.07	0	0.01	0	0.99	0.078	NT
Sonchus maritimus	0	0	0.08	0.01	0.01	0	0.99	0.884	NT
Equisetum ramosissimum	0	0	0.08	0.01	0.01	0	0.99	0.838	RD
Hordeum murinum leporinum	0	0	0.08	0.01	0	0	0.99	0.995	RD
Maresia nana	0	0	0.08	0.01	0.01	0	0.99	0.155	TP_other (N16)
Plantago crassifolia	0	0	0.07	0.01	0	0	0.99	0.994	NT
Dysphania atriplicifolia	0	0	0.08	0.01	0	0	0.99	0.999	NN
Paspalum vaginatum	0	0	0.05	0.01	0	0	0.99	0.98	NN
Silene beguinotii	0	0	0.05	0.01	0	0	0.99	0.976	TP_other (N16)
Sonchus arvensis	0	0	0.08	0.01	0	0	0.99	0.998	RD
Stachys maritima	0	0	0.08	0.01	0	0	0.99	0.768	TP
Ipomoea indica	0	0	0.06	0.01	0	0	0.99	0.988	NN
Helichrysum italicum italicum	0	0	0.08	0.02	0	0	0.99	0.998	TP_other (N16)
Pulicaria dysenterica	0	0	0.08	0.01	0	0	0.99	0.996	NT
Erica multiflora	0	0	0.07	0	0	0.01	1	0.86	TP_other (no dune)
Arenaria leptoclados leptoclados	0	0	0.06	0.01	0	0	1	0.992	NT

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Juncus subulatus	0	0	0.06	0.01	0	0	1	0.99	TP_other (no dune)
Urospermum picroides	0	0	0.08	0.01	0	0	1	0.996	NT
Carlina corymbosa	0	0	0.08	0.01	0.01	0	1	0.787	RD
Atriplex halimus	0	0	0.06	0.01	0	0	1	0.992	TP_other (no dune)
Lotus corniculatus	0	0	0.06	0.01	0	0	1	0.992	NT
Frankenia laevis laevis	0	0	0.05	0.01	0	0	1	0.99	TP_other (no dune)
Anethum foeniculum	0	0	0.06	0.01	0	0	1	0.987	RD
Carduus pycnocephalus pycnocephalus	0	0	0.06	0.01	0	0	1	0.987	RD
Geranium rotundifolium	0	0	0.06	0.01	0	0	1	0.987	NT
Lolium multiflorum	0	0	0.06	0.01	0	0	1	0.995	RD
Crepis vesicaria	0	0	0.06	0.01	0	0	1	0.993	NT
Trigonella sulcata	0	0	0.06	0.01	0	0	1	0.993	NT
Catapodium pauciflorum	0	0	0.06	0.01	0	0	1	0.993	NT
Sherardia arvensis	0	0	0.06	0.01	0	0	1	0.992	RD
Teucrium chamaedrys	0	0	0.06	0.01	0	0	1	0.992	TP_other (no dune)
Blackstonia perfoliata	0	0	0.07	0.01	0	0	1	0.979	NT
Tamarix africana	0	0	0.06	0.01	0	0	1	0.993	TP_other (no dune)
Carex hispida	0	0	0.06	0.01	0	0	1	0.993	NT
Elymus repens repens	0	0	0.06	0.01	0	0	1	0.993	RD
Fumaria capreolata capreolata	0	0	0.06	0.01	0	0	1	0.995	RD
Silene nummica	0	0	0.06	0.01	0	0	1	0.995	TP_other (N16)
Centaurium tenuiflorum tenuiflorum	0	0	0.05	0	0	0	1	0.981	NT
Limonium narbonense	0	0	0.05	0	0	0	1	0.981	TP_other (no dune)

Shifting Dunes Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Rumex crispus	0	0	0.06	0.01	0	0	1	0.991	NT
Silene conica	0	0	0.06	0.01	0	0	1	0.991	NT
Arenaria serpyllifolia	0	0	0.06	0.01	0	0	1	0.996	NT
Agrostis stolonifera	0	0	0.06	0.01	0	0	1	0.995	NT
Leontodon hispidus	0	0	0.06	0.01	0	0	1	0.995	NT
Lotus rectus	0	0	0.06	0.01	0	0	1	0.995	NT
Vitis vinifera	0	0	0.06	0.01	0	0	1	0.995	NT
Epilobium hirsutum	0	0	0.06	0.01	0	0	1	0.994	NT
Populus alba	0	0	0.06	0.01	0	0	1	0.994	NT
Symphyotrichum squamatum	0	0	0.06	0.01	0	0	1	0.994	NN
Anchusa undulata hybrida	0	0	0.06	0.01	0	0	1	0.989	TP_other (N16)
Cachrys sicula	0	0	0.06	0.01	0	0	1	0.989	NT
Beta macrocarpa	0	0	0.06	0.01	0	0	1	0.994	NT
Parapholis cylindrica	0	0	0.05	0	0	0	1	0.99	NT

