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Resurveying the most threatened habitats

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TABLE OF CONTENTS

SUPPLEMENTARY MATERIALS:

Appendix A: Supporting Information to Chapter I

Appendix B: Supporting information to Chapter II

Appendix C: Supporting information to Chapter III

Other papers arising from PhD research:

Appendix D:
Cini, E., Acosta, A. T. R., Malavasi, M., **Sarmati, S.**, Del Vecchio, S., Ciccarelli, D., & Marzialetti, F. (2025). Long-term dynamics of coastal dune landscapes and habitat diversity: Insights from a quarter century of resurveys in Castelporziano Presidential Estate. Conservation Science and Practice, e70101. https://doi.org/10.1111/csp2.70101

Appendix E:
Denaro, A., Caria, M. C., Malavasi, M., Rivieccio, G., Melis, R., Farris, E., Maccioni, A., Bruno, A., Fadda, M., Acosta, A.T.R., **Sarmati, S.**, Sperandii, M.G. & Bagella, S. (2025). Resurveying Mediterranean coastal dunes: insights from the ReSarDu database. Vegetation Ecology and Diversity, 62, e174934. https://doi.org/10.3897/ved.174934

Abstract

Mediterranean coastal dunes are among the most threatened ecosystems in Europe, undergoing accelerated transformations under global environmental change and anthropogenic pressures. To advance understanding of long-term vegetation dynamics in these habitats, this research was developed through three complementary steps and is based on a diachronic analysis of vegetation resurveys at both local and national scales across Italian dune ecosystems.

First, within the Castelporziano Presidential Estate, which hosts one of the most well-preserved coastal dune systems in Italy, 80 historical vegetation plots, originally surveyed approximately 30 years ago across all vegetation communities of the coastal zonation, were revisited to assess temporal changes in species composition, ecological indicator values, and functional traits.

In parallel, ReSurveyDunes, the first national database of resurveyed Italian coastal dune vegetation plots, was developed by integrating historical phytosociological relevés with resurveys conducted between 2023 and 2024. This database encompasses multiple dune habitats and enables long-term, national-scale assessments of their conservation status.

From ReSurveyDunes 519 historical plots distributed across 11 regions, originally sampled between 1974 and 2009, were extracted and analysed to produce the first national assessment of multi-decadal trends in coastal dune vegetation, encompassing herbaceous communities of upper beach, shifting dune, and dune grassland habitats.

Results revealed heterogeneous but interpretable patterns across spatial scales. In well-preserved sites such as Castelporziano, species richness and the abundance of typical psammophilous species remained stable or increased, reflecting limited anthropogenic disturbance and ongoing natural successional processes. At the national scale, overall species richness often increased, but this trend masked marked declines in habitat-specialist species, particularly in early-successional environments. These compositional changes were driven primarily by an increase in ruderal species and by species redistribution along the coastal zonation gradient, rather than by the widespread invasion of non-native taxa. Approximately one-third of revisited plots experienced transitions toward different habitat types, indicating the coexistence of inland-directed stabilisation and localised degradation in foredune zones.

Together, these findings demonstrate that apparent increases in diversity may conceal structural and functional erosion in dynamic dune ecosystems. Long-term resurvey approaches, such as those implemented in ReSurveyDunes, are essential for detecting subtle ecological shifts and for guiding conservation strategies aimed at preserving the integrity and resilience of Mediterranean coastal dune habitats under intensifying environmental pressures.

Riassunto

Le dune costiere mediterranee rappresentano uno degli ecosistemi più minacciati d'Europa, soggetti a trasformazioni sempre più rapide sotto l'effetto del cambiamento ambientale globale e delle pressioni antropiche. Al fine di approfondire la comprensione delle dinamiche della vegetazione in questi ambienti, utilizzando la rivisitazione della vegetazione sia a scala locale che nazionale negli ecosistemi dunali italiani, è stata condotta un'analisi diacronica attraverso tre distinte fasi.

In primo luogo, all'interno della Tenuta Presidenziale di Castelporziano, che comprende uno dei sistemi dunale meglio conservati del territorio italiano, sono stati rivisitati 80 rilievi vegetazionali storici, effettuati originariamente circa 30 anni fa lungo tutta la zonazione costiera. La rivisitazione ha permesso di analizzare i cambiamenti temporali nella composizione floristica, negli indicatori ecologici di Ellenberg e nei tratti funzionali delle comunità vegetali in un ambiente unicamente conservato. Parallelamente, è stato sviluppato ReSurveyDunes, il primo database di rilievi storici rivisitati della vegetazione dunale costiera lungo le coste italiane. Integrando rilievi fitosociologici storici risalenti in media a trent'anni fa su diversi habitat dunali del territorio italiano, con nuovi rilievi condotti tra il 2023 e il 2024, questo database consente valutazioni su scala nazionale e a lungo termine dello stato di conservazione di questi ambienti. Da questa fonte sono stati estratti dati provenienti da 519 rilievi distribuiti in 11 regioni italiane, originariamente campionati tra il 1974 e il 2009 e riesaminati nel periodo 2023-2024, al fine di produrre la prima valutazione nazionale delle tendenze della vegetazione dunale costiera degli ultimi decenni, includendo habitat erbacei delle dune pioniere, e delle dune mobili e fisse.

I risultati hanno evidenziato pattern eterogenei ma interpretabili a diverse scale spaziali. Nei siti ben conservati, come Castelporziano, la ricchezza specifica e l'abbondanza delle specie psammofile tipiche sono rimaste stabili o in aumento, riflettendo la presenza di processi di successione naturale e una limitata pressione antropica. A scala nazionale, al contrario, l'aumento complessivo della ricchezza specifica ha spesso mascherato un marcato declino delle specie tipiche degli habitat, in particolare negli ambienti di avanduna. Tali cambiamenti composizionali risultano guidati principalmente da un aumento della presenza di specie ruderali e da una ridistribuzione delle specie psammofile lungo il gradiente di zonazione costiera piuttosto che da forti cambiamenti nella composizione delle specie, per esempio attraverso la diffusione delle specie invasive. Circa un terzo dei rilievi riesaminati ha mostrato forti cambiamenti della vegetazione, con transizioni verso tipi di habitat differenti rispetto a quelli originari, indicando la coesistenza di processi di stabilizzazione, successione verso stadi più maturi, insieme a fenomeni di degrado localizzato nelle aree dunali più prossime alla linea di costa. Nel complesso, questi risultati dimostrano che apparenti incrementi della diversità possono celare fenomeni di degrado strutturale e funzionale negli ecosistemi dunali.

La rivisitazione di rilievi, come quelli adottati nell'ambito di ReSurveyDunes, risulta pertanto fondamentale per poter individuare cambiamenti ecologici sottili e per orientare strategie di conservazione volte a preservare l'integrità e la resilienza degli habitat dunali costieri mediterranei in un contesto di pressioni ambientali in crescente intensificazione.

Papers published or prepared during PhD

Paper 1:

Gianguzzi, L., Guarino, R., Bazan, G., Di Pietro, R., Acosta, A. T. R., Bajona, E., Bolliger, P., Bonomi, C., Camuffo, A., Console, C., Fascetti, S., Fortini, P., Frattaroli, A., Mei, G., Mondello, F., Olivari, S., Rizzieri, M., Rosati, L., **Sarmati, S.,** Scuderi, L., Simonazzi, M., Spampinato, G., Viegi, L., & Stinca, A. (2023). Itineraries of the Working Group for Vegetation Science of the Italian Botanical Society–1 (2022): Excursion to the Egadi Islands, Mount San Giuliano and Mount Cofano (Trapani, western Sicily, Italy). *Italian Botanist*, 16, 1-57. https://dx.doi.org/10.3897/italianbotanist.16.103989

Paper 2:

Pafumi, E., Angiolini, C., **Sarmati, S.**, Bacaro, G., Fanfarillo, E., Fiaschi, T., Foggi, B., Gennai, M., & Maccherini, S. (2024). Spatial patterns of coastal dune plant diversity reveal conservation priority hotspots in and out a network of protected areas. *Global Ecology and Conservation*, 54, e03085. https://doi.org/10.1016/j.gecco.2024.e03085

Paper 3 – Chapter I:

Sarmati, S., Sperandii, M. G., Di Biase, L., Acosta, A. T. R., & Del Vecchio, S. (2025). Three decades of coastal vegetation dynamics in the Castelporziano Presidential Estate: Analysing biodiversity shifts in an exceptionally intact coastal dune system. *Biodiversity and Conservation*, 34(7), 2565–2581. https://doi.org/10.1007/s10531-025-03087-w

Paper 4 – Chapter II:

Acosta, A. T. R., Di Biase, L., **Sarmati, S.**, Allevato, E., Angiolini, C., Bagella, S., Bazan, G., Bertacchi, A., Brancaleoni, L., Buffa, G., Calbi, M., Caria, M. C., Ciccarelli, D., Cutini, M, De Francesco, M. C., De Natale, A., Fantinato, E., Fiaschi, T., Gangale, C., Gerdol, R., Gianguzzi, L., Laface, V. L. A., Maccherini, S., Morabito, A., Mugnai, M., Musarella, C. M., Pafumi, E., Santangelo, A., Sciandrello, S., Siccardi, E., Spampinato, G., Stanisci, A., Strumia, S., Viciani, D., & Del Vecchio, S. (2025) ReSurveyDunes - a data resource of resurveyed coastal dune vegetation plots in Italy. *Vegetation Ecology and Diversity* 62:1–6. https://doi.org/10.3897/ved.139539

Paper 5 – Chapter III:

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Paper 6:

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Paper 7:
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Paper 8:
Denaro, A., Caria, M. C., Malavasi, M., Rivieccio, G., Melis, R., Farris, E., Maccioni, A., Bruno, A., Fadda, M., Acosta, A.T.R., **Sarmati, S.**, Sperandii, M.G. & Bagella, S. (2025). Resurveying Mediterranean coastal dunes: insights from the ReSarDu database. *Vegetation Ecology and Diversity*, 62, e174934. https://doi.org/10.3897/ved.174934

Paper 9:
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Paper 11:
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Paper 12:
Sarmati, S., Angiolini, C., Sperandii, M. G., Barták, V., Gennai, M., Acosta, A. T. R., Bertacchi, A., Bonari, G., Foggi, B., Maccherini, S., Viciani, D., & Bazzichetto, M. (2025). A complex interplay between natural and anthropogenic factors shapes plant diversity patterns in Mediterranean coastal dunes. *Landscape Ecology*, 40(1), 20. https://doi.org/10.1007/s10980-024-02025-5

Paper 13:
Nagy, D.U., Callaway, R. M., Flory, S.L., Barratt, C. D., Durka, W., … **Sarmati, S**., Scheepens, J.F.S., Shah, M.A., Sheng, M., Sikkema, P., Silliman, C, Slate, M.L., St. Clair, S.B., Stein, C., Stevermer, K., Suzuki, S.N., Tashpulatov, Y., Tsunoda, T., Turginov, T., Vakhlamova, T., van Dam, N.M., Wagner, V., Westberg, L., Xiao, S. Zhang, Z., Rosche, C. Rapid and repeated evolution of increased competitive ability in a global invader. *Nature*. **(submitted)**

GENERAL INTRODUCTION

Under an increasing anthropogenic pressure

European coastal ecosystems have been shaped by human activities since prehistoric times, including deforestation, agriculture, grazing, and vegetation management (Gao et al., 2020; Nordstrom & Jackson, 2021; Provoost et al., 2011). In recent decades, however, their ecological impacts have intensified due to population growth, coastal settlement, climate change, and sea-level rise (Schlacher et al., 2008). Traditional land-use practices have been altered, replaced, or abandoned, while tourism and urban development have expanded rapidly over the last 50-70 years (EEA, 2015; Gao et al., 2020; Heslenfeld et al., 2008). These processes have caused widespread habitat degradation, placing coastal dunes among Europe's most threatened ecosystems (Heslenfeld et al., 2008; Janssen et al., 2016). Over the twentieth century, approximately 70% of European coastal dune systems were lost as a result of urbanization (Brown & McLachlan, 2002).

The Mediterranean basin has been disproportionately affected due to its long history of human settlement and its role as a major global tourism destination (Malavasi et al., 2013, 2016; Sytnik & Stecchi, 2015). Urban expansion, tourism infrastructure, and associated disturbances (such as land-use change, trampling, and beach cleaning) have reduced landscape heterogeneity, diminished psammophilous vegetation cover, facilitated the invasion of alien species, and ultimately driven habitat loss (Ciccarelli, 2014; Farris et al., 2013; Molina et al., 2020; Prisco et al., 2020; Santoro et al., 2011). These cumulative pressures weaken dune structure and functioning, thereby reducing ecosystem resilience (La Bella et al., 2024).

In Italy, the situation is particularly severe. The Fourth Report of the EU Habitats Directive (92/43/EEC) classified 89% of Italian coastal sand dune habitats as "Unfavourable-Bad" and 11% as "Unfavourable-Inadequate" (Ercole, et al., 2021), reflecting persistent anthropogenic pressure consistent with broader Mediterranean trends (Janssen et al., 2016).

Although coastal dunes occupy a limited proportion of the terrestrial surface, they play a critical role in biodiversity conservation and ecosystem functioning. Strong environmental gradients structure dune vegetation into characteristic coastal zonation, supporting highly specialized and often threatened plant species while also providing habitat for invertebrates, amphibians, and reptiles (McLachlan et al., 2018). In addition, coastal dunes deliver key ecosystem services, including storm protection, microclimate regulation, groundwater storage, carbon sequestration, nutrient cycling, and cultural and recreational values (Arkema et al., 2013; Everard et al., 2010; Nordstrom & Jackson, 2021).

Despite their ecological importance, coastal dunes are increasingly vulnerable to sea-level rise, shoreline erosion, urbanisation, pollution, and other human-driven pressures (Bazzichetto et al., 2020; Calvão et al., 2013; Defeo et al., 2009; Malavasi et al., 2013; Poeta et al., 2014; Schlacher et al., 2008). Urban development and tourism directly remove vegetation or disrupt sediment dynamics and indirectly degrade plant communities through trampling, and the facilitation of alien species establishment (Carboni et al., 2010; Ciccarelli, 2014; Dimitrakopoulos et al., 2017; Santoro et al., 2012; Tzatzanis et al., 2003).

Land-use changes, including both grazing intensification and grazing abandonment, further threaten dune stability. Grazing can increase sand mobility, while abandonment often promotes shrub encroachment, reducing habitat openness and plant diversity (Gao et al., 2020; Van Der Hagen et al., 2023). In addition, alien species introductions, frequently associated with human disturbance, contribute to biotic homogenisation and reduced ecosystem resilience (Giulio et al., 2020; Makowski & Finkl, 2019). Finally, coastal erosion, intensified by anthropogenic activities and climate change, causes habitat fragmentation, declines in species richness, and the loss of shoreline plant communities (Antonioli et al., 2017, 2020; Bazzichetto et al., 2020; García-Mora et al., 1999; Pranzini et al., 2015; Vousdoukas et al., 2020).

Understanding temporal changes is essential for interpreting vegetation dynamics in Mediterranean coastal dunes, where human pressures are intense and long-standing (Martinez & Psuty, 2004). Over recent decades, dune dynamics have been investigated using permanent vegetation plots (Isermann, 2011; Kuiters et al., 2009; Pakeman et al., 2017; Prisco et al., 2016), community resurveys (Ciccarelli et al., 2025; Maliniemi et al., 2023; Sperandii et al., 2019; Valcheva et al., 2021), historical photographs, and remote-sensing approaches (Bazzichetto et al., 2020; Bertacchi et al., 2016; Cini et al., 2025; Malavasi et al., 2016; Molina et al., 2020; Santana-Cordero et al., 2016; Sciandrello et al., 2015). Collectively, these studies provided consistent evidence of temporal degradation of coastal dunes driven by land-use change, coastal development, and increasing human pressure, resulting in simplified vegetation structure and enhanced erosion (Malavasi et al., 2013; Pakeman et al., 2017).

Among available approaches, resurvey studies, based on the re-sampling of historical vegetation plots, are particularly effective for detecting long-term changes in species composition and community structure (Kapfer et al., 2017; Knollová et al., 2024). In Italy, however, such studies are mostly restricted to limited time spans or to site- and region-specific analyses (Ciccarelli et al., 2025; Del Vecchio et al., 2015; Sperandii et al., 2019). Moreover, a geographically representative national dataset is still lacking, despite their considerable potential for assessing broad-scale temporal changes in species composition, diversity, and functional structure (Finderup Nielsen et al., 2021; Hédl et al., 2017).

In addition, Mediterranean coastal dunes, no resurvey studies have explicitly focused on well-preserved coastal dune systems with intact vegetation zonation, which are essential for understanding natural successional dynamics in the absence of pervasive anthropogenic disturbance (Callaway & Davis, 1993; Martinez & Psuty, 2004; Van Der Maarel, 1988). Large-scale, harmonized resurvey vegetation datasets therefore represent a valuable yet still underexploited resource for evaluating long-term habitat change and contextualizing local patterns of degradation within a broader biogeographical framework (Jandt et al., 2011).

The resurvey approach: opportunities and limitations

Temporal changes in plant communities are commonly assessed using three approaches: (i) large vegetation databases, (ii) permanent plots, and (iii) resurveys of historical plots. These approaches differ in reliability, spatial representativeness, and logistical demands. Database-driven studies allow cost-effective detection of broad trends but cannot rely on direct plot-to-plot comparisons and may partly reflect spatial pseudo-turnover rather than true temporal change (Chytrý et al., 2014; Jandt et al., 2011). Permanent plots provide the highest precision but are constrained by high costs, limited spatial coverage, and often subjective plot placement (Bakker et al., 1996; Hédl et al., 2017).

Resurveying historical plots represents an effective compromise, enabling direct plot-to-plot temporal comparisons across broader spatial scales and at moderate cost. This approach has gained increasing attention, particularly within European phytosociology, which benefits from a long tradition of standardised vegetation surveys. Large-scale initiatives such as *ReSurveyEurope* further highlight the potential of historical data for long-term biodiversity monitoring (Knollová et al., 2024).

Resurvey studies are nonetheless subject to uncertainties, including relocation error, observer bias, and phenological differences between surveys. While relocation uncertainty is unavoidable in unmarked plots, its effects decrease in structurally homogeneous vegetation and with increasing sample size (Kapfer et al., 2017). Observer-related pseudo-turnover and phenological bias can be minimised through careful study design and temporal alignment of surveys (Archaux et al., 2006; Hédl et al., 2017; Ross et al., 2010). Although these sources of error cannot be fully eliminated, they can be quantified and substantially reduced.

Aims and structure of the study:

This study investigates long-term temporal changes in Mediterranean coastal dune habitats over an average period of approximately 30 years, using vegetation resurveying as a common methodological framework. By integrating local reference conditions with national-scale analyses, the study aims to analyse natural vegetation dynamics and anthropogenically driven changes in order to provide a comprehensive assessment of long-term trends in Italian coastal dune ecosystems. To achieve these objectives, the study is structured around three main aims, outlined below.

1) The first aim (Chapter I) is to assess long-term vegetation dynamics under minimal anthropogenic disturbance. Historical and recent vegetation plots from the Presidential Estate of Castelporziano, one of the last well-preserved Italian coastal dune systems, are compared to analyse changes in species composition, community structure, and Ellenberg Indicator Values (EIVs; Ellenberg, 1974; Dengler et al., 2023; Tichý et al., 2023) across all vegetation communities of the coastal zonation, encompassing both herbaceous and woody dune habitats. EIVs provide species-based proxies of environmental conditions and are particularly valuable where historical environmental data are lacking (Del Vecchio et al., 2015; Jantsch et al., 2013; Maliniemi et al., 2023). This chapter establishes a reference framework for natural successional dynamics and vegetation stability.

2) The second aim (Chapter II) introduces *ReSurveyDunes*, the first Italian database of resurveyed coastal dune vegetation plots. By integrating historical phytosociological relevés with resurveys conducted between 2023 and 2024, this dataset provides geographically representative coverage **across** multiple dune habitats of conservation concern and supports national-scale assessments of temporal change and conservation status under the EU Habitats Directive.

3) The third aim (Chapter III) quantifies long-term changes in species richness, vegetation cover, and community composition across Italian coastal dune habitats at the national scale. Using *ReSurveyDunes*, this chapter evaluates temporal trends in taxonomic diversity and the relative contribution of key ecological guilds (typical dune species, ruderal taxa, and non-native species), identifies species driving compositional change, and characterises transitions among EUNIS habitat types. Together, these analyses provide the first comprehensive national-scale assessment of long-term

vegetation change in Italian coastal dunes, offering insights into biodiversity loss, functional simplification, and habitat transformation along the Mediterranean coastline.

Chapter I (paper 1)

Biodiversity and Conservation https://doi.org/10.1007/s10531-025-03087-w

ORIGINAL RESEARCH

Three decades of coastal vegetation dynamics in the Castelporziano Presidential Estate: analysing biodiversity shifts in an exceptionally intact coastal dune system

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Abstract

Mediterranean coastal dunes are among the most threatened ecosystems in Europe. Analysing temporal trends in a site with exceptionally well-preserved zonation and minimal anthropogenic disturbance offers a unique opportunity to deepen our understanding of vegetation dynamics under low-impact conditions in these vulnerable ecosystems. This study examines the temporal dynamics of coastal dune ecosystems within the Castelporziano Presidential Estate, which hosts intact Mediterranean dune systems with complete vegetation zonation. Revisiting 80 historical plots initially surveyed 30 years ago, we analysed changes in plant species occurrence and abundance over time using ordination and similarity percentage analysis. Additionally, we assessed shifts in typical, ruderal, and alien species, ecological indicator values, and an index based on rhizomatous geophyte grasses to evaluate the system's erosion control capacity. Our results revealed no significant decline in species richness in foredunes and dune grasslands, contrasting with trends observed in other coastal dunes in Central Italy. Instead, we recorded an increase in typical species abundance in foredunes, likely resulting from limited human disturbance over the past 30 years. These changes are probably related to ongoing successional dynamics. Coastal shrublands underwent more pronounced changes, transitioning toward woodlands and experiencing an increase in typical species. These transformations suggest positive successional shifts. Our findings indicate that the coastal dune ecosystem is well-preserved, largely due to restricted human disturbance and effective management. This study underscores the value of resurveying methodologies for monitoring vegetation dynamics, offering critical insights to support conservation efforts for these unique Mediterranean habitats.

Introduction

Population growth along coastal areas has driven increasing urbanization, which, combined with the development of the tourism industry, has significantly altered the coastal landscape over the last 50 years (EEA 2020; Gao et al. 2020). Land degradation, coupled with widespread coastal erosion processes (Prăvălie 2021), has contributed to a decline in the species richness and diversity of psammophilous native species, ultimately leading to the loss of natural coastal habitats (Prisco et al. 2020; Singh et al. 2021).

Human activities have shaped European coastal ecosystems since prehistoric times, from early deforestation, agriculture, and grazing to recent urban expansion and vegetation management (Provoost et al. 2011; Gao et al. 2020). These pressures have profoundly altered dune systems, with urbanization in extreme cases replacing natural landscapes entirely (Provoost et al. 2011; Santana-Cordero et al. 2016; Garcia-Lozano et al. 2018; Molina et al. 2020). Land use changes, including vegetation removal for grazing, have intensified aeolian dynamics, while grazing abandonment has led to shrub encroachment and declining plant diversity (Damgaard et al. 2013; van der Hagen et al. 2023; Gao et al. 2020). Moreover, alien species introductions (both intentional and accidental) have profoundly altered dune plant communities (Makowski and Finkl 2019; Giulio et al. 2020).

Human interventions and management strategies have also played an important role in shaping coastal plant communities, particularly in relation to coastal erosion (Bossard and Nicolae Lerma 2020). Erosion is a key driver of biodiversity change, reducing vegetation cover and species richness, especially affecting species with shallow roots (Ciccarelli 2014; Bazzichetto et al. 2020; Antonioli et al. 2017; García-Mora et al. 1999). It can fragment habitats, eliminate plant communities close to the shoreline, and accelerate dune degradation through the loss of key stabilizing species (Ciccarelli 2014; García -Mora et al. 2000; Bazzichetto et al. 2020).

These pressures have affected most of the Mediterranean coastal areas, making dune systems one of the most threatened ecosystems in Europe (Janssen et al. 2016), with only a few sites left to maintain their ecological integrity. One such example is the Presidential Estate of Castelporziano, which, despite various changes in land use throughout its long history, has been preserved from significant anthropic impacts since at least 1977, and represents a unique opportunity to analyse vegetation dynamics under long-term minimal anthropic disturbance (Pratesi 2015; La Bella et al. 2021; Della Rocca et al. 2001; Acosta et al. 2003).

Although temporal changes in coastal dune ecosystems have been investigated using different approaches (e.g., using permanent plots, through the comparison of historical photos, or through remote sensing analyses (Sciandrello et al. 2015; Malavasi et al.

2016a; Santana-Cordero et al. 2016; Molina et al. 2020; Bazzichetto et al. 2020), the resurvey method has proven highly effective for tracking changes in such dynamic environments (Del Vecchio et al. 2015; Sperandii et al. 2018; Landi et al. 2012; Bonari et al. 2021a). Resurveying studies consist in the re-sampling of vegetation plots historically surveyed by other authors (Kapfer et al. 2017; Knollová et al. 2024), leveraging historical vegetation data to provide new opportunities for long-term biodiversity monitoring. This approach has gained increasing attention in recent years, as demonstrated by large-scale initiatives such as ReSurveyEurope (Knollová et al. 2024) and ReSurveyDunes (Acosta et al. 2025). However, no resurveying studies have yet analysed temporal vegetation changes across a well-preserved coastal dune system with intact vegetation zonation. Evaluating temporal trends in an area with exceptionally well-preserved zonation, free from the widespread anthropic disturbances that characterize Mediterranean coastal dunes, is critical to enhance our understanding of vegetation dynamics in these unique and highly threatened ecosystems (Van Der Maarel 1988; Callaway and Davis 1993; Martínez and Psuty 2004).

Trends in biodiversity changes over time can be more informative when considering not only species turnover but also changes in community structure and whether the species involved exhibit adaptations to specific ecological conditions. To this end, changes in the composition of species guilds, such as typical, ruderal, and alien species, may provide further insight into the ecological processes driving temporal changes (Sarmati et al. 2024). Furthermore, Ecological Indicator Values (EIVs) can be a valuable tool for rapidly assessing ecological conditions and their changes. Originally proposed by Ellenberg for the vascular plants of Central Europe (Ellenberg 1974) and later updated and extended to cover the flora of all Europe (Dengler et al. 2023; Tichý et al. 2023), these values describe plant 'preferences' for specific ecological conditions, expressed on an ordinal scale. When analysing temporal changes, EIVs values can be particularly useful in cases where information on past environmental conditions is lacking and may reveal changes in species composition involving similar adaptations (Jantsch et al. 2013; Del Vecchio et al. 2015; Maliniemi et al. 2023).

In this study, we repeated historical vegetation surveys conducted approximately 30 years ago within the Presidential Estate of Castelporziano. We aimed to: (i) analyse temporal trends in coastal dune vegetation zonation at both species and community levels, focusing on changes in species richness and abundance, as well as in ecologically relevant plant guilds (i.e. typical, ruderal, and alien species); (ii) examine trends in Ecological Indicator Values; (iii) evaluate changes in the contribution of plant species to mitigating the coastal erosion process.

Materials and methods

Study area

The Presidential Estate of Castelporziano, extending over about 6040 hectares, includes almost 5 km of coastline along the Tyrrhenian coast of Latium (Central Italy), a few kilometers south of the mouth of the Tiber River (Fig. 1). The history of this area dates back to Antiquity, when it was a residential area for wealthy Romans (III BC-IV AD). Subsequently, after being a property of the Papal State and aristocratic families, it was acquired by the Kingdom of Italy in 1872, and in 1948 became the property of the President of the Italian Republic. Moreover, in 1999, it was designated as a State Nature Reserve due to its high naturalistic value (Pratesi 2015; Presidential Decree 136/N of 1999; Nardone, 2021). Since 2000, the estate has been part of the Natura 2000 Network (SIC IT6030027 "Castelporziano coastal strip," SIC IT6030028"Castelporziano hygrophilous oak woods," ZPS IT6030084 "Castelporziano Presidential Estate") according to the Habitats Directive 92/43/EEC. Since 2017, the SICs have been designated as Special Areas of Conservation (SACs).

Despite being approximately 25 km from the center of Rome and surrounded by a greatly anthropized matrix, this protected area remains one of the last strips of the best preserved coastal dunes in Italy but also in the entire Mediterranean basin (Pratesi 2015; La Bella et al. 2021; Della Rocca et al. 2001; Acosta et al. 2003). Moreover, the coastal environment of the Presidential Estate is one of the few coastal stretches where the full

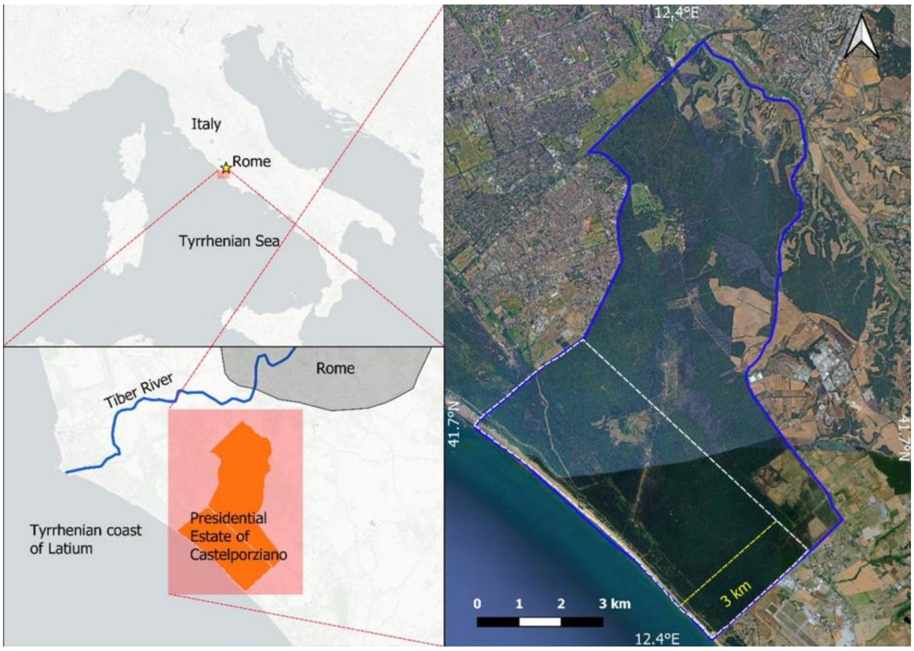

Fig. 1 Study area. The presidential estate of Castelporziano. Blue lines represent the boundary of the area. Dashed white borders delimited the area interested by the resurveyed plots. The yellow dashed line indicates the maximum distance from the coast

zonation of coastal dune vegetation, i.e. the spatial turnover of plant communities from the shoreline to the inland, driven by species' ecological preferences (Doing 1985; Acosta et al. 2003), remains intact, spanning from herbaceous foredunes to fixed dunes with shrubs and forests. The psammophilous vegetation of the dunes extends from the coastline, followed inland by an extensive area almost entirely occupied by Mediterranean shrubs and holm oak (*Quercus ilex*) woods (La Bella et al. 2021).

The dune system consists of sandy deposits primarily supplied by the Tiber River during the Holocene, with sediment deposition influenced by post-glacial sea-level rise and continuously reshaped by marine currents and wind (Capelli et al. 2007). From a phytoclimatic perspective, it falls within the Mediterranean and Transitional Mediterranean Region, with a meso-Mediterranean thermotype with an average annual temperature of 16 °C and an average annual rainfall of approximately 800 mm (Salvati et al. 2021).

Data selection

We searched for all vegetation surveys conducted in the past and available for the Presidential Estate of Castelporziano (CP-BioDb Castelporziano biodiversity database). Out of the 344 available historical plots we selected as follows. First, we filtered for plots that had been surveyed more than 20 years ago (n = 283), then selected those that were located within 3000 m of the coastline (n = 83) (Figs. 1 and 2). To reduce relocation bias, we retained only those historical plots with precise geographical information, i.e. either with GPS-derived coordinates available or with a position error of < 50 m. Furthermore,

Fig. 2 Main coastal vegetation types within the study area. **a** Foredunes; **b** Dune grasslands; **c** Shrublands; **d** Woody communities of fixed dunes

to enhance relocation accuracy and minimize seasonal bias, we filtered for those historical plots that provided information on plot size and sampling period (date, or month) (Vymazalová et al. 2012; Kapfer et al. 2017). When relocating historical plots, we also considered the description of the area, the original list of species, and the dominant species (Kapfer et al. 2017). Each plot was classified by assigning the corresponding Natura 2000 habitat following European and national guidelines (Biondi et al. 2009; Angelini et al. 2016; European Commission 2013).

The filtered dataset resulted in 80 historical vegetation plots covering almost all coastal dune habitats occurring in the Mediterranean, starting from foredune habitats (EU habitat 2110 and 2120) to inland *Quercus ilex* woods (EU habitat 9340) (Online Resource Table S1). The selected historical plots were originally surveyed from 1985 to 2000 and resurveyed in 2023, meaning that up to ca. 40 years have passed between the earliest and the most recent surveys (mean time span: 29.8 years). Plot size ranged between 5 and 1000 m^2 (median = 100 m^2; mean = 157.4 m^2).

Overall, we resurveyed 74 of the 80 historical plots (92.5%), with six plots remaining un-relocated and un-surveyed. These missing plots were situated in fixed and stable dunes. Two were originally classified as juniper-dominated formations of Mediterranean stable dunes (EU habitat 2250*), but they were currently inaccessible. The other four were herbaceous formations dominated by grasses and annuals (habitat 2240). According to previous descriptions, these plots occupied gaps in the garrigue, coexisting with *Helichrysum* spp. and *Juniperus* spp. (Lucchese and Pignatti 1987, 1990). Their inaccessibility was due to vegetation closure caused by shrub encroachment.

Vegetation resurvey

Resurveying was performed with the same approach as for the historical plots, during the same season and with the same plot size. The occurrence of all vascular plant species was recorded, and species abundance was visually estimated using the Braun-Blanquet percentage cover scale (Braun-Blanquet 1964), as in historical plots. We also estimated the overall abundance of all vascular plants for each plot. A standardized taxonomic nomenclature of historical and resurveyed plots was applied according to Bartolucci et al. (2018).

Data analysis

Temporal trends at the community level

Temporal changes in species composition were explored through multivariate analysis, using Detrended Correspondence Analysis (DCA) with log-transformation of species abundances (*decorana* function, "vegan" R package, Oksanen et al. 2022). To better balance the number of plots for each habitat, we combined historical plots based on coastal dune vegetation zonation. Specifically, plots were grouped according to their typical distance from the sea (and consequently similar environmental conditions) and structure similarity into the following macro-categories: foredunes (2110 and 2120 EU habitat), dune grasslands (2210 and 2230), shrublands (2250* and 2260, where 2250* is a EU priority habitat), and woody communities of fixed dunes (9340 and 91 F0; see Online Resource Table S1).

All statistical analyses were conducted within the R environment (R Core Team 2022).

Temporal trends at the species level: species richness and abundance in plant guilds

To identify the species that most explained the differences between the two sampling periods, we performed a similarity percentage analysis (SIMPER). This analysis tested for differences in composition between resurveyed and historical plots within habitat types grouped in the macro-categories using 999 random permutations (*simper* function, "vegan" R package, Oksanen et al. 2022).

For each plot, we calculated species richness (the total number of recorded species) and total abundance (sum of individual species cover). These metrics were computed both for all species collectively and for relevant ecological guilds, which have been demonstrated to be particularly useful in coastal dune ecosystems: typical, alien, and ruderal species (Del Vecchio et al. 2015; Sperandii et al. 2019; Bonari et al. 2021a). Typical species for each habitat type were defined according to the Italian Interpretation Manual of the 92/43/EEC Habitats Directive (Biondi et al. 2009; Biondi and Blasi 2015; Online Resource Table S1), while ruderal and alien species were classified following previous studies (Biondi et al. 2012; Del Vecchio et al. 2016; Prisco et al. 2017). While typical species are considered a proxy for a good conservation status of habitats, being fundamental to define the structure and to guarantee the functionality of habitats (Bonari et al. 2021b), ruderal and alien species are opportunistic species usually associated with disturbances (Biondi et al. 2012).

Trends in ecological indicator values over time

We assigned each species its corresponding ecological indicator value (EIV) for soil moisture (M) and temperature (T), based on the values provided in Tichý et al. (2023), by consulting the appropriate tables and matching the species to their respective indicators. These indicators were selected because temperature and soil moisture are critical factors for plant survival and growth. Both factors have undergone significant changes over the past century, including rising temperatures, reduced precipitation, and lower groundwater levels (Brunetti et al. 2004; Scanlon et al. 2023). Furthermore, these EIVs have been particularly effective in inferring environmental changes that characterize coastal dune ecosystems over time (Del Vecchio et al. 2015). Species classified as 'factor-independent' ('X values') were excluded from the calculations. For each plot, we then computed the unweighted averages of each EIV by summing the values of all species present in the plot and dividing by the number of species. Thus, we calculated the communities' unweighted mean EIVs (hereafter referred to as CM) using only the presence/absence (qualitative) data of the species in the plots (Tölgyesi et al. 2014; Diekmann 2003; Ellenberg et al. 1992).

Erosion control

We also analysed changes over time in the total abundance of psammophilous species commonly regarded as playing a sand-stabilizing role in mitigating coastal erosion processes. To this end, we calculated an index of "erosion control" (La Bella et al. 2024) by summing the abundance of the three most common rhizomatous species typical of the foredune (*Calamagrostis arenaria* subsp. *arundinacea*, *Sporobolus pungens*, and *Thinopyrum junceum*, referred to as Acal, Aspo, and Athy, respectively) in each plot, standardized by the total abundance (*Atotal*) recorded in that plot, according to the following formula:

$$\text{ErosionIndex} = \frac{\text{Acal} + \text{Aspo} + \text{Athy}}{\text{Atotal}}$$

The erosion control index, along with the temporal variation in species richness and abundances (calculated on both, total flora and for typical, alien, and ruderal species), and the community unweighted mean of EIVs, was compared between the two sampling periods using a non-parametric paired Wilcoxon signed-rank test with a posteriori Holm correction for multiple comparisons (Kapfer et al. 2017). This was done using the *pairwise_ wilcox_test* function from the "rstatix" R package (Kassambara 2021).

Results

Temporal trends at community level

The first axis of the DCA (eigenvalue 0.85, Fig. 3) reflected the typical Mediterranean coastal dune vegetation zonation, with a clear differentiation between foredune habitats and grasslands of fixed and semi-fixed dunes on the right side of the diagram, and between shrublands and woodlands of stable dunes on the left. This analysis shows that historical foredune plots shifted toward lower values of the first DCA axis, indicating a transition toward relatively stable dune grasslands (see also Fig. 4). The second axis of the DCA (eigenvalue = 0.58) primarily captured changes in the inland woody vegetation over time, revealing a consistent shift between historical and recent plots of coastal shrublands along this axis. Notably, resurveyed coastal shrubland plots show a trend toward coastal woodlands, which maintained a stable position in the scatter diagram.

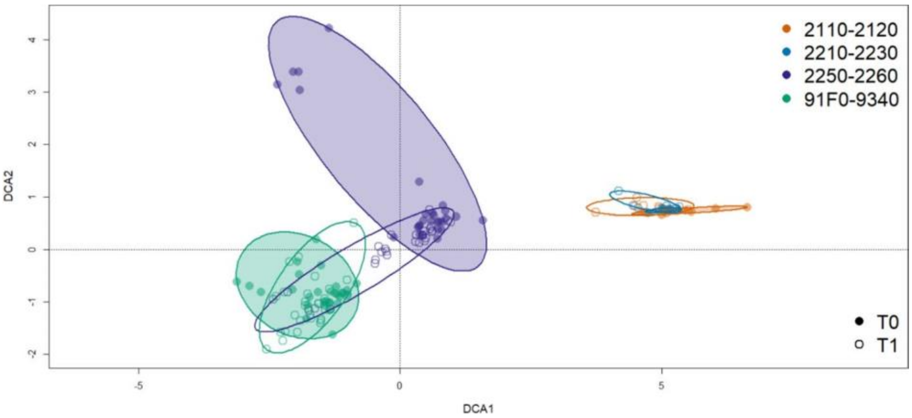

Fig. 3 Scatter diagram of detrended correspondence analysis (DCA) of historical versus resurveyed plots. Colours indicate habitat types grouped in vegetation categories. Dots represent historical and resurveyed plots. Ellipses collect all plots belonging to a specific vegetation category and time. Filled ellipses and dots are for historical plots (T0 = Time 0), while the empties are for revisited ones (T1 = Time 1). Top right legend lists EU habitat types of coastal dune zonation (foredunes: 2110 and 2120 EU habitat; dune grasslands: 2210 and 2230; shrubs: 2250* and 2260; woody communities of fixed dunes: 9340 and 91 F0)

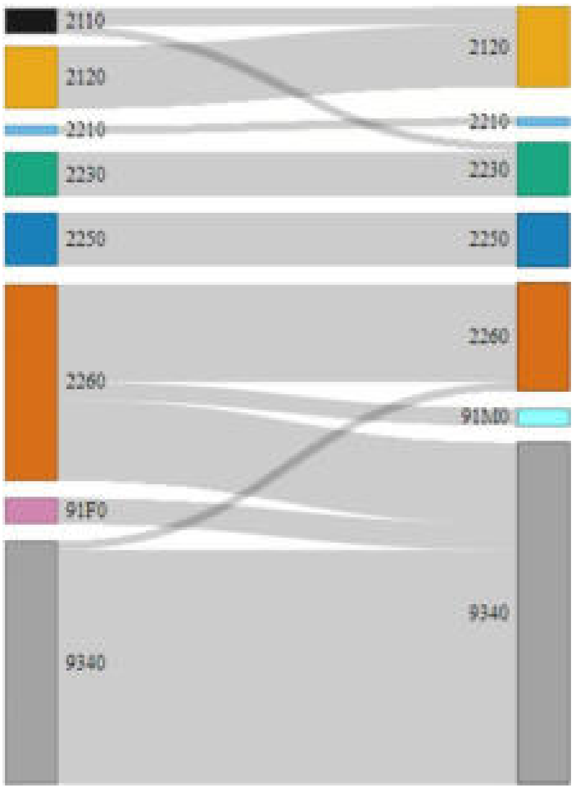

Fig. 4 Alluvial diagram showing how historical plots have changed habitat attribution over time. Each plot is represented by a grey line connecting its historical habitat type (on the left) to its actual habitat type after being resurveyed (on the right). Each colour describes a single habitat (for the list of habitat types see Table S1). The habitat 91M0 (broadleaved forest with *Carpinus betulus* and *Quercus cerris*) was observed only at the time of resurvey

Temporal trends at species level: species richness and abundance in plant guilds

During the resurvey, a total of 129 vascular plant species were recorded. A pairwise comparison between the two survey periods revealed that mean species richness significantly decreased in shrub communities and coastal woodlands (Fig. 5), while no significant changes were observed in foredunes and dune grasslands. Although the cover of typical species increased across all habitats, significant increases were observed only in shrublands and coastal woodlands (Fig. 5 and Online Resource Table S2). The presence of ruderal species declined, dropping from 9 species (4.86% of total species) to 5 species (3.88%) during the resurvey (Online Resource Table S2). Two previously unrecorded alien species, *Erigeron sumatrensis* and *Trachycarpus fortunei*, were observed during the resurvey, while the archeophyte *Avena sterilis*, recorded in the original plots, was not found.