Dune Grasslands Species	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Festuca fasciculata raggr.	**0.06**	**0.09**	**0.64**	**5.14**	**9.49**	**0.06**	**0.06**	**0.026**	**TP**
Ononis variegata	**0.04**	**0.09**	**0.46**	**3.96**	**6.26**	**0.04**	**0.16**	**0.024**	**TP**
Lotus creticus	**0.02**	**0.04**	**0.5**	**2.32**	**3.18**	**0.02**	**0.38**	**0.03**	**TP_other (N14)**
Medicago littoralis	**0.02**	**0.04**	**0.44**	**1.48**	**3.64**	**0.02**	**0.4**	**0.001**	**TP**
Silene colorata compl.	**0.02**	**0.03**	**0.63**	**2.51**	**2.52**	**0.02**	**0.42**	**0.04**	**TP**
Plantago coronopus aggr	**0.02**	**0.05**	**0.36**	**0.68**	**3.34**	**0.02**	**0.48**	**0.001**	**RD**
Juniperus macrocarpa	**0.02**	**0.04**	**0.39**	**0.29**	**2.7**	**0.02**	**0.5**	**0.001**	**TP_other (no dune)**
Calamagrostis arenaria arundinacea	**0.01**	**0.04**	**0.31**	**0.47**	**2.07**	**0.01**	**0.54**	**0.001**	**TP_other (N14)**
Cutandia maritima	**0.01**	**0.04**	**0.26**	**1.15**	**2.07**	**0.02**	**0.62**	**0.033**	**TP**
Carpobrotus sp.pl.	**0.01**	**0.03**	**0.25**	**0.81**	**0.82**	**0**	**0.63**	**0.034**	**NN**

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Sporobolus pungens	0.01	0.01	0.49	0.33	1.25	0.01	0.67	0.001	TP_other (N14)
Thymelaea tartonraira tartonraira	0.01	0.05	0.12	0.04	0.79	0.01	0.71	0.001	TP_other (no dune)
Erodium laciniatum laciniatum	0.01	0.02	0.27	0.25	1.03	0	0.71	0.03	NT
Rumex bucephalophorus	0.01	0.02	0.26	0.25	0.79	0	0.73	0.013	NT
Cistus salviifolius	0	0.04	0.11	0.05	0.69	0.01	0.74	0.002	TP_other (no dune)
Fumana procumbens	0	0.03	0.11	0.05	0.73	0	0.76	0.005	TP
Anchusa crispa crispa	0	0.03	0.14	0.19	0.42	0	0.77	0.043	TP
Crithmum maritimum	0	0.03	0.13	0.17	0.4	0	0.78	0.045	TP_other (no dune)
Sonchus bulbosus bulbosus	0	0.01	0.36	0.25	0.27	0	0.8	0.02	TP
Teucrium capitatum capitatum	0	0.01	0.24	0.11	0.37	0	0.81	0.011	TP
Pistacia lentiscus	0	0.01	0.21	0.08	0.43	0	0.82	0.005	TP_other (no dune)
Silene succulenta corsica	0	0.02	0.13	0.03	0.25	0.01	0.83	0.001	TP_other (N14)
Paronychia argentea	0	0.02	0.14	0.11	0.4	0	0.83	0.045	NT
Matthiola tricuspidata	0	0.01	0.23	0.12	0.3	0	0.84	0.017	TP
Ailanthus altissima	0	0.02	0.1	0	0.4	0	0.85	0.003	NN
Juniperus phoenicea	0	0.01	0.14	0.04	0.42	0	0.86	0.041	TP_other (no dune)
Anthemis arvensis	0	0.01	0.18	0.06	0.53	0.01	0.87	0.011	RD
Smilax aspera	0	0.01	0.38	0.11	0.24	0	0.87	0.007	TP_other (no dune)
Tripidium ravennae ravennae	0	0.01	0.16	0	0.3	0	0.87	0.001	TP_other (no dune)
Poterium sanguisorba	0	0.01	0.24	0.09	0.25	0.01	0.88	0.005	TP
Anisantha diandra	0	0.01	0.15	0	0.27	0	0.88	0.002	TP
Asparagus acutifolius	0	0.01	0.17	0.08	0.18	0	0.88	0.012	TP_other (no dune)

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Salsola kali aggr	0	0.01	0.27	0.09	0.16	0	0.88	0.011	TP_other (N12)
Daucus carota	0	0.01	0.2	0.09	0.24	0.01	0.89	0.008	RD
Dittrichia viscosa viscosa	0	0.01	0.18	0.03	0.28	0	0.89	0.002	RD
Schoenus nigricans	0	0.01	0.13	0.02	0.19	0	0.89	0.001	TP_other (no dune)
Seseli tortuosum tortuosum	0	0.01	0.23	0.06	0.25	0	0.89	0.048	TP
Quercus ilex	0	0.01	0.15	0	0.22	0	0.89	0.001	TP_other (no dune)
Lysimachia arvensis	0	0	0.32	0.04	0.22	0	0.9	0.005	RD
Tamarix gallica	0	0.01	0.14	0	0.25	0	0.9	0.001	TP_other (no dune)
Linum strictum	0	0.01	0.23	0.03	0.15	0.01	0.91	0.009	NT
Echium plantagineum	0	0.01	0.13	0	0.18	0	0.91	0.002	RD
Erigeron sp.pl.	0	0	0.31	0.02	0.2	0	0.91	0.001	NN
Rubia peregrina	0	0	0.28	0.05	0.14	0	0.91	0.002	TP_other (no dune)
Clematis flammula	0	0.01	0.2	0.02	0.29	0.01	0.92	0.001	TP_other (no dune)
Crataegus monogyna	0	0.01	0.11	0	0.16	0	0.92	0.001	NT
Urospermum dalechampii	0	0	0.26	0.02	0.17	0	0.92	0.001	RD
Clematis vitalba	0	0.01	0.13	0.06	0.13	0	0.92	0.028	RD
Periploca graeca	0	0.01	0.09	0	0.13	0	0.93	0.002	NT
Sonchus oleraceus	0	0.01	0.1	0.01	0.13	0	0.93	0.005	RD
Hypochaeris glabra	0	0	0.24	0	0.15	0	0.93	0.002	NT
Senecio leucanthemifolius	0	0	0.19	0.05	0.07	0	0.93	0.042	NT
Polycarpon tetraphyllum	0	0	0.24	0.03	0.14	0.01	0.94	0.002	TP
Daphne gnidium	0	0.01	0.12	0.01	0.14	0	0.94	0.038	TP_other (no dune)
Scabiosa triandra	0	0.01	0.11	0.02	0.13	0	0.94	0.016	NT
Erica multiflora	0	0.01	0.12	0	0.15	0.01	0.95	0.001	TP_other (no dune)

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Cerastium ligusticum	0	0	0.24	0	0.13	0	0.95	0.001	NT
Lavandula stoechas stoechas	0	0.01	0.12	0	0.16	0	0.95	0.001	TP_other (no dune)
Pinus pinaster pinaster	0	0.01	0.12	0	0.15	0	0.95	0.002	TP_other (no dune)
Chondrilla juncea	0	0	0.26	0.04	0.1	0	0.95	0.047	RD
Geranium molle	0	0	0.21	0.02	0.08	0	0.95	0.003	NT
Odontites luteus luteus	0	0	0.21	0.02	0.09	0	0.95	0.029	TP_other (no dune)
Centaurium erythraea	0	0.01	0.1	0	0.13	0	0.96	0.002	NT
Anacyclus radiatus radiatus	0	0.01	0.1	0	0.13	0	0.96	0.003	RD
Geranium purpureum	0	0	0.19	0	0.1	0	0.96	0.001	RD
Phragmites australis	0	0.01	0.1	0	0.13	0	0.96	0.003	NT
Orobanche minor	0	0	0.23	0.03	0.08	0	0.96	0.003	NT
Ononis reclinata	0	0.01	0.1	0	0.13	0	0.96	0.002	NT
Helichrysum italicum italicum	0	0	0.21	0.03	0.09	0	0.96	0.044	TP
Quercus robur	0	0	0.19	0	0.08	0	0.96	0.001	NT
Phillyrea angustifolia	0	0	0.17	0	0.08	0.01	0.97	0.001	TP_other (no dune)
Linum usitatissimum angustifolium	0	0	0.22	0	0.1	0	0.97	0.001	NT
Cenchrus sp.pl.	0	0	0.22	0.02	0.1	0	0.97	0.03	NN
Thapsia garganica	0	0	0.22	0.02	0.08	0	0.97	0.021	NT
Scabiosa columbaria	0	0	0.13	0	0.06	0	0.97	0.001	RD
Echium vulgare	0	0	0.19	0.02	0.06	0	0.97	0.025	RD
Trigonella wojciechowskii	0	0	0.17	0	0.06	0	0.97	0.002	NT
Veronica persica	0	0	0.2	0	0.07	0	0.97	0.001	NN
Silene italica	0	0	0.13	0	0.05	0	0.97	0.001	RD
Ervilia hirsuta	0	0	0.16	0	0.06	0	0.97	0.001	RD
Myosotis arvensis	0	0	0.16	0	0.06	0	0.97	0.001	RD
Brachypodium retusum	0	0	0.13	0	0.05	0	0.97	0.001	TP_other (no dune)