In the foredunes, the SIMPER analysis indicated a temporal increase in the abundance of many typical species, including *Anthemis maritima* subsp. *maritima* and *Cyperus capitatus,* but also species typical of dune grasslands such as *Medicago littoralis, Plantago macrorhiza,* and *Sixalix atropurpurea* increased (Online Resource Table S3). In contrast, the two key perennial grasses, *Calamagrostis arenaria* subsp. *arundinacea* and *Thinopyrum junceum*, showed a decrease in abundance, although this change was not significant.

In coastal grasslands, only a few species, such as *Echinophora spinosa*, *Cutandia maritima*, *Silene canescens* and *Thinopyrum junceum*, exhibited a significant decline in abundance.

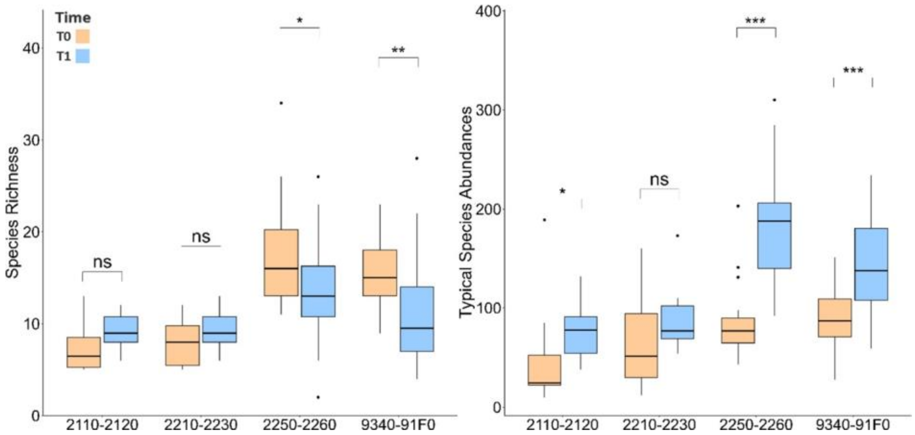

Fig. 5 Changes in total species richness and typical species abundance in historical (Time = 0) versus resurveyed plots (Time = 1) along the vegetation zonation of coastal dunes (foredunes: 2110 and 2120 EU habitat; dune grasslands: 2210 and 2230; shrubs: 2250* and 2260; woody communities of fixed dunes: 9340 and 91 F0; *P < 0.05; **P < 0.01; ***P < 0.0001; ns: P > 0.05)

Most species typical of coastal shrublands showed significant increases in abundance, including *Arbutus unedo*, *Erica multiflora*, *Phillyrea angustifolia*, *Pistacia lentiscus*, and *Juniperus oxycedrus*, with a particularly notable increase in *Quercus ilex* (+ 28.64%). Typical climbing species like *Smilax aspera*, *Rubia peregrina*, and *Hedera helix* subsp. *helix* also increased in abundance. In contrast, the abundance of *Cistus salviifolius* and *C. creticus* subsp. *eriocephalus*, species that often colonize garrigue habitats after fires, declined, though not significantly.

Species typical of coastal woodlands also increased, especially *Quercus ilex*, *Phillyrea latifolia*, and *Pistacia lentiscus*. Additionally, some species more characteristic of mesophilous broad-leaved forest, such as *Carpinus betulus*, *Populus alba*, and *Crataegus monogyna*, contributed notably to the changes observed in the resurveyed plots.

Trends in ecological indicator values over time

Ecological indicator values revealed that coastal woodlands experienced the most substantial changes (Fig. 6). Specifically, significant shifts in CM values for moisture and temperature were observed exclusively within these communities, with moisture levels increasing and temperature values decreasing. These changes were mainly driven by an increase in the abundance of species such as *Populus alba*, *Crataegus monogyna*, *Quercus robur*, and *Malus sylvestris*, as well as by the newly recorded occurrence of species such as *Carpinus betulus* and *Acer campestre*.

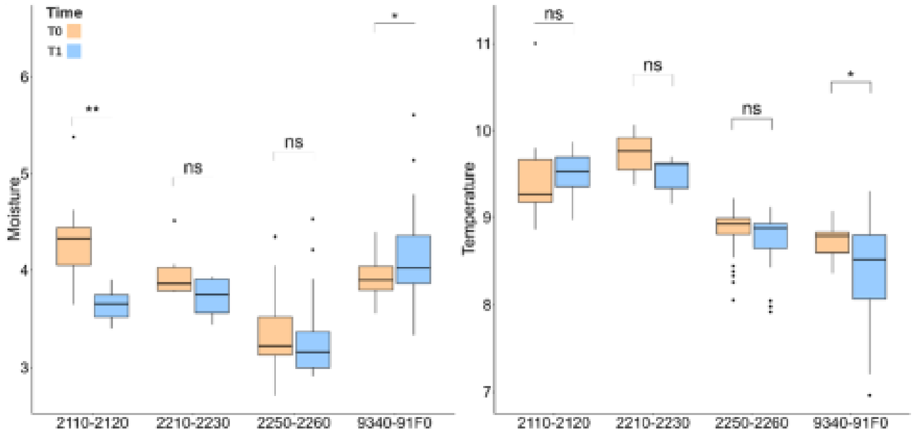

Fig. 6 Changes in Ecological indicator values over time for moisture and temperature along the vegetation zonation of coastal dunes (foredunes: 2110 and 2120 EU habitat; dune grasslands: 2210 and 2230; shrubs: 2250* and 2260; woody communities of fixed dunes: 9340 and 91 F0; *P < 0.05; **P < 0.01; ns: P > 0.05)

Erosion control

As previously noted, the two perennial grasses *Calamagrostis arenaria* subsp. *arundinacea* and *Thinopyrum junceum*, both key psammophilous species essential for the formation and stabilization of foredunes, showed a decrease in abundance in the revisited plots. However, the pairwise comparison of the erosion index between the historical and revised surveys did not reveal significant differences (erosion index, mean ± SD, at T0 = 0.42 ± 0.3; at T1 = 0.18 ± 0.13; Wilcoxon test, n = 10, P-value = 0.419).

Discussion

The systematic collection of quantitative floristic data from historical plots conducted approximately 30 years ago enabled us to perform a comprehensive analysis of temporal trends at both the community and species levels in the coastal dune ecosystems of the Presidential Estate of Castelporziano. Across the Mediterranean, human pressure, alone or combined with natural hazards such as coastal erosion or flooding, has led to landscape simplification, alterations in coastal zonation, and habitat loss (Malavasi et al. 2016b; García-Lozano et al. 2018; Molina et al. 2020).

This degradation has led to the decline of species essential for dune formation and stabilization, as well as those exclusive to dune ecosystems (Sperandii et al. 2019; Pintó et al. 2023). In contrast, the Castelporziano Estate represents an exceptionally well-preserved coastal dune system, where these degradation processes have not been observed. Previous studies have demonstrated that protection is an effective conservation strategy for coastal ecosystems (Prisco et al. 2020; García-Lozano et al. 2018; Pintó et al.2023), underscoring the importance of preserving well-conserved sites such as Castelporziano. The restricted access has preserved the integrity of its dune ecosystems, offering valuable insights for conservation efforts across the broader Mediterranean area.

This unique characteristic allowed us to conduct one of the few (if not the first) resurveying studies in the Mediterranean analysing temporal changes across the entire coastal dune vegetation zonation under minimal disturbance. Notably, previous resurveying studies in the region have primarily focused on herbaceous vegetation, only partially examined coastal zonation, or included areas subject to varying degrees of human pressure (Del Vecchio et al. 2015, 2016; Sperandii et al. 2019; Cascone et al. 2021).

Our results did not show a significant decrease in species richness in the foredunes and dune grasslands, which contrasts with findings from most coastal dune areas in central Italy (Sperandii et al. 2018). While relatively few changes were observed in the dune grasslands, we noted an increase in the abundance of dune grassland species in foredunes. The increase in species richness or abundance over time, along with species turnover, is a natural component of vegetation succession (Álvarez-Molina et al. 2012; Sperandii et al. 2019). However, these trends are challenging to disentangle, as they are influenced by multiple factors, including land use and the degree of human pressure (Malavasi et al. 2016b; van der Hagen et al. 2023). Given the highly restricted public access to the study area, we assume that typical disturbance factors linked to tourism, such as trampling, have been minimal over the past 30 years. Consequently, the temporal trends observed in foredunes, both at the species and community levels, are likely unrelated to human disturbance, instead suggesting a shift toward positive successional dynamics for foredunes and relatively stable fixed dune grasslands. Additionally, restricted access may have contributed to the low number of alien and ruderal species recorded in both historical and resurveyed plots. This limited presence of alien species, previously documented (La Bella et al. 2021), was reaffirmed in our study.

The abundance of the two perennial dune-building grasses, *Calamagrostis arenaria* subsp. *arundinacea* and *Thinopyrum junceum*, slightly decreased in our study. These species have crucial below-ground root systems with rhizomes contributing to stabilizing mobile sand (de Battisti and Griffin 2020; Sperandii et al. 2021), and their decline has been widely documented across the Mediterranean region (Prisco et al. 2020; Janssen et al. 2016; Malavasi et al. 2016b; Sperandii et al. 2019), contributing to coastal erosion. However, the erosion index did not show significant changes between the two surveyed periods. This suggests that the slight decline in key dune-building species is not currently a major concern in our study area. Nevertheless, this negative trend warrants careful ongoing monitoring.

Major changes were recorded in coastal shrublands and woodlands, where a number of plots transitioned to coastal woodlands. In coastal shrublands, most typical species increased, particularly *Quercus ilex* and *Phillyrea angustifolia*, whereas *Cistus* species declined. This decline, alongside the increase in typical coastal woodland species, may be linked to changes in the fire regime in the area, influenced by management strategies such as fire protection. *Cistus* species are highly combustible (Curt et al. 2011), and seed germination in many shrub species within the Cistaceae family is often triggered by fire (Paula et al. 2009). Thus, the significant transformations observed in the shrubland vegetation may also reflect positive successional dynamics, where shrublands naturally progress into more closed scrub or woodland formations. Regarding coastal woodlands, we observed a significant increase in typical species, along with new colonization by woody species characteristic of cooler and more humid environments. This pattern may suggest a slight successional shift towards mesophilous broad-leaved forest (Čarni 2017; Fascetti et al. 2013), which are more common further inland in the study area (Acosta et al. 2000), though further investigation is needed to confirm this hypothesis.

Overall, the coastal strip of the Presidential Estate of Castelporziano supports a well-developed coastal beach-dune ecosystem, where the typical zonation of dune habitats can still be identified, ranging from upper beach plant communities to coastal forests of the inner dunes, now very rare in the Mediterranean basin. The limited pressure from mass beach tourism and other disturbance factors, such as urban expansion, trampling, and dune levelling, has facilitated the preservation of the typical floristic composition and the complete sequence of coastal dune habitats, which have remained well preserved over the long term.

Conclusion

Our resurveying study, spanning an average of 30 years, allowed us to detect changes in species richness, abundance, and ecologically relevant plant guilds. Additionally, we assessed shifts in ecological conditions using Ecological Indicator Values and evaluated changes in plant species' contributions to mitigating the erosion process. Our results revealed relatively minor changes likely associated with management strategies and suggested potential positive successional trends. Although caution is warranted when interpreting results from a relatively small area, it is essential to emphasize that this protected area hosts a unique coastal dune ecosystem featuring a complete zonation of coastal dune vegetation, making it one of the last coastal biodiversity hotspots in the Mediterranean. Our findings highlight that, with appropriate management, coastal dune ecosystems can be preserved and continue evolving over the long term. This study further reinforces the importance of large protected natural areas for the conservation of coastal dune habitats, as they provide essential conditions for the long-lasting sustainability of these fragile ecosystems. Additionally, our research confirms the value of resurveying methods in capturing vegetation dynamics, providing a solid foundation for implementing effective conservation strategies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-025-03087-w.

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Author contributions AA conceived and designed the study. SS and SDV collected the data. SS analysed the data. AA, SS, and SDV interpreted the data. SS wrote the first draft of the manuscript. All authors made significant contributions to the manuscript and approved it for publication.

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Data availability Data that support the findings of this study are stored in the CP-BioDb Castelporziano biodiversity database.

Declarations

Conflict of interest The authors declare no conflict of interest.

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Chapter II (paper 2)

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ReSurveyDunes — a data resource of resurveyed coastal dune vegetation plots in Italy*

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Abstract

We present ReSurveyDunes — the first database of Italian coastal dune vegetation plots, developed through a collaborative network of Italian vegetation scientists. This paper describes the scope of the initiative, provides an overview of the available data, and highlights its key features, research applications, and future potential.

ReSurveyDunes currently comprises 972 vegetation plots distributed across 11 Italian regions (Abruzzo, Basilicata, Calabria, Campania, Emilia-Romagna, Lazio, Molise, Sardinia, Sicily, Tuscany, and Veneto). The original plots were surveyed between 1974 and 2009, with a primary focus on herbaceous psammophilous coastal zonation (habitats 1210, 2110, 2120, 2130*, 2210, 2230, and 2240, as defined by the 92/43/EEC Habitats Directive). Resurveys were conducted in 2023 and 2024. Each plot dataset

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includes (i) a complete list of vascular plant species with cover estimates; (ii) geographic coordinates (latitude and longitude); (iii) sampling dates; and (iv) plot size.

Designed to analyze fine-scale temporal trends in Italian coastal vegetation, ReSurveyDunes is a versatile tool for diverse ecological studies. It represents a valuable resource for evidence-based decision-making, enabling targeted conservation and management actions informed by up-to-date ecological data.

Keywords

Coastal dune habitats, Habitats Directive, psammophilous vegetation, resurvey, temporal trends, vegetation database

Introduction

According to the 4th Report under article 17 of the EU Habitats Directive 92/43/EEC (EEC 1992), the conservation status of Italian coastal sand dunes habitats is worryingly bad: the overall assessment reports 89% of habitats in Unfavorable Bad conservation status while the remaining 11% is reported as Unfavorable Inadequate (Prisco et al. 2020; Ercole et al. 2021). This critically poor conservation state has been assessed across all criteria and Biogeographical Regions, and it is particularly serious for key dune habitats that provide essential ecosystem services, such as "Shifting dunes with *Ammophila arenaria*", which are considered crucial for dune formation and protection against coastal erosion (La Bella et al. 2024). Even more alarmingly, the conservation status of Italian coastal dune habitats mirrors that of the broader Mediterranean biogeographical region (Janssen et al. 2016). Main pressures and threats stem from increasing human activities, including the development of residential, commercial, and industrial areas, as well as the expansion of alien and ruderal species (Géhu and Biondi 1994; Janssen et al. 2016; Gao et al. 2020; Prisco et al. 2020; Singh et al. 2021).

Plot-based vegetation samples, known as vegetation plots, document plant species diversity and community composition at specific locations and times. Resurveying studies, which involve re-sampling historically surveyed vegetation plots, are increasingly being used to detect temporal changes in the vegetation of various ecosystems (Knollová et al. 2024). These studies predominantly rely on phytosociological data due to the long tradition of phytosociological relevés and the recent compilation of large repositories that provide invaluable data across a variety of habitats (Dengler et al. 2011; Chytrý et al. 2016; Sabatini et al. 2021). Despite some degree of relocation error, revisitation studies are considered a valid and cost-effective tool for analysing temporal dynamics in plant communities (Hédl et al. 2017; Kapfer et al. 2017).

In Italy, resurveying coastal dune habitats has proven highly effective for identifying major temporal trends at both community and species levels. Del Vecchio et al. (2015a, 2015b) focused on resurveying phytosociological relevés, while Sperandii et al. (2019, 2021) based their resurveying on georeferenced random plots. However, all these studies have been conducted in relatively restricted areas or regions, and thus, no temporal trends on coastal dune vegetation at a widescale are currently available.

The great diversity of Italian coastal dune habitats has been widely recognized (Brullo et al. 2001; Biondi et al. 2009; Prisco et al. 2013). This relevant diversity, coupled with the undoubtedly poor conservation status of these fragile but resilient habitats (Santoro et al. 2012), underscores the need for more effective conservation measures. Such measures should be supported by detailed knowledge of biodiversity temporal trends preferentially derived from wide-scale monitoring activities, both inside and outside protected areas. Therefore, reliable estimates of long-term vegetation changes in these threatened habitats are urgently needed at the national level.

In this context, we introduce ReSurveyDunes — a new data resource of resurveyed coastal dune vegetation plots in Italy, compiled by a collaborative network of Italian vegetation scientists. This is the first database of Italian coastal dune resurveyed vegetation, collecting historical phytosociological information revisited during 2023/2024. Here, we provide an overview of the currently available data, illustrating the main characteristics of the database and its potential future uses.

Database compilation

In 2023, a call for collaboration was sent to vegetation experts of the Italian Society of Vegetation Science (SISV) to join the ReSurveyDune project, aiming to resurvey Italian coastal dune areas as comprehensively as possible. To be included in ReSurveyDune, all datasets needed to meet the following minimum requirements: (i) a complete list of vascular plants within defined plots, including information on species cover; (ii) plot location data, including longitude and latitude, along with information on the precision of the coordinates (specified geographic accuracy level); (iii) sampling date; and (iv) plot size.

Database structure, content taxonomic standardization and limitations

Overall, ReSurveyDune currently includes 972 vegetation plots located in 11 Italian administrative regions Abruzzo, Basilicata, Calabria, Campania, Emilia-Romagna, Lazio, Molise, Sardinia, Sicily, Tuscany, and Veneto (Fig. 1)**.** The historical dataset includes a total of 495 plots, comprising both published phytosociological vegetation records and additional unpublished data, all of which were revisited (Suppl. materials 1, 2 for detailed references and for the distribution of each habitat). Therefore, for each plot, the outcome of the revisitation is provided, and the plots that could not be located or that disappeared were marked as such. Sampling size varied from 1 to 450 m², but was relatively homogeneous within each habitat type. Resurveying was performed in 2023 and 2024 with the same approach as for the historical plots, during the same season and with the same plot size. The occurrence of all vascular plant species was recorded, and species abundance was visually estimated using the Braun-Blanquet percentage cover scale (Braun-Blanquet 1964), as in historical plots.

Taxonomic nomenclature was standardised according to Euro+Med 2006 database.

At this stage, we have included only herbaceous-chamephytic coastal dune habitats, although we plan to incorporate woody dune habitats in future updates. Each relevé has been assigned to a specific EU habitat type (as defined by the 92/43/EEC Habitats Directive; EEC 1992). Seven habitats were considered (Table 1): 1210, 2110, 2120, 2130* (priority habitat), 2210, 2230, and 2240 (Biondi et al. 2009), corresponding to three

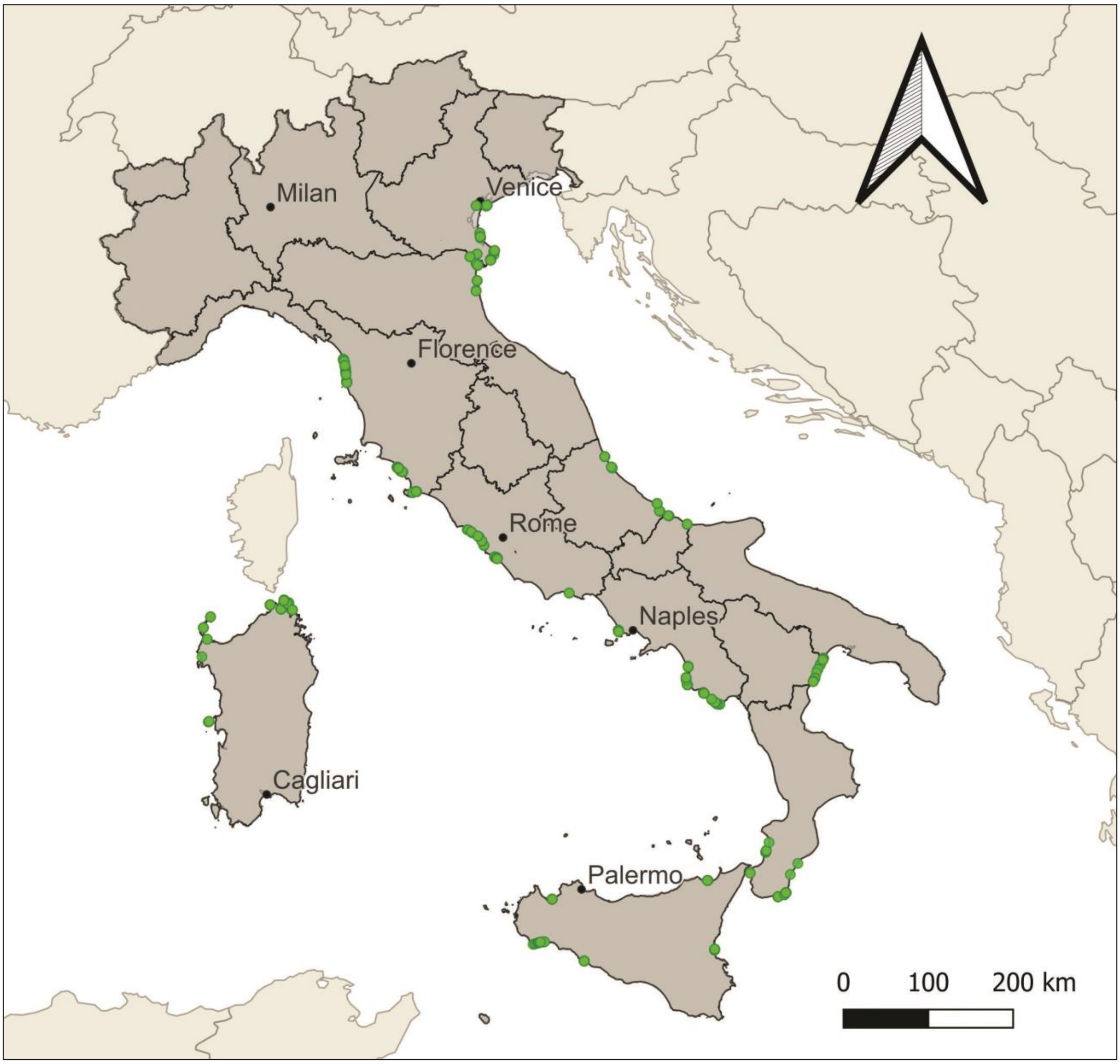

Figure 1. Distribution of resurveyed historical vegetation plots across 11 Italian administrative regions. Each green dot represents plot location. Black dots represent major cities with their names labelled.