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Vitis vinifera	0	0	0.1	0	0.13	0	0.98	0.004	NT
Lonicera caprifolium	0	0	0.12	0	0.04	0	0.98	0.001	NT
Salvia rosmarinus	0	0	0.12	0	0.04	0	0.98	0.002	TP_other (no dune)
Rubus ulmifolius	0	0	0.17	0	0.06	0	0.98	0.001	RD
Geranium columbinum	0	0	0.13	0	0.04	0	0.98	0.001	RD
Clinopodium nepeta	0	0	0.14	0	0.06	0	0.98	0.001	RD
Lysimachia foemina	0	0	0.17	0	0.06	0	0.98	0.002	NT
Linum trigynum	0	0	0.16	0	0.04	0	0.98	0.001	NT
Centaurea aplolepa subciliata	0	0	0.14	0	0.04	0	0.99	0.001	TP_other (N14)
Colutea arborescens	0	0	0.09	0	0.03	0	0.99	0.001	NT
Juniperus communis	0	0	0.09	0	0.03	0	0.99	0.001	TP_other (no dune)
Ruscus aculeatus	0	0	0.09	0	0.03	0	0.99	0.002	TP_other (no dune)
Pinus halepensis halepensis	0	0	0.09	0	0.02	0	0.99	0.002	TP_other (no dune)
Festuca incurva	0	0	0.1	0	0.03	0	0.99	0.002	NT
Moraea sisyrinchium	0	0	0.14	0	0.04	0	0.99	0.002	NT
Oxalis pes-caprae	0	0	0.14	0	0.04	0	0.99	0.002	NN
Senecio vulgaris	0	0	0.14	0	0.04	0	0.99	0.003	NT
Squilla pancration	0	0	0.14	0	0.05	0	0.99	0.002	TP_other (no dune)
Medicago lupulina	0	0	0.12	0	0.03	0	0.99	0.002	RD
Arundo donax	0	0	0.1	0	0.03	0	0.99	0.001	AR
Cytisus laniger	0	0	0.1	0	0.03	0	0.99	0.001	TP_other (no dune)
Limbarda crithmoides longifolia	0	0	0.1	0	0.03	0	0.99	0.002	TP_other (no dune)
Hypericum perforatum	0	0	0.09	0	0.02	0	0.99	0.001	NT
Luzula campestris	0	0	0.09	0	0.02	0	0.99	0.001	NT
Oxalis dillenii	0	0	0.09	0	0.02	0	0.99	0.001	NN

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Squilla maritima	0	0	0.1	0	0.03	0	0.99	0.003	TP_other (no dune)
Catapodium pauciflorum	0	0	0.09	0	0.02	0	0.99	0.002	NT
Poa annua	0	0	0.09	0	0.02	0	0.99	0.002	RD
Arabis hirsuta	0	0	0.09	0	0.02	0	0.99	0.001	RD
Brachypodium pinnatum	0	0	0.09	0	0.02	0	0.99	0.001	NT
Iris germanica	0	0	0.09	0	0.02	0	0.99	0.001	AR
Sedum gr maximum	0	0	0.09	0	0.02	0	0.99	0.001	NT
Vincetoxicum hirundinaria	0	0	0.09	0	0.02	0	0.99	0.001	NT
Medicago orbicularis	0	0	0.1	0	0.03	0	0.99	0.002	NT
Allium vineale	0	0	0.09	0	0.02	0	0.99	0.003	NT
Anacamptis morio	0	0	0.09	0	0.02	0	0.99	0.003	NT
Buglossoides arvensis	0	0	0.09	0	0.02	0	0.99	0.003	NT
Pteridium aquilinum	0	0	0.09	0	0.02	0	0.99	0.003	RD
Senecio inaequidens	0	0	0.09	0	0.02	0	0.99	0.002	NN
Romulea rollii	0	0	0.14	0	0.03	0	0.99	0.001	NT
Eudianthe coeli-rosa	0	0	0.1	0	0.02	0	0.99	0.003	NT
Avena sterilis	0	0	0.1	0	0.03	0.01	1	0.003	AR
Erica scoparia scoparia	0	0	0.1	0	0.03	0	1	0.001	NT
Euphorbia dendroides	0	0	0.1	0	0.02	0	1	0.002	NT
Convolvulus arvensis	0	0	0.1	0	0.03	0	1	0.003	RD
Reseda lutea	0	0	0.1	0	0.02	0	1	0.003	RD
Ajuga chamaepitys	0	0	0.1	0	0.02	0	1	0.002	NT
Colchicum autumnale	0	0	0.1	0	0.02	0	1	0.002	NT
Medicago polymorpha	0	0	0.1	0	0.02	0	1	0.002	RD
Koeleria splendens	0	0	0.1	0	0.02	0	1	0.003	NT
Arabis glabra	0	0	0.1	0	0.02	0	1	0.003	NT
Populusxcanadensis	0	0	0.1	0	0.02	0	1	0.003	NN

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Prunus spinosa	**0**	**0**	**0.1**	**0**	**0.02**	**0**	**1**	**0.003**	**NT**
Umbilicus rupestris	**0**	**0**	**0.14**	**0**	**0.02**	**0**	**1**	**0.001**	**NT**
Stachys maritima	**0**	**0**	**0.09**	**0**	**0.01**	**0**	**1**	**0.002**	**TP_other (N14)**
Petrorhagia prolifera	**0**	**0**	**0.1**	**0**	**0.02**	**0**	**1**	**0.003**	**NT**
Lotus conimbricensis	**0**	**0**	**0.09**	**0**	**0.01**	**0**	**1**	**0.002**	**NT**
Scorzonera laciniata	**0**	**0**	**0.1**	**0**	**0.02**	**0**	**1**	**0.003**	**NT**
Myosotis ramosissima ramosissima	**0**	**0**	**0.1**	**0**	**0.01**	**0**	**1**	**0.003**	**RD**
Ephedra distachya	0.05	0.13	0.41	5.68	5.67	0.06	0.12	0.996	TP
Helichrysum stoechas stoechas	0.04	0.09	0.46	4.85	2.15	0.05	0.21	0.999	TP
Crucianella maritima	0.03	0.07	0.37	3.07	2.46	0.03	0.24	0.992	TP
Centaurea sphaerocephala sphaerocephala	0.03	0.07	0.38	3.21	2.38	0.02	0.26	1	TP
Armeria pungens	0.02	0.06	0.4	2.91	1.88	0.03	0.29	1	TP
Pancratium maritimum	0.02	0.04	0.55	1.94	3.19	0.02	0.31	0.056	TP_other (N14)
Helichrysum italicum tyrrhenicum	0.02	0.06	0.33	2.94	1.78	0.03	0.34	0.997	TP
Thinopyrum junceum	0.02	0.04	0.52	1.75	3.5	0.02	0.36	0.058	TP_other (N14)
Anthemis maritima maritima	0.02	0.04	0.47	1.99	2.63	0.02	0.44	0.117	TP_other (N14)
Lomelosia rutifolia	0.02	0.06	0.28	1.88	1.8	0.02	0.46	0.971	TP
Medicago marina	0.01	0.03	0.46	1.07	2.51	0.01	0.51	0.092	TP_other (N14)
Cerastium semidecandrum	0.01	0.04	0.35	1.17	1.5	0.02	0.53	0.054	TP
Echinophora spinosa	0.01	0.02	0.54	1.28	1.39	0.02	0.56	0.175	TP_other (N14)
Phleum arenarium	0.01	0.05	0.27	1.51	0.75	0.01	0.57	0.981	TP
Cyperus capitatus	0.01	0.03	0.41	2.06	1.33	0.01	0.58	1	TP_other (N14)
Eryngium maritimum	0.01	0.03	0.39	1.71	0.94	0.01	0.59	0.998	TP_other (N14)
Lagurus ovatus	0.01	0.03	0.35	1	1.29	0.01	0.6	0.177	TP

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Rostraria litorea	0.01	0.04	0.26	0.53	1.74	0.01	0.63	0.072	TP
Sixalix atropurpurea	0.01	0.03	0.26	0.63	1.09	0.01	0.64	0.127	RD
Ambrosia psilostachya	0.01	0.03	0.24	0.8	0.62	0.01	0.65	0.957	NN
Silene rosulata sanctae-theresiae	0.01	0.04	0.19	1.04	0.4	0.01	0.66	0.88	NT
Daucus pumilus	0.01	0.03	0.28	0.9	1.26	0	0.67	0.056	TP
Poacynum venetum	0.01	0.05	0.13	0.86	0.37	0.01	0.68	0.902	TP
Scrophularia ramosissima	0.01	0.03	0.2	0.63	0.63	0.01	0.69	0.996	TP
Silene niceensis	0.01	0.02	0.3	0.47	0.83	0.01	0.7	0.17	TP
Achillea maritima maritima	0.01	0.02	0.26	0.84	0.52	0	0.7	0.992	TP_other (N14)
Anisantha rigida	0.01	0.02	0.25	0.33	0.88	0.01	0.72	0.3	RD
Convolvulus soldanella	0.01	0.01	0.39	0.75	0.52	0.01	0.73	0.989	TP_other (N14)
Euphorbia terracina	0	0.02	0.28	0.35	0.84	0	0.74	0.205	TP_other (N14)
Artemisia campestris variabilis	0	0.02	0.17	0.89	0.04	0.01	0.75	1	TP
Poa bulbosa	0	0.01	0.3	0.54	0.25	0	0.75	0.994	TP
Osyris alba	0	0.02	0.19	0.43	0.31	0.01	0.76	0.096	TP_other (no dune)
Plantago crassifolia	0	0.02	0.16	0.75	0	0	0.76	1	NT
Dasypyrum villosum	0	0.02	0.18	0.53	0.23	0.01	0.77	0.983	RD
Euphorbia paralias	0	0.01	0.33	0.29	0.38	0.01	0.78	0.365	TP_other (N14)
Trifolium nigrescens	0	0.02	0.17	0.53	0.17	0	0.78	0.96	NT
Verbascum niveum garganicum	0	0.01	0.23	0.18	0.51	0.01	0.79	0.08	NT
Anisantha sterilis	0	0.02	0.17	0.59	0.08	0	0.79	1	RD
Xanthium orientale	0	0.01	0.29	0.47	0.12	0	0.79	0.999	NN
Medicago minima	0	0.01	0.31	0.38	0.19	0.01	0.8	0.999	TP
Cynodon dactylon	0	0.01	0.45	0.27	0.3	0	0.8	0.147	RD
Echium sabulicola sabulicola	0	0.02	0.17	0.44	0.22	0.01	0.81	0.993	TP