Table 1. Summary of coastal EU habitats included in the database. For each habitat type, the EUNIS and Habitats Directive (Annex I) code and name, a brief description with most frequent species, and the number and the mean area per habitat of historical plots are provided.

EUNIS code and name	Habitats Directive code and name (Annex I)	Habitat description	Number of historical plots	Mean area per habitat (m²)	Most frequent species
N12 Mediterranean and Black Sea sandy beaches	**1210** Annual vegetation of drift lines	Pioneer communities of therophyticsalinophytic species	87	43.7	*Cakile maritima* *Xanthium orientale* *Thynopyrum junceum*
N14 Coastal mobile dune habitats of the Mediterranean, Macaronesia, and Black Sea	**2110** Embryonic shifting dunes	Pioneer communities of perennial species dominated by *Elymus farctus* ssp. *farctus*	156	33.3	*Thynopyrum junceum* *Eryngium maritimum* *Echinophora spinosa*
	2120 Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)	Semi-permanent cordons of the dune system dominated by *Ammophila arenaria* ssp. *australis*	154	45.3	*Calamagrostis arenaria* *Echinophora spinosa* *Eryngium maritimum*
	2130* Fixed coastal dunes with herbaceous vegetation (grey dunes)	Fixed dunes, stabilised and colonised by more or less closed perennial grasslands and abundant carpets of lichens and mosses	1	25	*Helianthemum nummularium* *Thymus pulegioides* *Catapodium rigidum*
N16 Mediterranean and Macaronesian coastal dune grasslands (grey dunes)	**2210** *Crucianellion maritimae* fixed beach dunes	Fixed dunes with chamaephytic communities dominated by *Crucianella maritima* and *Pancratium maritimum*	54	45	*Pancratium maritimum* *Thynopyrum junceum* *Eryngium maritimum*
	2230 *Malcolmietalia* dune grasslands	Fixed dunes with therophytic grasslands	40	37.9	*Festuca fasciculata* *Cyperus capitatus* *Lagurus ovatus*
	2240 *Brachypodietalia* dune grasslands with annuals	Dune mediterranean xeric grasslands rich in therophytes	3	7.33	*Aira elegans* *Anthemis arvensis* *Cerastium ligusticum*

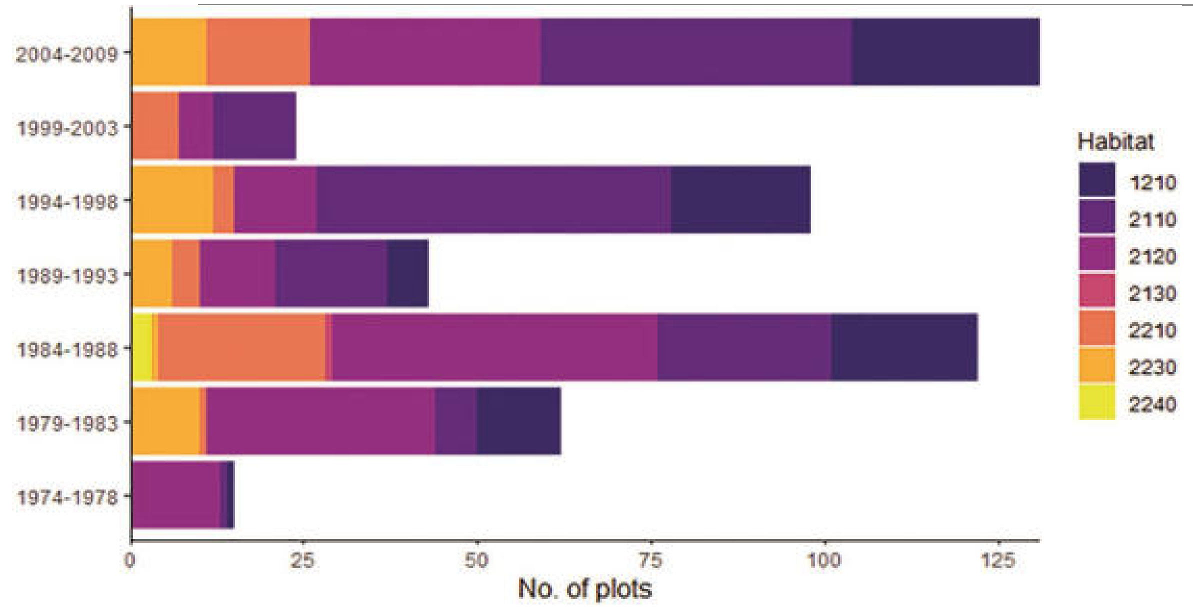

Figure 2. Number of historical vegetation plots originally surveyed across different time periods, grouped in 5-year intervals (except the last interval, which spans 6 years), and categorized by habitat type (as defined by the 92/43/EEC Directive).

EUNIS habitat types N12, N14, N16 (https://eunis.eea.europa.eu/habitats). The number of vegetation plots per habitat is shown in Fig. 2. The oldest historical plot dates to 1974, while the most recent one was recorded in 2009. As the original data (historical plots) were sampled for various purposes using the phytosociological approach, despite harmonisation of basic attributes upon integrating the datasets into ReSurveyDunes, there remains variation in relevant features such as plot location accuracy and plot size.

Data accessibility

ReSurveyDunes is an independent resurvey database, with data ownership retained by the contributors. Decisions on data sharing will be made individually for each data request. By the end of the ReSurveyDune project, we plan to integrate this database into larger data repositories to ensure easy access and interoperability of the data. One such repository is ReSurveyEurope, which is currently being developed and is closely connected to the European Vegetation Archive, EVA (Knollová et al. 2024).

Application and future perspectives

In this article, we introduced ReSurveyDunes, the first Italian dataset of fine-scale resurveyed coastal dune vegetation habitats. This dataset provides a comprehensive overview of the diversity of Italian coastal dune habitats and serves as a crucial tool for analysing temporal changes in these fragile ecosystems at a national scale.

Because the vegetation plots are georeferenced, they can be integrated with additional information (i.e. remote sensing data), facilitating the analysis of a wide range of impacts, including human pressure, coastal erosion, alien species invasion, or climatic changes. Additionally, the plot records can be overlaid with protected area boundaries to identify major conservation gaps. They can also be used to pinpoint priority areas for future surveys. Moreover, the information in this dataset can support the evaluation of changes in the conservation status of Annex I habitats, as required by the Habitats Directive.

Overall, ReSurveyDunes not only offers a valuable resource for studying coastal dune vegetation dynamics and their responses to environmental changes, enhancing our understanding of these highly threatened habitats, but also contributes to informed decision-making for habitat conservation and management.

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Supplementary material 1

References for the historical plots

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Data type: docx

Link: https://doi.org/10.3897/ved.139539.suppl1

Supplementary material 2

Distribution maps

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Daniele Viciani, Silvia Del Vecchio

Data type: tif

Link: https://doi.org/10.3897/ved.139539.suppl2

Chapter III (paper 3)

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; Janssen et al., 2016). 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).

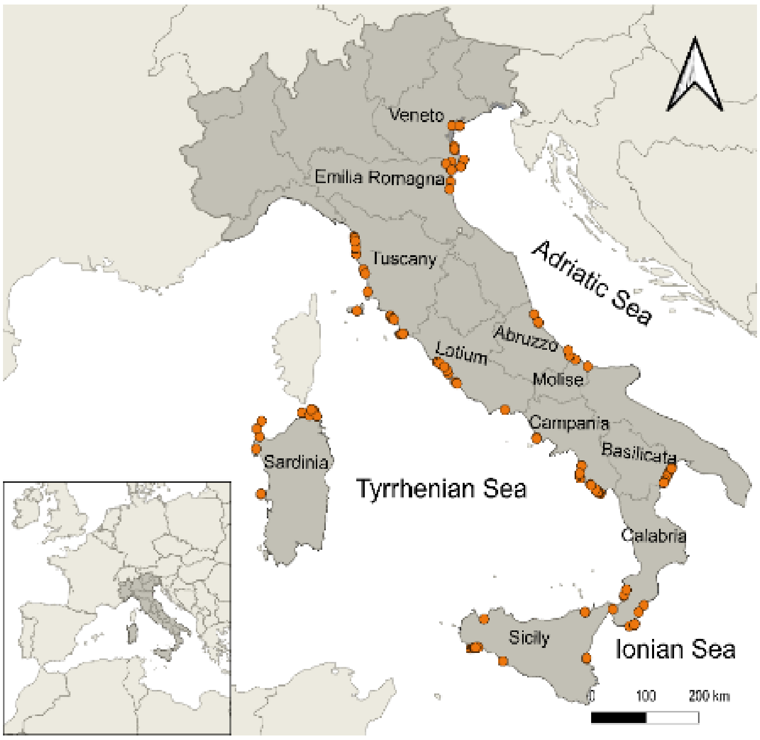

Fig. 1. **Study area**. Distribution of resurveyed historical plots (marked in orange) along the Italian coastal dunes.

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. *corsica, 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 and 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).

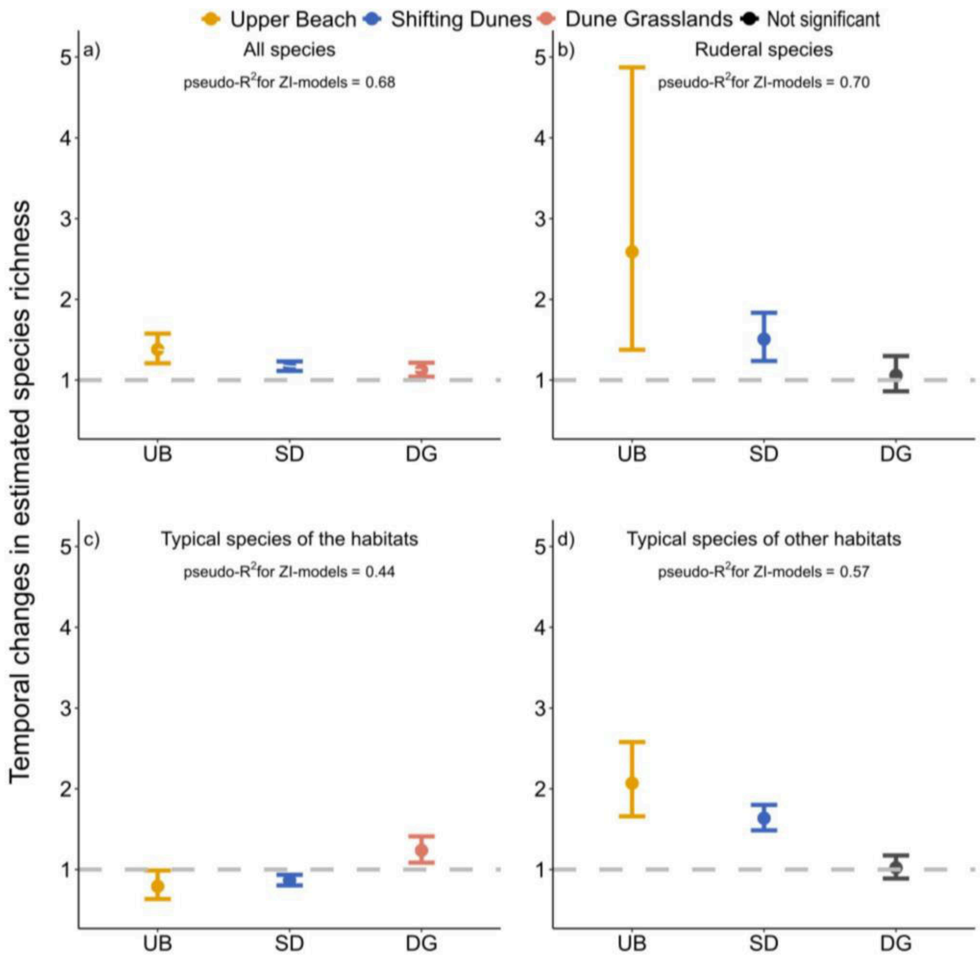

Fig. 2. Results of mixed models assessing temporal changes in species richness. Panels (a–d) show modelled changes in species richness for (a) all species, (b) ruderal species, (c) typical species of the habitat, and (d) typical species of other habitats. These changes are depicted across three habitat 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 back-transformed estimated marginal mean contrasts between historical and revisited surveys 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.

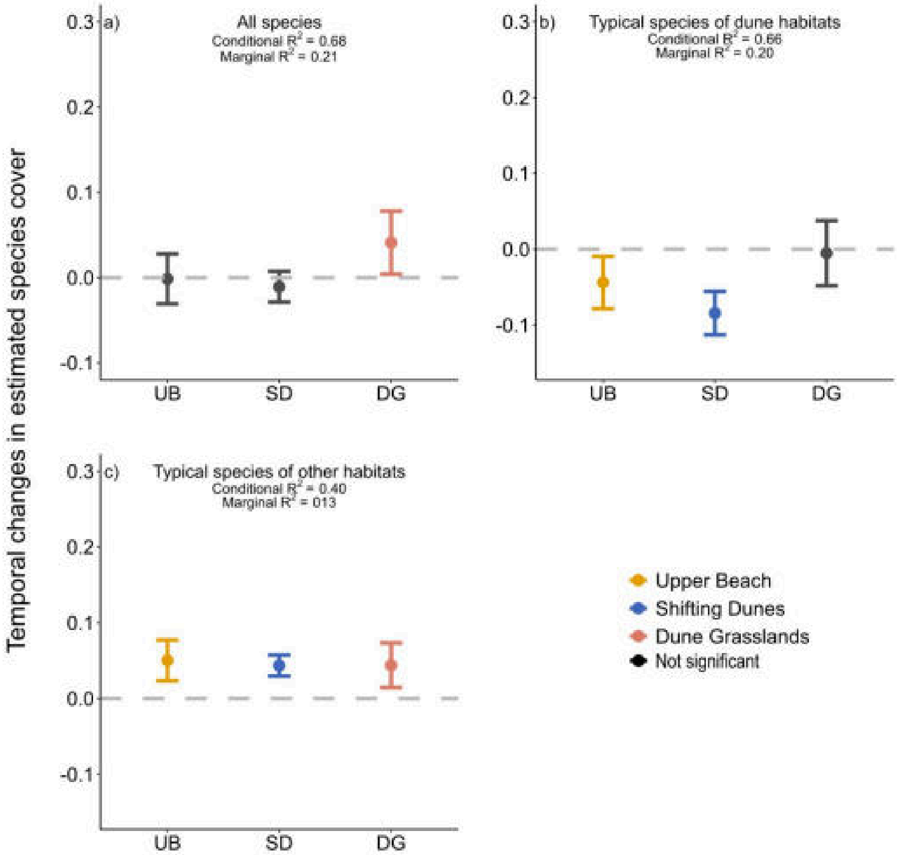

Fig. 3. Results of mixed models assessing temporal changes in species cover. Panels (a–c) display modelled temporal changes in cover for (a) all species, (b) typical species of the habitat, and (c) typical species of other habitats across three habitat types, represented by different colours: (EUNIS 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 back-transformed estimated marginal mean contrasts between historical and revisited surveys from mixed 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.

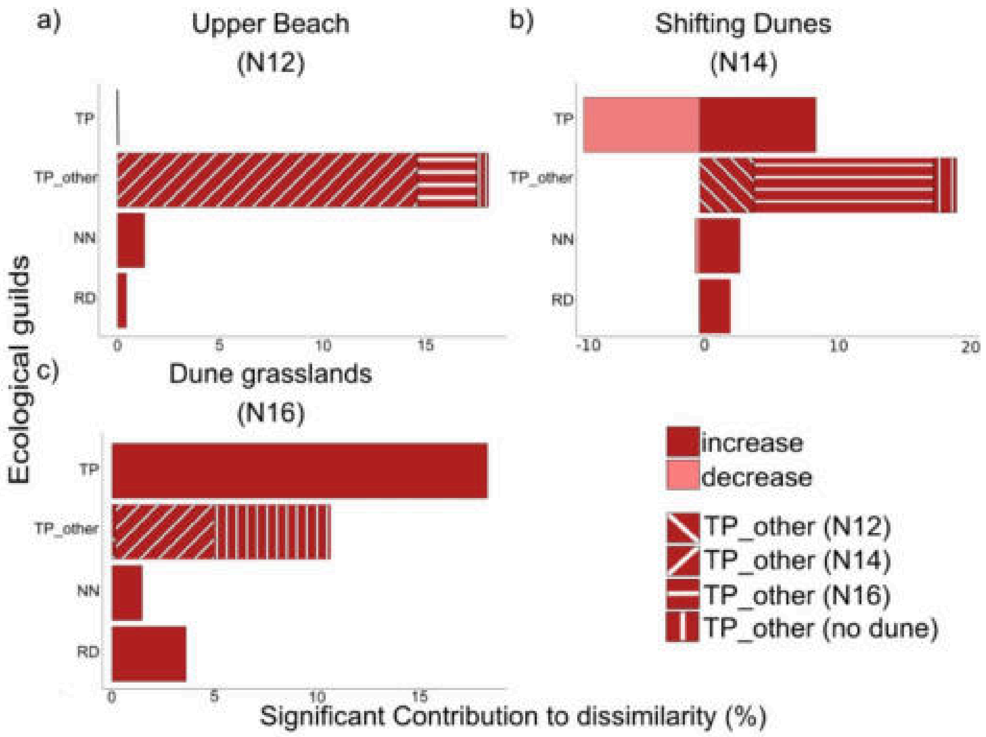

Fig. 4. Significant contributions of ecological guilds to community dissimilarity based on SIMPER analysis. Bars represent the cumulative significant contributions of species within each ecological guild to the total dissimilarity between historical and revisited plots across habitat types (EUNIS N12: 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.

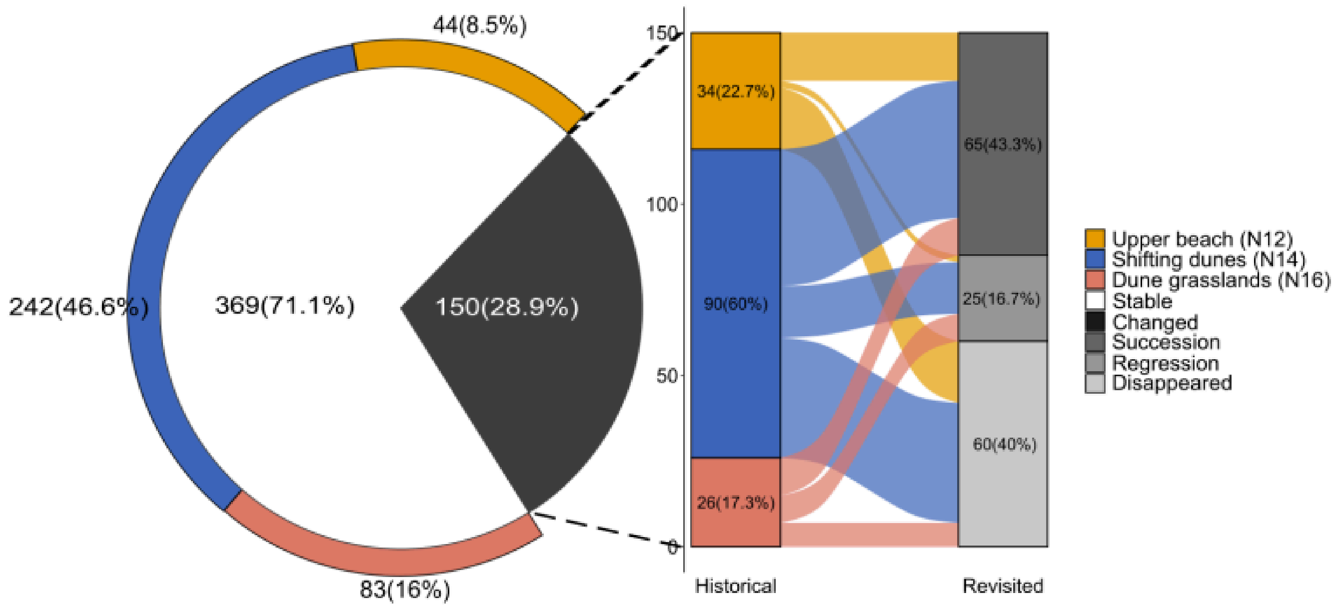

Fig 5. Changes in habitat classification between historical and revisited plots. The left panel shows the proportion of historical plots that remained stable (white area) or changed to a different habitat type (black area). Surrounding the stable plots, coloured semicircular bands represent the percentage 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, while ruderal species and typical species of other habitats became more abundant. The observed increase in ruderal species is consistent with findings reported for other Italian coastal systems (Santoro et al., 2012; Sarmati et al., 2025a; Sperandii et al., 2019). This pattern indicates substantial changes in terms of 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, in most disturbed sites, this successional trajectory appeared to be accompanied by an increase in species typical of dune (e.g. *Helichrysum stoechas* subsp. *stoechas,* and *Daucus pumilus*), together with a rise in ruderal taxa. Collectively, the simultaneous increase of shifting dunes species and the expansion of dune grasslands and ruderal taxa 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 and facilitate the ingression of synanthropic species (Ciccarelli et al., 2012; Miot da Silva et al., 2008; Prisco et al., 2016b). Consistently, synanthropic taxa, such as *Cynodon dactylon,* contributed to temporal dissimilarity in upper beach. These species, characterised by high ecological plasticity, rapid reproduction, and resistance to trampling, can quickly colonise disturbed habitats and are favoured by soil compaction and nutrient enrichment (Biondi et al., 2012; García-Mora et al., 1999; Martínez & García-Franco, 2004; Šilc et al., 2020; Wang et al., 2020).