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Hormuzakia aggregata	0	0.02	0.14	0.41	0.13	0	0.81	0.996	TP
Hypochaeris radicata	0	0.01	0.51	0.25	0.27	0.01	0.82	0.975	RD
Parapholis filiformis	0	0.03	0.1	0.37	0.03	0	0.82	0.997	NT
Lomelosia argentea	0	0.01	0.21	0.25	0.48	0	0.82	0.074	TP
Anisantha tectorum	0	0.01	0.22	0.16	0.23	0	0.83	0.058	RD
Arenaria serpyllifolia	0	0.01	0.25	0.31	0.12	0	0.83	0.999	NT
Reichardia picroides	0	0.01	0.47	0.25	0.24	0.01	0.84	0.994	NT
Silene conica	0	0.01	0.26	0.29	0.13	0	0.84	0.999	NT
Marcus-kochia ramosissima	0	0.01	0.18	0.17	0.17	0	0.84	0.986	TP
Seseli tortuosum maritimum	0	0.01	0.2	0.19	0.28	0.01	0.85	0.693	TP
Helianthemum nummularium	0	0.02	0.11	0.41	0.02	0	0.85	1	NT
Anisantha madritensis	0	0.01	0.23	0.25	0.13	0	0.85	0.999	RD
Cakile maritima maritima	0	0.01	0.37	0.17	0.2	0.01	0.86	0.927	TP_other (N12)
Silene otites otites	0	0.01	0.39	0.16	0.23	0	0.86	0.933	TP
Vicia pseudocracca	0	0.01	0.25	0.19	0.21	0	0.86	0.367	NT
Andryala integrifolia	0	0.01	0.22	0.2	0.24	0	0.86	0.337	TP
Trifolium scabrum	0	0.01	0.37	0.21	0.16	0	0.87	0.229	NT
Silene nummica	0	0.01	0.18	0.28	0.04	0	0.88	1	TP
Erodium cicutarium	0	0	0.36	0.2	0.13	0	0.88	0.964	NT
Catapodium rigidum	0	0	0.33	0.14	0.12	0	0.89	0.969	RD
Corynephorus sp.pl.	0	0.01	0.27	0.1	0.14	0.01	0.9	0.305	TP
Euphorbia cyparissias	0	0	0.33	0.13	0.12	0	0.9	0.387	RD
Oenothera sp.pl.	0	0	0.34	0.1	0.15	0	0.9	0.412	NN
Carex liparocarpos	0	0	0.33	0.12	0.12	0	0.9	0.295	NT
Silene vulgaris	0	0	0.32	0.13	0.1	0	0.9	0.838	RD
Thinopyrum acutum	0	0.01	0.19	0.09	0.16	0	0.91	0.803	NT
Petrorhagia saxifraga	0	0	0.3	0.12	0.08	0	0.91	0.613	TP
Equisetum ramosissimum	0	0	0.3	0.14	0.07	0	0.91	0.999	RD

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Scirpoides holoschoenus	0	0.01	0.15	0.06	0.15	0	0.91	0.161	TP_other (no dune)
Lobularia maritima	0	0	0.24	0.16	0.03	0	0.92	0.932	TP_other (no dune)
Sabulina tenuifolia	0	0.01	0.15	0.13	0.06	0	0.92	0.733	NT
Rhamnus alaternus alaternus	0	0.01	0.15	0.13	0.08	0	0.92	0.82	TP_other (no dune)
Verbascum sinuatum	0	0	0.26	0.06	0.11	0	0.92	0.059	RD
Cuscuta sp.pl.	0	0	0.26	0.1	0.05	0	0.92	0.998	NN
Trifolium campestre	0	0	0.28	0.15	0.04	0.01	0.93	0.998	RD
Matthiola sinuata	0	0	0.27	0.1	0.09	0	0.93	0.998	TP_other (N12)
Plantago lanceolata	0	0	0.3	0.09	0.09	0	0.93	0.316	RD
Raphanus raphanistrum	0	0	0.27	0.08	0.09	0	0.93	0.89	RD
Arenaria leptoclados leptoclados	0	0	0.26	0.11	0.05	0	0.93	1	NT
Solidago virgaurea litoralis	0	0	0.23	0.14	0	0	0.93	1	NT
Bromus hordeaceus	0	0	0.28	0.18	0	0	0.94	1	RD
Festuca ambigua	0	0	0.23	0.14	0.02	0	0.94	0.999	NT
Diplotaxis tenuifolia	0	0.01	0.13	0.18	0	0	0.94	1	RD
Lotus hirsutus	0	0	0.26	0.07	0.06	0	0.94	0.999	TP_other (no dune)
Euphorbia peplis	0	0	0.22	0.09	0.04	0	0.94	0.895	TP_other (N12)
Stachys romana	0	0.01	0.1	0.13	0	0	0.94	0.999	NT
Thymus pulegioides	0	0.01	0.11	0.13	0.02	0	0.94	0.998	NT
Jasione montana	0	0	0.22	0.03	0.12	0	0.94	0.067	NT
Hedypnois rhagadioloides	0	0	0.19	0.15	0.06	0	0.95	0.102	NT
Oenanthe lachenalii	0	0.01	0.1	0.13	0	0	0.95	0.999	NT
Cistus creticus	0	0.01	0.11	0.15	0	0	0.95	1	TP_other (no dune)
Dactylis glomerata	0	0	0.2	0.1	0.02	0	0.95	0.867	RD
Bassia laniflora	0	0	0.23	0.06	0.06	0	0.95	0.192	NT
Blackstonia perfoliata	0	0	0.18	0.05	0.05	0	0.95	0.948	NT

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Sonchus arvensis	0	0.01	0.11	0.15	0	0	0.95	1	RD
Veronica arvensis	0	0	0.24	0.11	0.02	0	0.95	1	NT
Trifolium arvense	0	0	0.24	0.13	0	0.01	0.96	1	NT
Launaea fragilis	0	0	0.21	0.05	0.07	0	0.96	0.948	NT
Glaucium flavum	0	0	0.21	0.04	0.06	0	0.96	0.088	TP_other (N12)
Avena barbata	0	0	0.21	0.04	0.06	0	0.96	0.087	RD
Tribulus terrestris	0	0	0.21	0.08	0.02	0	0.96	0.997	RD
Pinus pinea	0	0	0.16	0.06	0	0	0.96	0.999	TP_other (no dune)
Plantago arenaria	0	0	0.21	0.09	0.02	0	0.96	0.999	TP
Stachys recta	0	0	0.22	0.04	0.06	0	0.96	0.132	TP
Catapodium balearicum	0	0	0.16	0.05	0.03	0	0.97	0.966	RD
Teucrium flavum	0	0	0.15	0.13	0.06	0	0.97	0.936	TP_other (no dune)
Trifolium striatum	0	0	0.19	0.04	0.04	0	0.97	0.199	NT
Avellinia festucoides	0	0	0.19	0.06	0.03	0	0.97	0.999	TP
Leontodon rosanoi	0	0	0.16	0.07	0	0	0.97	0.999	NT
Polygonum maritimum	0	0	0.14	0.04	0.02	0	0.97	0.128	TP_other (N12)
Teucrium chamaedrys	0	0	0.19	0.08	0	0	0.97	1	TP_other (no dune)
Parapholis incurva	0	0	0.16	0.04	0.02	0	0.97	0.977	NT
Hordeum murinum leporinum	0	0	0.16	0.06	0	0	0.97	0.999	RD
Valerianella locusta	0	0	0.16	0.02	0.04	0	0.97	0.06	NT
Rostraria cristata	0	0	0.16	0.05	0.02	0	0.97	0.98	NT
Scolymus hispanicus	0	0	0.15	0.04	0.02	0.01	0.98	0.999	RD
Rumex acetosella	0	0	0.17	0.05	0.02	0	0.98	0.998	RD
Euphorbia pithyusa cupanii	0	0	0.13	0.05	0	0	0.98	0.999	TP_other (no dune)
Helianthemum apenninum	0	0	0.17	0.05	0.02	0	0.98	0.978	NT
Muscari comosum	0	0	0.16	0.04	0.02	0	0.98	0.756	NT
Limonium contortirameum	0	0	0.13	0.05	0	0	0.98	0.999	TP_other (no dune)

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Reseda alba alba	0	0	0.16	0.06	0	0	0.98	1	RD
Anthoxanthum odoratum	0	0	0.16	0.04	0.02	0	0.98	0.673	NT
Poa sylvicola	0	0	0.17	0.04	0.02	0	0.98	0.998	NT
Sherardia arvensis	0	0	0.17	0.07	0	0	0.98	1	RD
Silene gallica	0	0	0.17	0.07	0	0	0.98	1	TP
Urospermum picroides	0	0	0.17	0.06	0	0	0.98	0.999	NT
Tuberaria guttata	0	0	0.17	0.06	0	0	0.98	1	NT
Centranthus calcitrapae calcitrapae	0	0	0.13	0.05	0	0	0.98	1	NT
Phleum subulatum	0	0	0.1	0.13	0	0	0.98	0.999	NT
Bromus squarrosus	0	0	0.14	0.05	0	0	0.98	0.998	NT
Aeluropus littoralis littoralis	0	0	0.13	0.05	0	0	0.98	1	TP_other (no dune)
Sporobolus pumilus	0	0	0.13	0.02	0.03	0	0.98	0.308	NN
Juniperus turbinata	0	0	0.12	0.04	0	0	0.98	1	TP_other (no dune)
Lysimachia linum-stellatum	0	0	0.09	0.03	0	0	0.98	0.998	NT
Linum tenuifolium	0	0	0.14	0.02	0.03	0	0.98	0.347	NT
Arabidopsis thaliana	0	0	0.13	0.02	0.02	0	0.98	0.183	RD
Lolium rigidum	0	0	0.14	0.06	0	0	0.98	1	RD
Allium carinatum	0	0	0.13	0.02	0.02	0	0.98	0.105	NT
Beta vulgaris maritima	0	0	0.13	0.04	0	0.01	0.99	0.999	RD
Trigonella sulcata	0	0	0.13	0.04	0	0	0.99	0.999	NT
Trifolium stellatum	0	0	0.13	0.02	0.02	0	0.99	0.974	NT
Alyssum alyssoides	0	0	0.13	0.04	0	0	0.99	0.998	NT
Draba verna	0	0	0.14	0.04	0	0	0.99	0.998	RD
Pallenis spinosa spinosa	0	0	0.14	0.05	0	0	0.99	0.999	RD
Maresia nana	0	0	0.14	0.02	0.02	0	0.99	0.941	TP
Avena fatua	0	0	0.14	0.02	0.02	0	0.99	0.348	AR
Sesamoides interrupta	0	0	0.1	0.03	0	0	0.99	0.999	NT