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 (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, anthropogenic pressures, and coastal erosion (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 grasslands structure and functioning (Lazzaro et al., 2020; Trotta et al., 2020). Taken together, these 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 multiple coastal dune sites at the national scale.

Although a considerable proportion of plots showed transitions consistent with successional advancement, indicating stabilization processes, a similarly large proportion of early-successional dune habitats (upper beach and shifting dunes) exhibited high levels of plot disappearance. 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). Disappeared plots were more frequent along the Tyrrhenian and Ionian coasts, consistent with projected shoreline retreat and beach surface loss due to sea-level rise (Celata & Gioia, 2024).

Our results further indicated that some plots, particularly 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. Overall, these findings suggest the coexistence of two contrasting and spatially heterogeneous trajectories: inland-directed successional advancement on one hand, and regression towards early-successional stages on the other.

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. 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. Overall, these findings indicate that current coastal dune dynamics are characterised by heterogeneous and locally contrasting processes rather than by a uniform, unidirectional change. 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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GENERAL CONCLUSIONS

This thesis provides a multi-scale, long-term assessment of vegetation dynamics in Mediterranean coastal dune ecosystems, integrating plot-based resurvey studies spanning an average period of approximately 30 years. By combining a detailed local case study under minimal anthropogenic disturbance (Chapter I), the development of the first national database of resurveyed coastal dune vegetation plots (Chapter II), and a national-scale analysis of vegetation change along the Italian coastline (Chapter III), the thesis offers a comprehensive picture of long-term changes in Mediterranean coastal dune habitats.

At the local scale, resurveys conducted in the Presidential Estate of Castelporziano demonstrate that, in the absence of pervasive human pressure, coastal dune ecosystems can maintain a high degree of structural and compositional stability over multiple decades. The persistence of the complete coastal zonation sequence, from upper beach communities to inner dune woodlands, highlights the critical role of long-term protection and restricted access in preserving natural successional dynamics. Observed changes were largely attributable to internal successional processes and management-related factors rather than to habitat degradation, confirming that well-managed protected areas can function as robust reference systems for Mediterranean coastal dunes (Garcia-Lozano et al., 2018; Pintó et al., 2023; Prisco et al., 2020).

At the European and global level, several initiatives provide frameworks for large-scale vegetation monitoring and comparative analyses, including *ReSurveyEurope* (Knollová et al., 2024) and major vegetation-plot repositories such as the European Vegetation Archive (EVA; http://euroveg.org/eva-database) and the global *sPlot* database (https://www.idiv.de/de/splot.html). Within this context, national datasets such as *ReSurveyDunes* complement these efforts by providing geographically representative, thematically focused data specifically for Italian coastal dunes. By harmonising historical phytosociological relevés and their subsequent resurveys across broad geographical gradients, *ReSurveyDunes* enables, for the first time, a national-scale evaluation of long-term vegetation dynamics in Italian coastal dunes. Beyond its analytical contribution, *ReSurveyDunes* provides a flexible framework for integrating vegetation data with remote sensing products, conservation planning tools, and policy-oriented assessments, thereby strengthening the interface between ecological research and habitat management under the EU Habitats Directive.

National-scale analyses reveal that long-term changes in Italian coastal dune vegetation are widespread but highly heterogeneous. The observed increase in overall species richness frequently mask ecologically divergent trends, whereby declines in habitat-specialist psammophilous species are accompanied by the expansion of ruderal, non-typical, and, to a lesser extent, non-native taxa. These patterns are most pronounced in highly dynamic and disturbance-sensitive habitats, such as upper beaches and shifting dunes, whereas dune grasslands exhibit more variable trajectories, reflecting the combined influence of disturbance, stabilisation, and successional progression.

Compositional and habitat-based analyses consistently indicate that vegetation change is driven primarily by shifts in species abundances and redistribution along the coastal zonation gradient, rather than by complete species turnover. The reassignment of nearly one-third of the resurveyed plots to different EUNIS habitat types, together with plot loss in seaward habitats, points to the coexistence of two contrasting yet interconnected trajectories: inland-directed stabilisation and successional advancement on the one hand, and degradation, erosion, and habitat loss on the other. Notably, successional trajectories previously documented mainly in exceptional protected sites, such as Castelporziano, were also detected at broader spatial scales, suggesting that these processes are part of a wider, spatially heterogeneous mosaic of change.

Overall, this thesis demonstrates that Mediterranean coastal dune ecosystems do not follow a single, unidirectional pathway of degradation. Instead, their long-term dynamics emerge from interactions among local disturbance regimes, management histories, environmental gradients, and protection status. These findings underscore the importance of integrated, long-term monitoring approaches based on vegetation resurveys, which uniquely enable the simultaneous assessment of species-, community-, and habitat-level changes. From a conservation perspective, the results highlight the urgency of protecting early-successional and disturbance-dependent dune habitats, which are both the most dynamic and the most vulnerable to irreversible loss. At the same time, they reaffirm the value of large, well-managed protected areas as benchmarks for understanding natural vegetation dynamics and for informing effective conservation and restoration strategies in Mediterranean coastal dune systems.

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Supplementary Information

Table S1. List of European habitat types of the historical plots. List of the habitat types (Habitats Directive 92/43/EEC) of the historical vegetation plots (T0), grouped in macro-categories according to dune zonation ("vegetation categories"). For each habitat type, the code reported in the Habitats Directive (92/43/EEC) and a shorter description is provided, together with a selected list of typical species representative of the study area according to Biondi et al. (2009). Species nomenclature follows Bartolucci et al. 2018. N = number of historical vegetation plots (T0).

Vegetation category	**Code**	**Description**	**N**	**Typical species**
Foredunes (2110-2120)	2110	Embryonic shifting dunes. First stage of sand accumulation forming mobile dune systems characterized by *Thinopyrum junceum* (= *Elymus farctus*)	3	*Thinopyrum junceum*, *Achillea maritima* subsp. *maritima*, *Convolvulus soldanella, Cyperus capitatus*, *Echinophora spinosa*, *Eryngium maritimum*, *Euphorbia peplis, Sporobolus pungens*
	2120	Shifting dunes. Semi-permanent dune systems along the shoreline with *Calamagrostis arenaria subsp. arundinacea (= Ammophila arenaria)* (white dune)	7	*Calamagrostis arenaria* subsp. *arundinacea, Achillea maritima* subsp. *maritima, Anthemis maritima* subsp. *maritima, Cyperus capitatus*, *Echinophora spinosa*, *Eryngium maritimum*, *Euphorbia paralias*, *Lotus cytisoides*, *Medicago marina*, *Pancratium maritimum*

Dune grassland (2210-2230)	2210	Perennial grassland of chamaephitic and suffrutice vegetation with *Crucianellion maritimae* growing in the inland slope of fixed dunes	1	*Crucianella maritima*, *Helichrysum stoechas, Lomelosia rutifolia, Pancratium maritimum*, *Seseli tortuosum*
	2230	*Malcolmietalia* dune grasslands. Annual species-rich communities that colonise grasslands clearings of the fixed and semi-fixed dunes	5	*Aetheorhiza bulbosa*, *Bromus diandrus*, *Cutandia maritima, C. divaricata, Daucus pumilus*, *Festuca fasciculata* (= *Vulpia fasciculata*), *Lagurus ovatus, Medicago littoralis*, *Phleum arenarium*, *Ononis variegata*, *Silene canescens*
Coastal dune shrubs (2250*-2260)	2250*	Coastal stable dunes with *Juniperus* spp. communities	6	*Juniperus oxycedrus*, *J. phoenicea*, *Asparagus acutifolius*, *Clematis flammula*, *Lonicera implexa* subsp. *implexa, Myrtus communis*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rhamnus alaternus* subsp. *alaternus, Rubia peregrina*, *Ruscus aculeatus*, *Smilax aspera*
	2260	Stable dunes with *Cisto-Lavanduletalia* sclerophyllous shrubs	22	*Asparagus acutifolius*, *Cistus* sp. pl. *(C. salviifolius, C. monspeliensis, C. creticus* ssp. *eriocephalus*), *Clematis flammula*, *Erica multiflora*, *Lonicera implexa* subsp. *implexa, Osyris alba*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rhamnus alaternus* subsp. *alaternus, Rubia peregrina*, *Salvia rosmarinus*, *Smilax aspera*

Coastal dune woods (91F0-9340)	91F0	Relictual woods of meso-igrophilous species	3	*Fraxinus angustifolia, Popolus tremula, Ulmus minor*
	9340	*Quercus ilex* forests	27	*Quercus ilex, Arbutus unedo, Cyclamen hederifolium, C. repandum, Erica arborea, Lonicera implexa, Phillyrea angustifolia, Rhamnus alaternus* subsp. *alaternus, Rubia peregrina, Smilax aspera, Viburnum tinus*

Table S2. Number of species observed in the dune vegetation categories and across all categories for each species guild. Historical (T0) and resurveyed plots (T1). Alien = alien species; Other = plant species not included in any other guild; Ruderal = ruderal species; Typical = typical species for each community.

	Foredunes 2110-2120				Dune grassland 2210-2230				Coastal dune shrubs 2250*-2260				Coastal dune woods 9340-91F0				Total species list			
	T0		T1		T0		T1		T0		T1		T0		T1		T0		T1	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Alien	--	--	--	--	--	--	--	--	1	0.93	1	1.52	--	--	1	1.35	1	0.54	2	1.55
Other	1	4.55	2	8.0	2	10.0	6	22.27	67	62.04	30	45.45	55	61.80	43	58.11	113	61.08	69	53.49
Ruderal	1	4.55	1	4.0	2	10.0	--	--	4	3.70	4	6.06	4	4.49	3	4.05	9	4.86	5	3.88
Typical	20	90.91	22	88.0	16	80.0	16	72.73	36	33.33	31	46.97	30	33.71	27	36.49	62	33.51	53	41.09

Table S3. Species that contributed to dissimilarity (SIMPER) between historical (T0) and resurveyed plots (T1) for each habitat type. Avg.: average between groups dissimilarity with standard deviation (sd); Diss.: cumulative contributions of each species to dissimilarity; T0 and T1 percentage of average abundance of each species in each sampling period. P-value: statistically significative contributions to dissimilarity are highlighted in bold; Guild: ecological guild to which the species belongs: A = alien species; O = plant species not included in any other guild; OT = typical species of other dune communities; R = ruderal species; T = typical species for foredunes.

Foredunes (2110-2120 EU habitat types)							
Species	**avg**	**sd**	**diss.**	**T0 avg. abund. (%)**	**T1 avg. abund. (%)**	**p-value**	**guild**
Calamagrostis arenaria s. *arundinacea*	0.10	0.11	0.13	15.9	5.7	0.999	T
Anthemis maritima s. ***maritima***	**0.10**	**0.09**	**0.26**	**2.9**	**13.6**	**<0.01**	T
Cyperus capitatus	**0.09**	**0.09**	**0.38**	**4.1**	**13.4**	**<0.05**	T
Ononis variegata	0.09	0.10	0.49	2.2	12	0.062	OT
Thinopyrum junceum	0.08	0.09	0.60	9.5	8	0.993	T
Convolvulus soldanella	0.04	0.08	0.66	4	2.6	0.937	OT
Sixalix atropurpurea	**0.03**	**0.09**	**0.70**	**0**	**4.1**	**<0.05**	OT
Silene canescens	**0.03**	**0.02**	**0.74**	**0.5**	**4**	**<0.001**	OT
Medicago littoralis	**0.03**	**0.04**	**0.77**	**0**	**3.2**	**<0.01**	OT
Echinophora spinosa	0.02	0.03	0.80	2.4	2.2	0.599	T
Plantago macrorhiza	**0.02**	**0.04**	**0.83**	**0**	**2.9**	**<0.01**	O
Cutandia maritima	**0.02**	**0.05**	**0.86**	**0**	**2**	**<0.001**	OT
Eryngium maritimum	0.01	0.02	0.88	1.7	0.5	1	T
Pancratium maritimum	0.01	0.03	0.89	0.2	1.3	0.124	T
Daucus pumilus	0.01	0.01	0.90	0.2	1.4	0.159	OT
Cakile maritima s. *maritima*	0.01	0.01	0.92	1.1	0	0.271	OT

Sporobolus pungens	0.01	0.01	0.93	1	0.3	0.982	T
Medicago marina	0.01	0.01	0.94	0.9	0	0.882	T
Juniperus oxycedrus	**0.01**	**0.01**	**0.94**	**0**	**0.5**	**<0.01**	OT
Festuca fasciculata	**0.01**	**0.01**	**0.95**	**0**	**0.5**	**<0.01**	OT
Anisantha rigida	0.00	0.01	0.96	1.3	0	1	OT
Salsola kali	0.00	0.01	0.96	0.4	0	0.99	OT
Xanthium orientale	0.00	0.01	0.97	0.4	0	0.99	O
Daucus carota	**0.00**	**0.01**	**0.97**	**0**	**0.3**	**<0.05**	R
Lagurus ovatus ovatus	**0.00**	**0.01**	**0.97**	**0**	**0.3**	**<0.05**	OT
Crucianella maritima	0.00	0.01	0.98	0.2	0	0.991	OT
Phleum arenarium s. *caesium*	0.00	0.00	0.98	0.5	0	1	OT
Asparagus acutifolius	**0.00**	**0.01**	**0.98**	**0**	**0.3**	**<0.05**	OT
Clematis flammula	**0.00**	**0.01**	**0.99**	**0**	**0.3**	**<0.05**	OT
Helichrysum stoechas	**0.00**	**0.01**	**0.99**	**0**	**0.3**	**<0.05**	OT
Maresia nana	**0.00**	**0.01**	**0.99**	**0**	**0.2**	**<0.01**	OT
Senecio vulgaris	**0.00**	**0.01**	**0.99**	**0**	**0.3**	**<0.05**	O
Raphanus raphanistrum s. landra	0.00	0.01	1.00	0.3	0	0.994	R
Euphorbia peplis	0.00	0.00	1.00	0.2	0	0.994	OT
Rubia peregrina	0.00	0.00	1.00	0.2	0	1	OT
overall average dissimilarity between the two groups was 0.78.							
Dune grassland (2210-2230 EU habitat types)							
Species	**avg**	**sd**	**diss.**	**T0 avg. abund. (%)**	**T1 avg. abund. (%)**	**p-value**	**guild**
Ononis variegata	0.200	0.180	28.667	36.330	0.283	0.831	T
Plantago macrorhiza	0.073	0.083	0.333	14.830	0.387	0.067	O
Crucianella maritima	0.072	0.122	6.667	6.330	0.489	0.944	T

Anthemis maritima s. *maritima*	0.069	0.055	11.167	13.830	0.588	0.951	OT
Cyperus capitatus	0.049	0.052	10.333	3.170	0.657	0.966	OT
Echinophora spinosa	**0.039**	**0.050**	**1.167**	**5.330**	**0.712**	**<0.05**	OT
Thinopyrum junceum	**0.031**	**0.036**	**0.833**	**5.330**	**0.756**	**<0.05**	OT
Cutandia maritima	**0.027**	**0.049**	**0.000**	**3.170**	**0.795**	**<0.05**	T
Medicago littoralis	0.027	0.052	0.000	6.830	0.832	0.091	T
Silene canescens	**0.022**	**0.016**	**0.833**	**4.670**	**0.864**	**<0.001**	T
Eryngium maritimum	0.018	0.016	3.833	1.000	0.889	0.172	OT
Medicago marina	0.012	0.027	0.000	2.170	0.905	0.114	OT
Centaurium erythraea	0.012	0.027	0.000	2.170	0.922	0.114	O
Pancratium maritimum	0.010	0.008	1.333	1.500	0.936	0.318	T
Daucus pumilus	0.007	0.010	0.333	1.000	0.946	0.581	T
Juniperus oxycedrus	0.007	0.008	0.500	0.830	0.956	0.858	OT
Sporobolus pungens	0.006	0.007	0.667	1.000	0.965	0.783	OT
Cuscuta sp.	0.003	0.007	0.000	0.500	0.969	0.104	O
Medicago orbicularis	0.003	0.006	0.000	0.500	0.973	0.114	O
Festuca fasciculata	0.003	0.006	0.333	0.000	0.976	0.888	T
Cuscuta cesattiana	0.003	0.006	0.333	0.000	0.980	0.888	O
Daucus carota s. *maritimus*	0.003	0.006	0.333	0.000	0.984	0.888	O
Convolvulus soldanella	0.002	0.005	0.333	0.000	0.986	0.914	OT
Helichrysum stoechas	0.002	0.004	0.000	0.500	0.989	0.16	T
Rostraria litorea	0.002	0.004	0.000	0.500	0.991	0.16	O
Cakile maritima maritima	0.002	0.004	0.333	0.000	0.994	0.945	OT
Euphorbia peplis	0.002	0.004	0.333	0.000	0.996	0.945	OT
Raphanus raphanistrum s. *landra*	0.002	0.004	0.333	0.000	0.998	0.945	R
Lysimachia arvensis	0.001	0.003	0.000	0.330	1.000	0.16	O

overall average dissimilarity between the two groups was 0.70.

Coastal dune shrubs (2250*-2260 EU habitat types)							
Species	**avg**	**sd**	**diss.**	**T0 avg. abund. (%)**	**T1 avg. abund. (%)**	**p-value**	**guild**
Quercus ilex	**0.111**	**0.127**	**0.135**	**2.893**	**31.536**	**<0.001**	OT
Cistus creticus s. *eriocephalus*	0.080	0.082	0.233	22.143	10.786	1	T
Phillyrea angustifolia	**0.079**	**0.072**	**0.329**	**3.857**	**24.679**	**<0.001**	T
Arbutus unedo	**0.065**	**0.051**	**0.407**	**7.429**	**21.464**	**<0.01**	T
Juniperus oxycedrus	**0.045**	**0.067**	**0.462**	**4.286**	**11.536**	**<0.01**	T
Cistus salviifolius	0.042	0.073	0.513	11.679	0.929	1	T
Erica multiflora	0.040	0.059	0.562	5.643	9.786	0.998	T
Smilax aspera	**0.037**	**0.029**	**0.607**	**3.393**	**13.071**	**<0.001**	T
Pistacia lentiscus	**0.032**	**0.045**	**0.647**	**1.571**	**9.464**	**<0.001**	T
Salvia rosmarinus	**0.027**	**0.037**	**0.680**	**2.964**	**7.036**	**<0.05**	T
Hedera helix* s. *helix	**0.025**	**0.040**	**0.710**	**0.679**	**7.571**	**<0.001**	OT
Juniperus phoenicea	**0.024**	**0.040**	**0.739**	**2.214**	**5.571**	**<0.05**	T
Rubia peregrina	**0.018**	**0.018**	**0.760**	**0.821**	**5.714**	**<0.001**	T
Daphne gnidium	**0.016**	**0.016**	**0.779**	**1.393**	**4.821**	**<0.001**	T
Phillyrea latifolia	**0.013**	**0.033**	**0.795**	**0.536**	**3.179**	**<0.001**	OT
Asparagus acutifolius	**0.012**	**0.014**	**0.809**	**1.321**	**4.286**	**<0.001**	T
Carpinus betulus	**0.012**	**0.045**	**0.824**	**0.000**	**3.607**	**<0.001**	O
Quercus cerris	**0.012**	**0.044**	**0.838**	**0.000**	**3.607**	**<0.001**	O
Erica arborea	**0.012**	**0.027**	**0.852**	**0.571**	**2.750**	**<0.001**	OT
Lotus hirsutus	0.011	0.020	0.866	3.036	2.000	0.98	T
Teucrium flavum	0.007	0.011	0.874	0.750	1.893	0.087	O
Lonicera implexa s. *implexa*	0.007	0.007	0.883	1.679	1.643	0.093	T
Helichrysum stoechas	0.005	0.007	0.889	1.250	0.964	1	T
Clematis flammula	0.005	0.007	0.895	0.536	1.429	0.152	T

Macrobriza maxima	0.004	0.011	0.900	1.250	0.000	1	O
Rhamnus alaternus* s. *alaternus	**0.004**	**0.010**	**0.905**	**0.143**	**1.250**	**<0.01**	T
Centaurium erythraea	0.003	0.004	0.910	0.679	0.607	1	O
Carex flacca	0.003	0.008	0.913	0.679	0.286	1	O
Tripidium ravennae* s. *ravennae	**0.002**	**0.009**	**0.916**	**0.000**	**0.571**	**<0.001**	O
Osyris alba	0.002	0.007	0.918	0.536	0.107	1	T
Ruscus aculeatus	**0.002**	**0.008**	**0.920**	**0.000**	**0.571**	**<0.001**	T
Linum strictum	0.002	0.003	0.923	0.500	0.107	1	O
Sixalix atropurpurea	0.002	0.003	0.925	0.214	0.393	0.999	T
Malus sylvestris	**0.002**	**0.009**	**0.927**	**0.000**	**0.464**	**<0.001**	O
Tuberaria guttata	0.002	0.008	0.929	0.571	0.000	1	O
Asphodelus ramosus s. *ramosus*	0.002	0.008	0.931	0.571	0.000	1	O
Myrtus communis	**0.002**	**0.008**	**0.933**	**0.071**	**0.464**	**<0.01**	T
Lagurus ovatus ovatus	0.002	0.003	0.935	0.429	0.071	1	OT
Rubus ulmifolius	**0.002**	**0.004**	**0.937**	**0.000**	**0.393**	**<0.001**	R
Rubus caesius	**0.002**	**0.008**	**0.939**	**0.000**	**0.464**	**<0.001**	O
Trigonella sulcata	0.002	0.004	0.941	0.429	0.000	1	O
Emerus major major	**0.001**	**0.008**	**0.943**	**0.000**	**0.464**	**<0.001**	O
Schoenus nigricans	**0.001**	**0.004**	**0.945**	**0.000**	**0.429**	**<0.001**	O
Teucrium capitatum s. *capitatum*	0.001	0.003	0.946	0.214	0.214	1	O
Fumana thymifolia	0.001	0.003	0.948	0.286	0.107	1	O
Trigonella wojciechowskii	0.001	0.007	0.950	0.464	0.000	1	O
Coleostephus myconis	0.001	0.003	0.951	0.357	0.000	1	O
Cephalanthera longifolia	0.001	0.003	0.953	0.357	0.000	1	O
Pinus pinea	**0.001**	**0.006**	**0.954**	**0.000**	**0.464**	**<0.001**	O
***Carex* sp.**	**0.001**	**0.003**	**0.956**	**0.000**	**0.393**	**<0.001**	O
Coronilla juncea	**0.001**	**0.006**	**0.957**	**0.000**	**0.464**	**<0.001**	O
Scirpoides holoschoenus	0.001	0.003	0.959	0.143	0.214	0.999	O