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Lathyrus sphaericus	0	0	0.14	0.02	0.02	0	0.99	0.901	NT
Medicago rigidula	0	0	0.1	0.03	0	0	0.99	0.999	NT
Hippocrepis biflora	0	0	0.09	0.02	0	0	0.99	0.998	NT
Sedum sexangulare	0	0	0.14	0.04	0	0	0.99	1	NT
Hyparrhenia hirta	0	0	0.09	0.02	0	0	0.99	0.998	NT
Pulicaria dysenterica	0	0	0.1	0.03	0	0	0.99	0.998	NT
Ambrosia maritima	0	0	0.1	0.03	0	0	0.99	1	TP
Cynanchica pyrenaica cynanchica	0	0	0.1	0.03	0	0	0.99	1	NT
Carlina corymbosa	0	0	0.14	0.04	0	0	0.99	0.999	RD
Lonicera implexa implexa	0	0	0.1	0.03	0	0	0.99	0.999	TP_other (no dune)
Macrobriza maxima	0	0	0.1	0.03	0	0	0.99	0.999	RD
Trifolium lappaceum	0	0	0.13	0.01	0.01	0	0.99	0.338	NT
Picris hieracioides hieracioides	0	0	0.1	0.03	0	0	1	0.999	RD
Corrigiola litoralis litoralis	0	0	0.1	0.02	0	0	1	0.999	TP
Plantago lagopus	0	0	0.1	0.02	0	0	1	0.999	TP
Sonchus asper	0	0	0.1	0.02	0	0	1	0.999	RD
Hirschfeldia incana incana	0	0	0.1	0.02	0	0	1	0.999	NT
Trifolium cherleri	0	0	0.1	0.02	0	0	1	0.999	NT
Triticum vagans	0	0	0.1	0.02	0	0	1	0.999	NT
Crepis bellidifolia	0	0	0.1	0.03	0	0	1	0.999	NT
Frankenia laevis laevis	0	0	0.1	0.03	0	0	1	0.999	TP_other (no dune)
Rubus caesius	0	0	0.1	0.02	0	0	1	1	NT
Asparagus horridus	0	0	0.1	0.02	0	0	1	0.999	TP_other (no dune)
Hornungia petraea	0	0	0.1	0.02	0	0	1	0.998	NT
Potentilla verna	0	0	0.1	0.02	0	0	1	0.998	NT
Saxifraga tridactylites	0	0	0.1	0.02	0	0	1	0.998	RD
Ziziphora acinos	0	0	0.1	0.02	0	0	1	0.998	RD
Sedum acre	0	0	0.1	0.02	0	0	1	0.998	NT

Dune Grasslands Species (continued)	average dissimilarity	sd	ratio	historical average abundance	revisited average abundance	contribution (%)	cumulative contribution (%)	p-value	Species guilds
Tragus racemosus	0	0	0.1	0.02	0	0	1	0.998	NT
Jacobaea maritima bicolor	0	0	0.1	0.02	0	0	1	0.999	TP_other (no dune)
Fumaria capreolata capreolata	0	0	0.1	0.02	0	0	1	0.999	RD
Euphorbia helioscopia	0	0	0.1	0.02	0	0	1	1	RD
Ranunculus bulbosus	0	0	0.1	0.02	0	0	1	1	NT
Capsella bursa-pastoris	0	0	0.1	0.02	0	0	1	1	RD
Filago germanica	0	0	0.1	0.02	0	0	1	1	NT
Lolium perenne	0	0	0.1	0.02	0	0	1	1	RD
Phagnalon saxatile	0	0	0.1	0.02	0	0	1	0.999	NT
Salvia pratensis	0	0	0.1	0.02	0	0	1	1	RD
Lepidium campestre	0	0	0.1	0.02	0	0	1	0.999	RD
Sonchus maritimus	0	0	0.1	0.02	0	0	1	1	NT
Petrorhagia dubia	0	0	0.1	0.01	0	0	1	0.999	NT
Senecio transiens	0	0	0.1	0.01	0	0	1	0.999	TP