Hypochaeris achyrophorus	0.001	0.003	0.960	0.286	0.000	1	O
Pinus halepensis	0.001	0.003	0.961	0.286	0.000	1	O
Catapodium rigidum	0.001	0.002	0.962	0.071	0.286	0.181	R
Anthoxanthum odoratum	0.001	0.003	0.964	0.286	0.000	1	O
Helichrysum italicum	0.001	0.002	0.965	0.286	0.000	1	T
Aira caryophyllea	0.001	0.002	0.966	0.286	0.000	1	O
Achnatherum bromoides	0.001	0.003	0.967	0.179	0.071	1	O
Dianthus sylvestris	**0.001**	**0.003**	**0.968**	**0.036**	**0.214**	**<0.05**	O
Trifolium campestre	**0.001**	**0.002**	**0.969**	**0.000**	**0.250**	**<0.001**	R
Trigonella smallii	0.001	0.002	0.970	0.214	0.000	1	O
Cytisus scoparius s. *scoparius*	0.001	0.003	0.971	0.214	0.000	1	O
Festuca myuros	0.001	0.002	0.972	0.214	0.000	1	O
Daucus carota maritimus	0.001	0.002	0.973	0.214	0.000	1	O
Rumex bucephalophorus	0.001	0.002	0.974	0.214	0.000	1	O
Ononis diffusa	0.001	0.002	0.974	0.214	0.000	1	OT
Aira elegans elegans	0.001	0.002	0.975	0.214	0.000	1	O
Carex distachya	0.001	0.002	0.976	0.071	0.107	0.999	O
Plantago afra	0.001	0.002	0.977	0.179	0.000	1	O
Medicago littoralis	0.001	0.002	0.977	0.179	0.000	1	OT
Quercus suber	**0.001**	**0.003**	**0.978**	**0.000**	**0.107**	**<0.001**	O
Lysimachia talaverae	0.000	0.002	0.979	0.143	0.000	1	O
Briza minor	0.000	0.002	0.979	0.143	0.000	1	O
Gaudinia fragilis	0.000	0.002	0.980	0.143	0.000	1	O
Anthemis arvensis	0.000	0.002	0.980	0.143	0.000	1	O
Teucrium polium	0.000	0.002	0.981	0.071	0.071	1	O
Logfia gallica	0.000	0.002	0.981	0.143	0.000	1	O
Urospermum picroides	0.000	0.002	0.982	0.143	0.000	1	O
Muscari comosum	0.000	0.002	0.982	0.143	0.000	1	O

Viburnum tinus s. *tinus*	0.000	0.002	0.983	0.107	0.000	1	T
Trifolium cherleri	**0.000**	**0.001**	**0.983**	**0.000**	**0.143**	**<0.001**	O
Erica scoparia s. *scoparia*	0.000	0.002	0.984	0.107	0.000	1	O
Asphodelus albus	**0.000**	**0.002**	**0.984**	**0.000**	**0.107**	**<0.001**	O
Ononis variegata	0.000	0.001	0.985	0.107	0.000	1	OT
Crataegus monogyna	**0.000**	**0.002**	**0.985**	**0.000**	**0.107**	**<0.001**	T
Medicago minima	**0.000**	**0.002**	**0.986**	**0.000**	**0.107**	**<0.001**	R
Triticum neglectum	0.000	0.002	0.986	0.107	0.000	1	O
Cladanthus mixtus	0.000	0.002	0.986	0.107	0.000	1	O
Moehringia pentandra	**0.000**	**0.002**	**0.987**	**0.000**	**0.071**	**<0.001**	O
Medicago marina	0.000	0.002	0.987	0.071	0.000	1	OT
Odontites luteus	**0.000**	**0.002**	**0.987**	**0.000**	**0.107**	**<0.001**	O
Linum usitatissimum s. *angustifolium*	0.000	0.001	0.988	0.071	0.000	1	O
Pulicaria odora	0.000	0.001	0.988	0.071	0.000	1	O
Oenanthe pimpinelloides	0.000	0.001	0.988	0.071	0.000	1	O
Cynosurus echinatus	0.000	0.001	0.989	0.071	0.000	1	O
Cynosurus cristatus	0.000	0.001	0.989	0.071	0.000	1	O
Plantago lagopus	0.000	0.001	0.990	0.071	0.000	1	O
Trachycarpus fortunei	**0.000**	**0.001**	**0.990**	**0.000**	**0.107**	**<0.001**	A
Avena barbata	0.000	0.001	0.990	0.071	0.000	1	O
Ononis reclinata	0.000	0.001	0.990	0.071	0.000	1	O
Clinopodium nepeta	**0.000**	**0.001**	**0.991**	**0.000**	**0.071**	**<0.001**	O
Hypericum perforatum	**0.000**	**0.001**	**0.991**	**0.000**	**0.071**	**<0.001**	O
Trisetaria panicea	**0.000**	**0.001**	**0.991**	**0.000**	**0.071**	**<0.001**	O
***Verbascum* sp.**	**0.000**	**0.001**	**0.992**	**0.000**	**0.071**	**<0.001**	O
***Helianthemum* sp.**	**0.000**	**0.001**	**0.992**	**0.000**	**0.107**	**<0.001**	O
Halimium halimifolium s. *halimifolium*	0.000	0.001	0.992	0.071	0.000	1	T
Medicago lupulina	0.000	0.001	0.993	0.071	0.000	1	O

Plantago bellardii	0.000	0.001	0.993	0.071	0.000	1	O
Euphorbia amygdaloides	**0.000**	**0.001**	**0.993**	**0.000**	**0.071**	**<0.001**	O
Centaurium maritimum	0.000	0.001	0.993	0.071	0.000	1	O
Hypochaeris glabra	0.000	0.001	0.994	0.071	0.000	1	O
Ornithopus pinnatus	0.000	0.001	0.994	0.071	0.000	1	O
Trifolium ligusticum	0.000	0.001	0.994	0.071	0.000	1	O
Moenchia mantica mantica	0.000	0.001	0.995	0.071	0.000	1	O
Oloptum miliaceum	0.000	0.001	0.995	0.071	0.000	1	O
Quercus frainetto	0.000	0.001	0.995	0.071	0.000	1	O
Pteridium aquilinum s. *aquilinum*	0.000	0.001	0.995	0.071	0.000	1	O
Trifolium resupinatum	0.000	0.001	0.996	0.071	0.000	1	O
Petrorhagia prolifera	0.000	0.001	0.996	0.071	0.000	1	O
Rumex acetosa acetosa	0.000	0.001	0.996	0.071	0.000	1	O
Vicia hybrida	0.000	0.001	0.996	0.071	0.000	1	O
Delphinium halteratum s. *halteratum*	0.000	0.001	0.997	0.071	0.000	1	O
Avena sterilis	0.000	0.001	0.997	0.071	0.000	1	A
Sherardia arvensis	0.000	0.001	0.997	0.071	0.000	1	O
Festuca danthonii s. *danthonii*	0.000	0.001	0.998	0.071	0.000	1	O
Trifolium lappaceum	0.000	0.001	0.998	0.071	0.000	1	O
Stachys romana	0.000	0.001	0.998	0.071	0.000	1	O
Filago germanica	0.000	0.001	0.998	0.071	0.000	1	O
Rostraria litorea	0.000	0.001	0.999	0.071	0.000	1	O
Phleum pratense s. *pratense*	0.000	0.001	0.999	0.071	0.000	1	O
Euphorbia exigua s. *exigua*	0.000	0.001	0.999	0.071	0.000	1	O
Convolvulus cantabrica	0.000	0.001	0.999	0.071	0.000	1	O
Cynodon dactylon	0.000	0.001	1.000	0.071	0.000	1	R
Festuca fasciculata	**0.000**	**0.001**	**1.000**	**0.000**	**0.071**	**<0.001**	OT
Anthemis maritima s. *maritima*	0.000	0.001	1.000	0.036	0.000	1	OT

overall average dissimilarity between the two groups was 0.82.							
Coastal dune woods (9340-91F0 habitat types)							
Species	**avg**	**sd**	**diss.**	**T0 avg. abund. (%)**	**T1 avg. abund. (%)**	**p-value**	**guild**
Quercus ilex	**0.142**	**0.119**	**0.229**	**43.17**	**71.33**	**<0.01**	OT
Phillyrea latifolia	**0.062**	**0.058**	**0.328**	**9.8**	**21**	**<0.01**	OT
Pistacia lentiscus	**0.058**	**0.065**	**0.421**	**2**	**18.1**	**<0.001**	OT
Erica arborea	0.049	0.060	0.499	10.53	8.37	1	OT
Quercus suber	0.028	0.055	0.544	3.37	5.5	0.259	O
Rubus ulmifolius	0.021	0.033	0.577	4.37	3.37	0.987	R
Brachypodium sylvaticum s. *sylvaticum*	0.018	0.032	0.606	4.57	2.5	1	O
Quercus robur	0.017	0.052	0.634	1.3	4.23	0.109	T
Hedera helix s. *helix*	0.017	0.028	0.661	4.33	3.23	1	T
Smilax aspera	0.010	0.013	0.678	3.13	3.17	0.987	T
Carpinus betulus	**0.009**	**0.047**	**0.693**	**0**	**2.37**	**<0.001**	O
Populus alba	**0.009**	**0.024**	**0.708**	**0.3**	**2.67**	**<0.001**	O
Ruscus aculeatus	**0.009**	**0.011**	**0.722**	**2.6**	**0.4**	**<0.001**	OT
Crataegus monogyna	**0.008**	**0.011**	**0.735**	**0.8**	**2.43**	**<0.05**	T
Asparagus acutifolius	**0.008**	**0.008**	**0.748**	**1.67**	**1.87**	**<0.001**	OT
Moehringia pentandra	**0.007**	**0.023**	**0.760**	**0.2**	**2.33**	**<0.001**	O
Achnatherum bromoides	0.007	0.014	0.770	0.7	1.6	0.287	O
Fraxinus angustifolia s. oxycarpa	0.006	0.026	0.780	1.77	0	1	T
Alliaria petiolata	**0.006**	**0.020**	**0.790**	**0**	**2.1**	**<0.001**	O
Ulmus minor minor	0.006	0.015	0.800	1.37	0.43	1	O
Oloptum miliaceum	0.006	0.011	0.809	0.6	1.37	0.073	O
Pinus pinea	**0.006**	**0.023**	**0.818**	**0.2**	**1.5**	**<0.01**	O

Myrtus communis	**0.005**	**0.015**	**0.826**	**0.63**	**1.27**	**<0.01**	OT
Cyclamen repandum* s. *repandum	**0.005**	**0.008**	**0.834**	**1.4**	**0.1**	**<0.01**	T
Carex distachya	0.005	0.008	0.841	0.83	0.67	0.057	O
Phillyrea angustifolia	**0.004**	**0.022**	**0.848**	**0**	**1.27**	**<0.001**	T
Catapodium rigidum	**0.004**	**0.008**	**0.854**	**0**	**1.13**	**<0.001**	R
Juniperus turbinata	**0.003**	**0.012**	**0.859**	**0**	**0.87**	**<0.001**	O
Carex flacca	0.003	0.006	0.863	0.47	0.53	0.393	O
Rubia peregrina	0.003	0.004	0.868	0.67	0.2	0.129	T
Arbutus unedo	0.003	0.004	0.872	0.77	0	0.136	T
Arisarum vulgare s. *vulgare*	0.003	0.008	0.876	0.8	0	1	O
Cistus salviifolius	**0.003**	**0.009**	**0.880**	**0.07**	**0.87**	**<0.001**	OT
Lonicera implexa s. *implexa*	0.003	0.008	0.884	0.77	0	1	T
Osyris alba	**0.002**	**0.009**	**0.888**	**0.07**	**0.6**	**<0.01**	OT
Juniperus phoenicea	0.002	0.008	0.892	0.27	0.43	0.559	OT
Clinopodium nepeta	0.002	0.004	0.896	0.3	0.5	0.58	O
Clematis flammula	0.002	0.003	0.899	0.6	0.1	0.18	OT
Euphorbia amygdaloides	0.002	0.006	0.903	0.3	0.5	0.997	O
Anemone apennina	0.002	0.004	0.906	0.6	0	0.965	O
Malus sylvestris	**0.002**	**0.008**	**0.910**	**0**	**0.87**	**<0.001**	O
Juncus inflexus s. *inflexus*	0.002	0.009	0.913	0.6	0	1	O
Erigeron sumatrensis	**0.002**	**0.008**	**0.917**	**0**	**0.63**	**<0.001**	A
Fraxinus ornus* s. *ornus	**0.002**	**0.008**	**0.920**	**0**	**0.6**	**<0.001**	O
Stellaria media	**0.002**	**0.004**	**0.923**	**0.07**	**0.5**	**<0.01**	O
Dioscorea communis	0.002	0.003	0.926	0.53	0	0.179	O
Rubus caesius	0.002	0.004	0.929	0.13	0.4	0.057	T
Carex sylvatica	0.002	0.004	0.931	0.5	0	1	O
Juniperus oxycedrus	0.002	0.003	0.934	0.47	0.07	0.997	OT
Prunus spinosa s. *spinosa*	0.002	0.006	0.937	0.23	0.43	0.992	O

Ligustrum vulgare	0.002	0.006	0.940	0.13	0.43	0.188	O
Clematis vitalba	0.002	0.003	0.942	0.47	0	1	R
Cytisus scoparius s. scoparius	0.002	0.007	0.945	0.5	0	1	O
Acer monspessulanum s. *monspessulanum*	0.002	0.008	0.947	0.43	0	1	O
Rhamnus alaternus s. *alaternus*	0.002	0.003	0.950	0.33	0.1	1	T
Tanacetum parthenium	**0.001**	**0.003**	**0.952**	**0**	**0.47**	**<0.001**	O
Daphne gnidium	0.001	0.003	0.954	0.23	0.2	1	OT
Pyrus spinosa	**0.001**	**0.006**	**0.956**	**0**	**0.43**	**<0.001**	O
Acer campestre	**0.001**	**0.006**	**0.958**	**0**	**0.43**	**<0.001**	O
Viburnum tinus s. tinus	0.001	0.003	0.960	0.33	0	1	OT
Cynosurus echinatus	0.001	0.003	0.961	0.13	0.2	0.941	O
Lagurus ovatus s. *ovatus*	0.001	0.003	0.963	0.13	0.2	0.984	OT
Vitis vinifera	**0.001**	**0.006**	**0.965**	**0**	**0.43**	**<0.001**	T
***Pyrus* sp.**	**0.001**	**0.006**	**0.967**	**0**	**0.43**	**<0.001**	O
Juncus effusus* s. *effusus	**0.001**	**0.005**	**0.968**	**0**	**0.43**	**<0.001**	O
Phleum nodosum	**0.001**	**0.005**	**0.970**	**0**	**0.43**	**<0.001**	O
Melica uniflora	0.001	0.003	0.971	0.23	0	1	O
Solanum nigrum	**0.001**	**0.003**	**0.972**	**0**	**0.2**	**<0.001**	O
Filago germanica	**0.001**	**0.003**	**0.973**	**0**	**0.2**	**<0.001**	O
Stachys sylvatica	0.001	0.002	0.974	0.13	0	1	O
Cytisus villosus	0.001	0.002	0.975	0.07	0.1	0.409	O
Carex pendula	0.001	0.002	0.976	0.17	0	1	O
Spartium junceum	0.001	0.002	0.977	0.07	0.1	0.984	O
Persicaria hydropiper	**0.000**	**0.002**	**0.978**	**0**	**0.17**	**<0.001**	O
Parietaria judaica	0.000	0.003	0.979	0.1	0	1	O
Rubus hirtus	0.000	0.003	0.979	0.1	0	1	O
Macrobriza maxima	0.000	0.002	0.980	0.13	0	1	O
Cyclamen hederifolium	0.000	0.002	0.981	0.13	0	1	T

Geranium purpureum	0.000	0.002	0.982	0.13	0	1	O
Holcus lanatus s. *lanatus*	0.000	0.002	0.982	0.07	0.1	1	O
***Convolvulus* sp.**	**0.000**	**0.002**	**0.983**	**0**	**0.1**	**<0.001**	O
Sonchus oleraceus	**0.000**	**0.001**	**0.984**	**0**	**0.13**	**<0.001**	O
Celtis australis s. *australis*	0.000	0.002	0.984	0.1	0	1	O
Anthoxanthum odoratum	**0.000**	**0.002**	**0.985**	**0**	**0.1**	**<0.001**	O
Trifolium lappaceum	**0.000**	**0.002**	**0.985**	**0**	**0.1**	**<0.001**	O
Trisetaria panicea	**0.000**	**0.002**	**0.986**	**0**	**0.1**	**<0.001**	O
Stachys romana	**0.000**	**0.002**	**0.986**	**0**	**0.1**	**<0.001**	O
Capsella bursa-pastoris* s. *bursa-pastori	**0.000**	**0.002**	**0.987**	**0**	**0.1**	**<0.001**	O
Quercus frainetto	0.000	0.002	0.987	0.1	0	1	O
Trifolium campestre	**0.000**	**0.002**	**0.988**	**0**	**0.1**	**<0.001**	O
Gaudinia fragilis	**0.000**	**0.002**	**0.988**	**0**	**0.1**	**<0.001**	O
Mentha suaveolens	**0.000**	**0.002**	**0.989**	**0**	**0.1**	**<0.001**	O
Geranium robertianum	0.000	0.002	0.989	0.07	0	1	O
Limodorum abortivum	0.000	0.002	0.990	0.07	0	1	O
Polypodium cambricum	0.000	0.002	0.990	0.07	0	1	O
Arum italicum s. italicum	0.000	0.001	0.991	0.07	0	1	O
Euphorbia peplis	0.000	0.001	0.991	0.07	0	1	OT
Blackstonia perfoliata	0.000	0.001	0.992	0.07	0	1	O
Daphne sericea	0.000	0.001	0.992	0.07	0	1	OT
Geranium molle	0.000	0.001	0.992	0.07	0	1	O
Cephalanthera longifolia	0.000	0.001	0.993	0.07	0	1	O
Dasypyrum villosum	0.000	0.001	0.993	0.07	0	1	O
Pteridium aquilinum* s. *aquilinum	**0.000**	**0.001**	**0.994**	**0**	**0.1**	**<0.001**	O
Allium triquetrum	0.000	0.001	0.994	0.07	0	1	O
Geranium rotundifolium	0.000	0.001	0.994	0.07	0	1	O
Limniris pseudacorus	0.000	0.001	0.995	0.07	0	1	O

Rhamnus cathartica	0.000	0.001	0.995	0.07	0	1	O
Aira elegans **s.** ***elegans***	**0.000**	**0.001**	**0.995**	**0**	**0.07**	**<0.001**	O
Carex divisa	0.000	0.001	0.996	0.07	0	1	O
Euonymus europaeus	0.000	0.001	0.996	0.07	0	1	O
Luzula forsteri	0.000	0.001	0.997	0.07	0	1	O
Clinopodium vulgare	0.000	0.001	0.997	0.07	0	1	O
Rosa sempervirens	**0.000**	**0.001**	**0.997**	**0**	**0.1**	**<0.001**	O
Briza minor	**0.000**	**0.001**	**0.998**	**0**	**0.1**	**<0.001**	O
Pulicaria odora	0.000	0.001	0.998	0.07	0	1	O
Laurus nobilis	0.000	0.001	0.998	0.07	0	1	O
Oenanthe pimpinelloides	0.000	0.001	0.999	0.07	0	1	O
Asplenium onopteris	0.000	0.001	0.999	0.07	0	1	O
Carex halleriana	0.000	0.001	0.999	0.07	0	1	O
Dittrichia viscosa	0.000	0.001	1.000	0.07	0	1	R
Cistus creticus s. eriocephalus	0.000	0.001	1.000	0.07	0	1	OT
overall average dissimilarity between the two groups 0.62							

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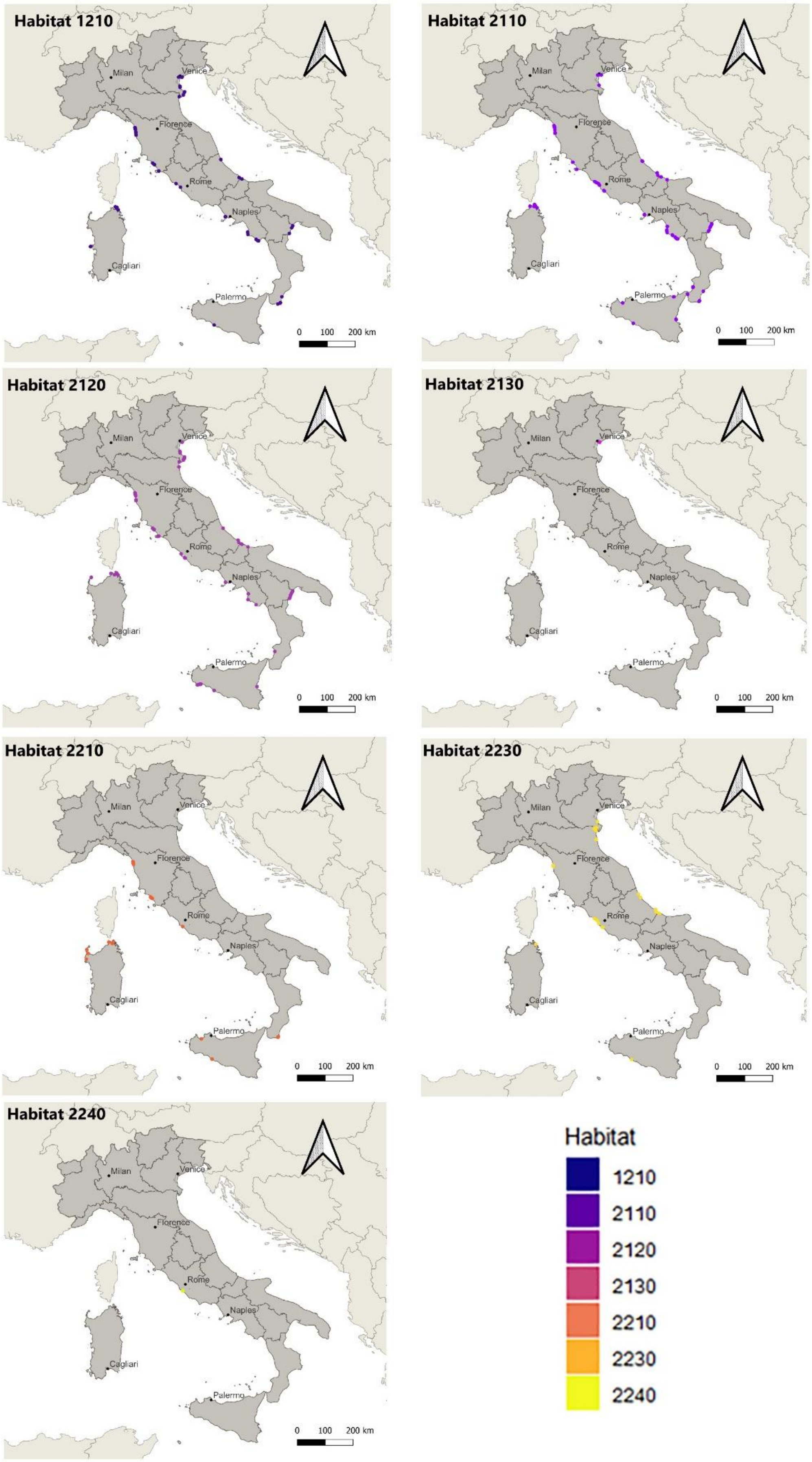
Distribution maps



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 species 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 dune habitat, and typical species of other habitat types (not specific to the dune habitats surveyed).

Species guilds	Upper beach (N12)				Shifting Dunes (N14)				Dune Grassland (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 dune 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 species guilds. Mixed models results 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 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.

Species richness	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 Dune Habitats	Upper Beach (N12)	↓	0.79	0.11	-2.07	0.039
Typical Species of Dune Habitats	Shifting dunes (N14)	↓	0.87	0.04	-3.74	0.002
Typical Species of Dune Habitats	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 species 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.

Species Cover	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 Dune Habitats	Upper Beach (N12)	↓	0.32	0.16	-2.74	0.006
Typical Species of Dune Habitats	Shifting dunes (N14)	↓	0.34	0.07	-7.39	< 0.0001
Typical Species of Dune Habitats	Dune Grasslands (N16)	--	0.44	0.11	-0.24	0.809
Other Typical Species	Upper Beach (N12)	↑	0.67	0.18	4.10	< 0.0001
Other Typical Species	Shifting dunes (N14)	↑	0.64	0.08	7.15	< 0.0001
Other Typical 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 analysed, 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 vestigated.

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 investigated 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 guild
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**
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)
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
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)
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
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 guild
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)**
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
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)
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
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
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**
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)
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
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
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
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)
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
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)**
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)**
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)**
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**
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**
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
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
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
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
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)
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
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
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

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Long-term dynamics of coastal dune landscapes and habitat diversity: Insights from a quarter century of resurveys in Castelporziano Presidential Estate

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Abstract

Coastal dunes are dynamic ecosystems vulnerable to human impact. Traditional monitoring relies on costly field surveys, but high-resolution satellite imagery offers an efficient alternative. This study integrates remote sensing (RS) and field data to analyze vegetation and landscape changes over 25 years in the highly protected Castelporziano Presidential Estate. We examined three habitat groups—Herbaceous Dune Vegetation (HDV), Woody Dune Vegetation (WDV), and Broadleaf Mixed Forest (BMF)—using 58 resurveyed plots and land cover maps. Landscape dynamics and vegetation compositional changes were assessed, and temporal patterns were calculated for three buffer sizes (25, 75, and 125 m), using Bray–Curtis dissimilarity and differences in landscape metrics. Random forest models evaluated the relationship between landscape and vegetation compositional changes. The results revealed a reduction in artificial surfaces, greater vegetation encroachment, and clear signs of natural succession. HDV exhibited a shift toward grassland species, reflecting ongoing changes in vegetation composition. WDV experienced the most pronounced compositional change, while BMF showed signs of structural homogenization. Habitat proportion emerged as the strongest predictor of compositional changes, especially at the finest scale. These findings confirm the value of combining RS and field data for long-term monitoring and provide useful insights for managing coastal dune habitats.

KEYWORDS

coastal habitats, conservation status monitoring, historical vegetation plot resurvey, landscape ecology, long-term changes, machine learning, Mediterranean coastal dune, protected area, remote sensing imagery

1 | INTRODUCTION

Coastal dune ecosystems develop in the interface between marine and terrestrial environments, hosting specialized plant communities along a distinct sea-inland gradient and forming part of the Coastal Transition Zone (Doody, 2013; Nordstrom, 2004). These ecosystems play a critical role in biodiversity conservation (Acosta et al., 2009) and offer essential ecosystem services, including carbon sequestration, coastal defense against climate change, and recreational opportunities (Barbier et al., 2011; Drius et al., 2019). However, these systems face significant threats from urbanization, erosion, tourism, trampling, and invasive species, contributing to their global decline (Acosta et al., 2009). These pressures alter sea-inland zonation patterns, resulting in fragmented and heterogeneous plant communities (Ciccarelli, 2014; Maun, 2009). Over recent decades, widespread coastal dune degradation has been reported in the literature, especially in Mediterranean coast dune ecosystems (Acosta, 2021; Doody, 2013; Intergovernmental Panel on Climate Change [IPCC], 2022; Martínez et al., 2013; Rooney, 2010). The European Union's Fourth National Monitoring Report indicates that most coastal dune habitats are in poor conservation status, with a worsening trend (Prisco et al., 2020).

Coastal dune ecosystems are highly dynamic and spatially heterogeneous, requiring fine approaches for monitoring their long-term structural and compositional changes (Ciccarelli et al., 2023). Vegetation resurveying represents a conventional method for assessing long-term ecological changes in coastal ecosystems (Charbonneau et al., 2023; Chelli et al., 2022; Del Vecchio et al., 2015; Sperandii et al., 2018, 2020). Despite its robustness, it is constrained by intensive field efforts, high costs, and time demands, as well as potential relocation inaccuracies and observer biases (Hédl et al., 2017; Kapfer et al., 2017). In recent years, the increasing availability of high-resolution aerial and satellite imagery has provided new opportunities to enhance ecological monitoring (Kwok, 2018). Historical imagery archives allow for the evaluation of spatiotemporal changes in habitat composition and configuration over extended time frames (Lillesand et al., 2015). Due to the fine-scale heterogeneity of coastal dune systems, high-resolution imagery is essential for capturing detailed land cover dynamics, fragmentation processes, and ecological connectivity. In this context, integrating photointerpretation techniques with landscape metrics has proven effective in assessing changes in habitat extent, structural complexity, and conservation effectiveness (Alphan & Çelik, 2014; Carranza et al., 2010; Malavasi et al., 2013, 2018; Tomaselli et al., 2023).

Landscape metrics provide insights into composition (land cover class diversity, e.g., Pland [PL]) and configuration (spatial arrangement of land cover units, e.g., Edge Density [ED]), serving as key indicators of ecosystem change (Fahrig, 2013; McGarigal et al., 2023; Walz, 2011). Several previous studies have applied these metrics to assess habitat fragmentation, alien species invasion, and conservation effectiveness in dune systems (Ajedegba et al., 2019; Austrich et al., 2021; Carranza et al., 2010; Chefaoui, 2014; Malavasi et al., 2013, 2014; Pafumi et al., 2024).

The increasing availability of high spatial and temporal resolution aerial and satellite orthophotos offers new opportunities to complement and enhance traditional field surveys, facilitating a more efficient and cost-effective monitoring framework. Given that vegetation compositional changes over time are influenced by landscape alterations (Walz, 2011), integrating vegetation field data with remote sensing (RS)-based landscape assessments offers a robust and cost-effective framework for understanding long-term ecological dynamics in coastal dunes (Malavasi et al., 2016).

However, few studies have investigated the link between vegetation and landscape-scale changes, particularly in Mediterranean coastal ecosystems (Bertacchi & Lombardi, 2014; Malavasi et al., 2016; Sciandrello et al., 2015). Thanks to the increasing availability of resurvey vegetation data and aerial/satellite orthophotos, examining this relationship could inform the development of novel methodologies to enhance resurvey efficiency and reduce monitoring intervals. Such an approach would be highly beneficial for improving conservation strategies in both protected and unprotected dune ecosystems.

Our study focuses on the Castelporziano Presidential Estate (Latium, Italy), one of the last well-preserved Tyrrhenian coastal dune systems and, probably, in the entire Mediterranean basin (Sarmati et al., 2025). This protected area (PA) is characterized by restricted human access even during peak tourist seasons at least from 1999 (Official Gazette of the Italian Republic, 1999; Torta & Recanatesi, 2021). Despite its high conservation status, Castelporziano is surrounded by densely populated urban areas and intensive agricultural zones, which exert considerable anthropogenic pressures (Figure 1). Given its unique conservation context, this site offers an ideal case study for analyzing long-term landscape and vegetation compositional changes in low-disturbance coastal dune systems, which are currently exceptionally rare across the entire Mediterranean basin. This study proposes a methodological approach to integrate multitemporal high-resolution RS-derived landscape maps with vegetation field data from two temporal snapshots, providing an in-depth analysis of coastal dune dynamics and conservation outcomes. To better understand the potential complementarity between field-based resurvey data and RS,

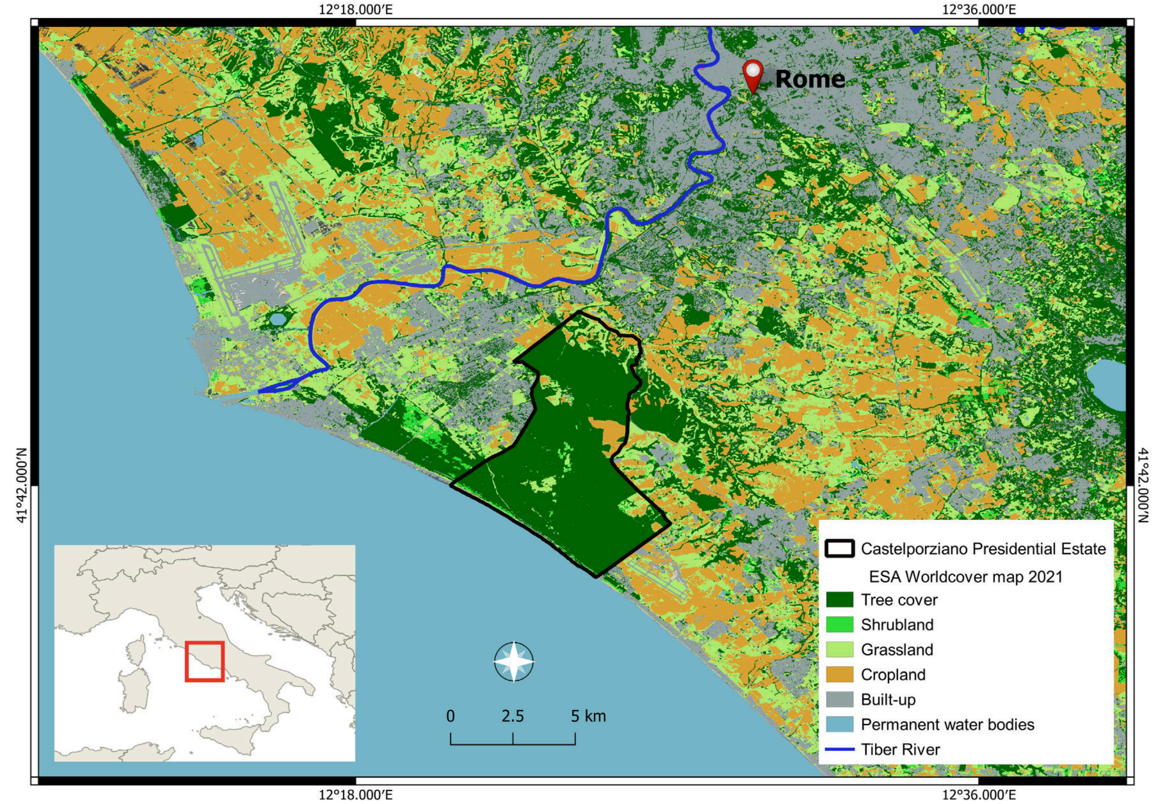

FIGURE 1 Study area in Lazio region—Central Italy (red rectangle) within Castelporziano Presidential Estate (black rounded). The basemap is European Space Agency Worldcover for global land cover mapping obtained from © ESA WorldCover project 2021/contains modified Copernicus Sentinel data (2021) processed by ESA WorldCover consortium (https://esa-worldcover.org; Zanaga et al., 2022).

we aim to identify how their integration can support the detection of long-term ecosystem changes. For these two temporal snapshots taken 25 years apart, our specific objectives are to: (a) evaluate changes in land cover and landscape dynamics, (b) analyze vegetation compositional changes within habitat groups, and (c) investigate whether a relationship exists between landscape and compositional changes. If such a relationship is found, it could help optimize and improve the resurvey schedules.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is situated within the PA of Castelporziano Presidential Estate (Natura2000 site code: IT6030084), along the Tyrrhenian coast in the Latium region of central Italy, near the mouth of the Tiber River (Figure 1). Castelporziano encompasses 6039 hectares and spans approximately 5 km of Holocene coastal dunes. It is characterized by a Mediterranean climate, with an average annual temperature of 16°C and an average annual rainfall of approximately 800 mm (Salvati et al., 2021). Established in 1872 as a government-owned hunting reserve, the area became a Presidential Estate in the 1950s, subject to landscape protection for its natural beauty. In 1999, it was officially designated as a State Nature Reserve (Nardone, 2021; Official Gazette of the Italian Republic, 1999). Since 2000, Castelporziano has been recognized as containing two Special Areas of Conservation (SAC), aimed at preserving both coastal and forest ecosystems (IT6030027 and IT6030028). The coastline of this area is influenced by a north–south longshore drift current, which significantly affects sediment transport and coastal morphology (Bonamano et al., 2024). This dynamic process plays a crucial role in shaping the coastal dunes and managing sediment balance, thereby influencing the stability and evolution of the landscape within the PA.

2.2 | Land cover mapping and landscape changes detection

We produced two land cover maps through the visual inspection of free satellite/aerial Red-Green-Blue (RGB) orthophotos in the QGIS 3.34.7 environment

TABLE 1 Land cover classes for image photointerpretation adapted from Acosta et al. (2013) and Malavasi et al. (2016).

CORINE code	Name	Definition	Detailed description	Acronym
1.	Artificial surfaces	Artificial surfaces	Human-made landscape including streets and infrastructures	ART
3.1.1.1.	Broadleaf Mixed Forests	Forests dominated by oaks and other broadleaf evergreens	Mediterranean mixed evergreen forests. Habitats: 9340 *Quercus ilex* and *Quercus rotundifolia* forests 91F0 Mixed oak-elm-ash forests of great rivers	BMF
3.1.2.1.	Afforestation	Afforestation	Afforestation on coastal dunes mainly with *Pinus*.	AFF
3.2.3.1.	Woody Dune Vegetation	Mediterranean macchia	Woody dune vegetation dominated by *Juniperus* and *Cistus* on fixed dunes. Habitats: 2250 Fixed coastal dunes with *Juniperus* spp. 2260 *Cisto-Lavanduletalia* dune sclerophyllous scrubs	WDV
3.2.4.2.	Semi-natural Herbaceous Vegetation	Semi-natural herbaceous ruderal vegetation	Semi-natural herbaceous vegetation in degraded and urbanized areas dominated by ruderal species	SHV
3.3.1.1.	Beach Pioneer Vegetation	Open sand	Open sand with sparse communities of the drift lines, dominated by annual species. Habitat: 1210 Annual vegetation of drift lines	BPV
3.3.1.2.	Herbaceous Dune Vegetation	Partially vegetated dunes and densely vegetated dunes	Herbaceous vegetation of shifting and mobile dunes and inner grasslands. Habitats: 2110 Embryonic shifting dunes tussock grass 2120 Shifting dunes along the shoreline with *Ammophila arenaria* Community 2210 *Crucianellion maritimae* fixed beach dunes 2230 *Malcolmietalia* dune grasslands	HDV
5.1.	Inland waters	Inland waters	River	CID
5.2.	Marine waters	Marine waters	Tyrrhenian Sea	SEA

(https://qgis.org/it/site/) for the years 1998 (T_0) and 2023 (T_1). For T_0, we used the freely available 1 m resolution RGB orthophotos from the Web Map Service of Italian National Geoportal (https://gn.mase.gov.it/portale/home) of July 1998. For T_1, we mapped coastal areas using satellite 1 m resolution RGB orthophotos of July 2023 produced by Airbus and by TerraMetrics and freely available on Google Earth. Specifically, we mapped approximately 2800 m wide strip starting from the coastline toward inland and 300 m seaward. The coastal dune landscape was classified into nine land cover classes (hereafter "land cover classes"), following previous studies in similar ecosystems (Malavasi et al., 2016), using CORINE land cover legend expanded to a fourth level of detail (Table 1): Afforestation (AFF), Artificial surfaces (ART), Broadleaf Mixed Forests (BMF), Beach Pioneer Vegetation (BPV), Herbaceous Dune Vegetation (HDV), Inland waters (CID), Marine waters (SEA), Semi-natural Herbaceous Ruderal Vegetation (SHV), and Woody Dune Vegetation (WDV).

The accuracy assessment of the land cover maps was based on using 100 random control points collected to construct the confusion matrix and calculating accuracy metrics (overall accuracy and Cohen's κ) for T_0 and T_1, classifying these control points with the official map of the Latium Region from 2008, which is freely available on https://dati.lazio.it/, and with field campaign of 2024, respectively. Both maps achieved high accuracy levels (overall accuracy >0.88, Cohen's κ >0.85), allowing us to proceed with the analysis (Table S1a,b).

Next, the landscape changes between 1998 and 2023 for each land cover class were calculated through a transition matrix and visualized using a chord diagram using the R package "circlize" (Gu et al., 2014; Table S2).

2.3 | Vegetation data selection and compositional change analysis

We focus on the coastal section of Castelporziano, covering an area of about 1000 ha. Its coastal dune ecosystems include almost all the habitats of the Mediterranean coastal psammophilous zonation (La Bella et al., 2021, Table 2). To analyze vegetation compositional change, we identified a subset of the land cover classes that could be clearly matched with specific habitat types listed in

TABLE 2 Habitat types according to European Union Habitat Directive (92/43/EEC), description and the corresponding "habitat groups."

EU habitat	Description	Habitat groups	Acronym
1210 Annual vegetation of drift lines	Pioneer coastal vegetation, located on the upper beach and colonized by specialized halonitrophilous therophytes, such as *Cakile maritima* Scop. subsp. *maritima*	Beach Pioneer Vegetation	BPV
2110 Embryonic shifting dunes tussock grass	Embryonic dunes on sandy coasts are formed by perennial psammophilous plants, primarily stabilized by *Thinopyrum junceum* (L.) Á. Löve	Herbaceous Dune Vegetation	HDV
2120 Shifting dunes along the shoreline with *Ammophila arenaria* Community	Coastal mobile dunes primarily stabilized by *Calamagrostis arenaria* (L.) Roth subsp. *arundinacea* (Husn.) Banfi, Galasso & Bartolucci, enable dune formation and maintenance with its extensive rhizome network		
2210 *Crucianellion maritimae* fixed beach dunes	This habitat develops on the inner slopes of coastal dunes, where the soil is more stable, named after the characteristic species *Crucianella maritima* L.		
2230 *Malcolmietalia* dune grasslands	These grasslands grow in interdunal areas, dominated by *Ononis variegata* L., *Silene canescens* Ten, and various annual species in diverse, species-rich associations		
2250 Fixed coastal dunes with *Juniperus* spp.	The fixed dunes host a low shrubland dominated by *Juniperus macrocarpa* Sm., transitioning to taller Mediterranean sclerophylls, creating an heterogeneous habitat	Woody Dune Vegetation	WDV
2260 *Cisto-Lavenduletalia* dune sclerophyllous scrubs	The sclerophyll shrublands are located further inland with a more stabilized substrate dominated by *Cistus creticus* L. subsp. *eriocephalus* (Viv.) Greuter & Burdetistus		
9340 *Quercus ilex* and *Quercus rotundifolia* forests	Evergreen maquis of the dune slack dominated by *Q. ilex* L.	Broadleaf Mixed Forests	BMF
91F0 Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)	Hardwood forests along riverbeds with dominant woody species including *Quercus* sp. pl. supported by a well-developed undergrowth.		

Annex I of the Habitats Directive (92/43/EEC), based on the availability of vegetation plot data and their detectability in RS imagery. These were grouped into four habitat groups (hereafter "habitat groups"): BPV (habitat code: 1210), HDV (habitat code: 2110, 2120, 2210, 2230), WDV (habitat code: 2250, 2260) and BMF (habitat code: 9340, 91F0). While the land cover classes represent the entire set of visually interpreted categories, the habitat groups correspond to those classes for which vegetation plots were available and that could be associated with Directive habitats. Therefore, not all land cover classes were included among the habitat groups used in the vegetation analysis.

To closely align with the 1998 imagery, we selected 58 historical vegetation plots from Observatory of Castelporziano "Centre for the multidisciplinary Study of Mediterranean Coastal Ecosystems" sampled between 1992 and 2000 (T_0): 15 in HDV, 15 in WDV, and 28 in BMF, ensuring a representative sample for each habitat group (see Tables S3 and S4). These plots were revisited in 2023 (T_1) following the same approach used in the historical ones, at T_0 (Acosta et al., 2025; Figure S1). Regrettably, no vegetation data was available for BPV, making it necessary to rely solely on landscape-level monitoring to assess changes in this group.

For each plot, we have information on ID, coordinates, habitat type, plot area, year of collection, and vascular plant species abundance at both initial (T_0) and subsequent (T_1) resurvey times. Then each plot was assigned to its corresponding group (HDV, WDV, and

BMF; Table S4). As the plots were mostly established for phytosociological purposes, their size was not standardized but adapted to the characteristics of the plant community, ranging from 5 to 1000 m^2 (HDV: 10–100 m^2; WDV: 20–200 m^2; BMF: 5–1000 m^2; Tables S3 and S4). To visualize vegetation compositional changes, defined as shifts in species composition and their relative abundances between T_0 and T_1, we constructed rank-abundance curves using the "goeveg" R package (Shimadzu et al., 2015; von Lampe & Schellenberg, 2016) for the three habitat groups. A consistent taxonomic nomenclature was applied to both historical and resurveyed plots following Bartolucci et al. (2024).

2.4 | Relationship between landscape and vegetation compositional changes

Firstly, to assess landscape changes, we converted the land cover maps of T_0 and T_1 from vector to raster format with a 1-m resolution using the "rasterize" tool in QGIS Desktop, version 3.34 Prizren (https://qgis.org/). Circular buffers of 25, 75, and 125 m were delineated around the centroid of each resurveyed plot. The land cover maps were masked by these buffers to evaluate landscape changes in the areas surrounding the surveyed plots over time. Each buffer was assigned a corresponding plot ID and habitat group to standardize the data for subsequent analyses. The buffer sizes were chosen based on their relevance to study the dynamics of various coastal habitats (Fahrig, 2013; Malavasi et al., 2018). Next, we calculated some landscape metrics (PL, mean patch area [MPA], Patch Density [PD], and ED, for their description see below) that provide essential insights into ongoing ecological processes (Carranza et al., 2015; Malavasi et al., 2018; McGarigal et al., 2023). Using the "landscapemetrics" R package (Hesselbarth et al., 2019), we computed these metrics for each buffer size at T_0 and T_1 and then calculated their differences (Δ) to assess landscape changes over time in both the focal landscape—defined as the corresponding land cover class (e.g., the proportion of BMF within a buffer centered on a BMF plot)—and the artificial class. This approach allowed us to evaluate key ecological dynamics, such as habitat loss or expansion, fragmentation, changes in connectivity, and human-driven modifications (McGarigal et al., 2023; Table S5).

For habitat composition, we used PL as an index of habitat proportion, calculated as the percentage of the focal landscape covered by that class. An increase in ΔPL indicates habitat gain, while a decrease suggests habitat loss. For habitat configuration, MPA represents the average size of patches within a certain area. The ΔMPA decrease indicates fragmentation process which may be due to or an expanding class or a reduction process (Durán & Moore, 2013; Malavasi et al., 2018). ED, on the other hand, quantifies the extent of boundaries between patches, offering insight about the complexity or simplicity of class shapes and a class's interaction with surrounding land cover types; higher values of ΔED indicate greater interaction with surrounding land cover types, while lower values suggest a connectivity loss. Another important metric is PD, which measures the number of patches within a given area and is typically associated with a measure of patches aggregation (Cini et al., 2024; McGarigal et al., 2023). To assess potential human impact, we also calculated PL for the artificial class (PL_{ART}), where an increase corresponds to urbanization gain and a decrease suggests habitat encroachment.

Vegetation compositional change was calculated as an overall measure of shifts in species presence and abundances over time, using a temporal β-diversity index—specifically, the Bray–Curtis dissimilarity (Bray–Curtis, Equation 1; Shimadzu et al., 2015) at plot level. This index was applied to species abundances and calculated using the "vegan" R package (Oksanen et al., 2025). In this context, A_i and B_i represent the abundances of the "*i*-th" species in the two samples, while "*s*" denotes the total number of species.

$$\text{Bray}-\text{Curtis} = \frac{\sum_{i=1}^{s} |A_i - B_i|}{\sum_{i=1}^{s} |A_i + B_i|}. \quad (1)$$

The random forest (RF) models were used to evaluate whether there is a relationship between landscape and vegetation compositional changes within each habitat groups, owing to the strong detection capacity of interaction terms (Denisko & Hoffman, 2018). The influence of landscape on compositional changes was investigated using RF models separately for the three buffer sizes (25, 75, and 125 m) using "caret" R package (Kuhn, 2008). Specifically, the RF model was configured by applying an internal 10-fold cross-validation and utilizing the "train" function within the "caret" package in R (Kuhn, 2008). A substantial number of uncorrelated decision trees (num. trees = 500) were selected as default value (Liaw & Wiener, 2002). The number of randomly chosen variables at each decision tree node (m.try) ranged from 2 to the total number of variables. RF models were chosen for their robustness, computational efficiency, and ability to assess variable importance (Cutler et al., 2007).

The RF models were calculated with Bray–Curtis index of compositional change as dependent variable and Δ of landscape metrics for the focal landscape and for artificial class as independent variables, as follows (Equation 2):

$$\text{Bray} - \text{Curtis} \sim \Delta\, \text{Landscape metrics} + \text{Habitat groups}. \quad (2)$$

The model performance metrics, including R^2, root mean squared error (RMSE), and mean absolute error (MAE) were calculated for each RF model. We employed the highest R^2 to determine the best model. Subsequently, we calculated variable importance through "varImp" function in "caret" R package for the best model at the three buffer sizes (Kuhn, 2008).

Finally, we employed partial dependence plots (PDP) to illustrate the marginal effect of a specific explanatory variable on the predicted values of the RF model keeping the model's functional form and other variables constant (Elith et al., 2008). With PDPs, we visually observed the shape of the relationship between Δ of landscape metrics and Bray–Curtis of compositional changes separately for the three habitat groups (Greenwell, 2017).

3 | RESULTS

3.1 | Landscape changes

Overall, the chord diagram (Figure 2) reveals a general trend of re-naturalization, with several artificial or human-modified areas being replaced by natural classes, particularly forested and dune habitats. Specifically, it pointed out that, in the analyzed period, BMF class had an interchange with SHV, while some areas of artificial class (ART, 33%) and AFF (8%) have turned into BMF. Additionally, 12% of the sea cover type (SEA) shifts to the BPV class. Other changes could also highlight that almost half of the BPV class (47%) is shifting to HDV, while part of the HDV is shifting to WDV (13%). Moreover, it is noteworthy that only 44% of the ART class remained

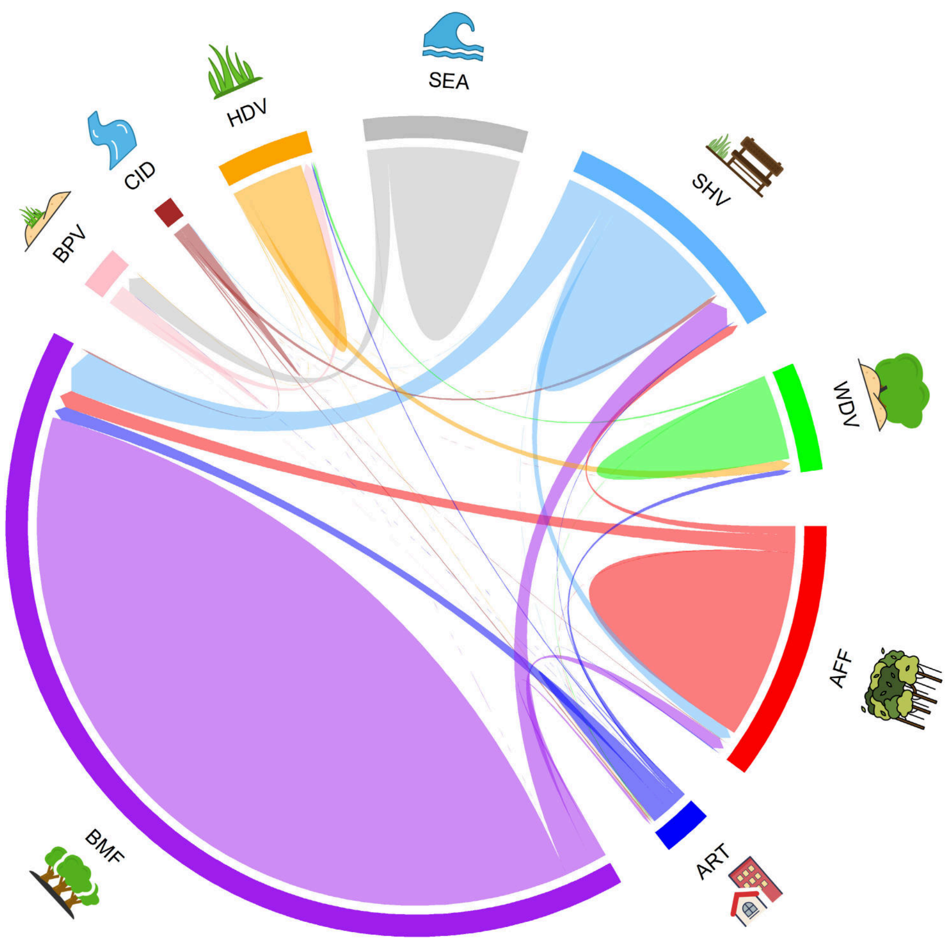

FIGURE 2 Chord diagram with arrows representing the changes between 1998 and 2023 in land cover classes: AFF, Afforestation; ART, Artificial; BPV, Beach Pioneer Vegetation; BMF, Broadleaf Mixed Forests; CID, Inland waters; HDV, Herbaceous Dune Vegetation; SEA, Marine waters; SHV; Semi-natural Herbaceous Ruderal Vegetation; WDV, Woody Dune Vegetation.

unchanged, while 13% changed into WDV. Finally, part of the river class (22% of CID) shifted to SHV.

3.2 | Vegetation compositional change within the habitat groups

Across all habitat groups, compositional change reflects a gradual successional shift rather than a wholesale loss of dune specialists, as revealed by changes in the rank-abundance curves (Figure 3). In the HDV, there was a slight increase in the number of species from 27 to 31 (+14.8%), and the increase in the dominance of dune grassland species such as *Ononis variegata* L. and *Anthemis maritima* L. subsp. *maritima*, with *O. variegata* keeping its first rank but increasing the relative abundance. On the other hand, two key role grasses typical of embryonic and shifting dunes, *Calamagrostis arenaria* (L.) Roth subsp. *arundinacea* (Husn.) Banfi & Galasso and *Thinopyrum junceum* (L.) Á.Löve decreased their abundances (Figure 3a).

In the WDV group, significant differences were observed between T_0 and T_1, primarily due to the reduction of *Cistus creticus* L. subsp. *eriocephalus* (Viv.) Greuter & Burdet, which was highly dominant in T_0 (from more than 20% of relative abundance to less than 10%) and to the higher species equipartition in T_1 (Figure 3b). Focusing on T_1, there is a comparable number of species (43 at T_0 vs. 40 at T_1, −3%) and similar relative abundance of *Arbutus unedo* L. over the last 25 years. We assist also in a strong increase in *Phillyrea angustifolia* L. and in maquis species such as *Juniperus macrocarpa* Sm. and *Quercus ilex* L, which are primarily associated with the emergence of new plants.

In the BMF group, the rank-abundance curves indicate an increase in the dominance of typical species of Mediterranean broadleaf forests, such as *Q. ilex* (Figure 3c). Notably, there was a significant decrease in the number of species between T_0 and T_1, from 113 to 76 species (−37%), related to a decrease in species, typical of the undergrowth. Additionally, the reduction of *Cistus* species was also verified accompanied by a temporal increase of *Phillyrea* sp. pl.

Overall, these dynamics reveal a shift from dune-building specialists toward grassland-associated species in early successional dunes, accompanied by a replacement of low scrub species with shrubby maquis, indicating a successional progression toward the later-stage vegetation communities across the coastal dune system.

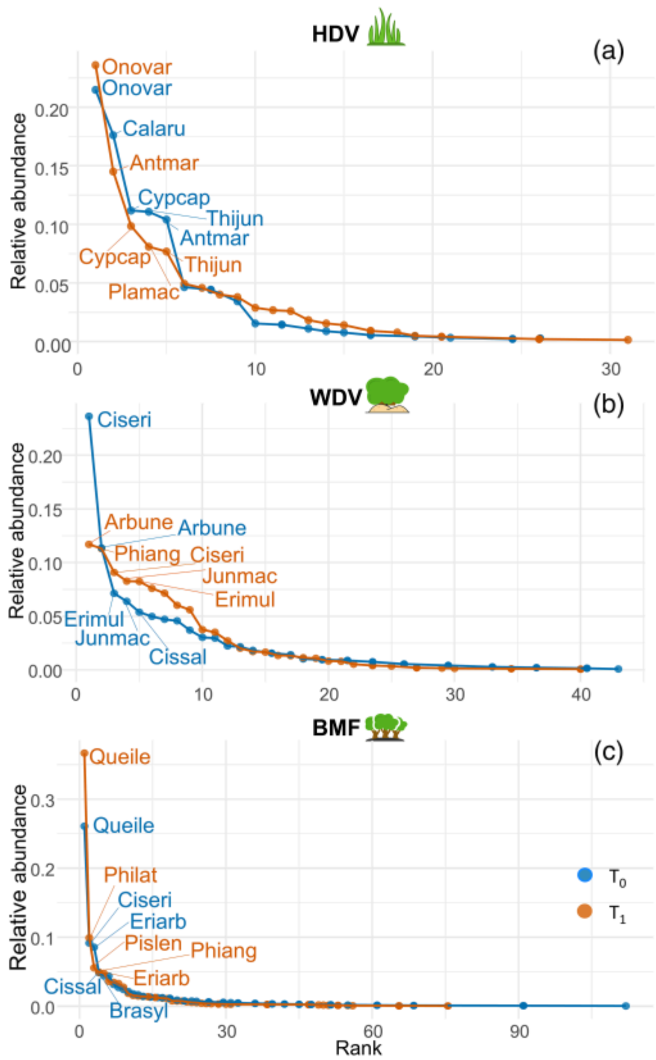

FIGURE 3 Rank-abundance curves for Herbaceous Dune Vegetation—HDV (a), Woody Dune Vegetation—WDV (b) and Broadleaf Mixed Forests—BMF (c) in T_0 (blue) and T_1 (red) on the basis of resurveyed historical vegetation plots. The species name abbreviations are reported as follows: Antmar, *Anthemis maritima* L. subsp. *maritima*; Arbune, *Arbutus unedo* L.; Brasyl, *Brachypodium sylvaticum* (Huds.) P.Beauv. subsp. *sylvaticum*; Calaru, *Calamagrostis arenaria* (L.) Roth subsp. *arundinacea* (Husn.) Banfi, Galasso & Bartolucci; Ciseri, *Cistus creticus* L. subsp. *eriocephalus* (Viv.) Greuter & Burdet; Cissal, *Cistus salvifolius* L.; Cypcap, *Cyperus capitatus* Vand.; Eriarb, *Erica arborea* L.; Erimul, *Erica multiflora* L.; Junmac, *Juniperus macrocarpa* Sm.; Onovar, *Ononis variegata* L.; Philat, *Phillirea latifolia* L.; Phiang, *Phillirea angustifolia* L.; Pislen, *Pistacia lentiscus* L.; Plamac, *Plantago macrorhiza* Poir.; Queile, *Quercus ilex* L.; Thijun, *Thinopyrum junceum* (L.) Á.Löve.

3.3 | Relationship between landscape and vegetation compositional changes over time

The RF model based on the 25 m buffer outperformed those using the other tested buffer sizes, achieving the highest explained variance ($R^2 = 0.49 \pm 0.31$; Figure 4, Table S6), and thereby demonstrating superior predictive power. Consequently, we concentrated our interpretation and discussion on the 25 m buffer results. However, we could evidence that all models showed similar patterns across all three habitat groups, allowing for a unified discussion of the results (Figures S2 and S3).

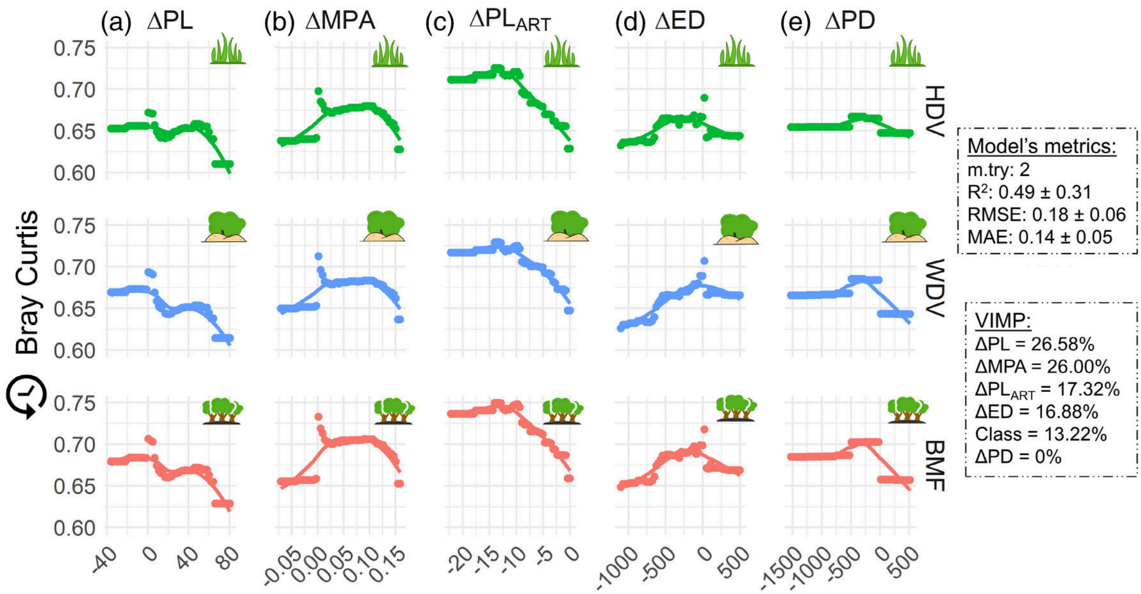

FIGURE 4 Visualization of random forest partial dependence plots at 25 m buffer size as it resulted in the best size for monitoring the relationship between landscape changes and vegetation compositional changes. Here are reported the models with *y*-axis the Bray–Curtis, and *x*-axis, respectively: (a) ΔPL (Pland), (b) ΔMPA (mean patch area), (c) ΔPL_{ART} (Pland of artificial class), (d) ΔED (Edge Density), and (e) ΔPD (Patch Density). On the right, the model's metrics (m.try, R^2, root mean squared error [RMSE], and mean absolute error [MAE]) and the variable importance values (VIMP) are reported. In red, green, and blue are respectively reported the graphs for Broadleaf Mixed Forests (BMF), Herbaceous Dune Vegetation (HDV), and Woody Dune Vegetation (WDV).

In this RF model, the most influential variables were the changes in habitat proportion (ΔPL: 26.58%), followed by the changes in patches fragmentation (ΔMPA: 26.00%; Figure 4). Furthermore, the changes in artificial proportion (ΔPL_{ART}) and in patches connectivity (ΔED) showed 17.32% and 16.88% of variable importance, respectively (Figure 4).

The relationship between changes in habitat proportion (ΔPL) and vegetation compositional changes was associated with a decreasing trend, in which the high species change was related to habitat loss (negative ΔPL), while low species shift was verified in areas with habitat gain (positive ΔPL; Figure 4a).

Regarding the relationship with changes in fragmentation process (ΔMPA), a parabolic trend was observed. The most intense compositional change was concentrated in patches that maintained a relatively stable mean area (ΔMPA ≈ 0), while fewer compositional change occurred in buffers where the fragmentation either decreased or increased (Figure 4b).

Furthermore, the RF model highlighted the decrease of artificial proportion (negative ΔPL_{ART}) in each buffer (Figure 4c). High vegetation compositional change was observed with intense artificial loss, while almost stable ΔPL_{ART} was related to low species shift (Figure 4c).

The relationship between habitat connectivity (ΔED) and compositional changes reveals that most shifts occur when ED remains stable, whereas fewer changes are observed with a significant reduction or increase in connectivity (Figure 4d). Finally, considering the changes in aggregation of patches (ΔPD), we found that most compositional changes took place in those areas where the PD has remained stable. On the other hand, reduced changes were registered where the PD has increased or reduced (Figure 4e).

The PDP of RF models at 75 and 125 buffer areas were reported in Figures S2 and S3.

4 | DISCUSSION

By utilizing high-resolution orthophotos alongside resurveyed field data, we were able to analyze coastal dune dynamics with a fine-grained perspective, focusing on the relationship between landscape and species changes. Our key finding is the demonstrated link between vegetation composition and landscape changes, indicating that RS-derived metrics can reliably serve as proxies for detecting vegetation shifts in coastal dune systems. At Castelporziano Estate, unlike most European coastal dunes (Foti et al., 2021; Garcia-Lozano et al., 2018; Molina et al., 2020; Sperandii et al., 2018; Vos et al., 2024), we observed a slight transition from artificial toward natural cover types, with notable Mediterranean forest encroachment—patterns that likely reflect ongoing positive successional dynamics toward later-stage communities. These results underscore the added value of integrating RS data into the long-term monitoring and management of protected coastal areas.

4.1 | Landscape changes

First of all, between T_0 and T_1, we observed a clear shift from sea to open sand, highlighting the sand accretion trend which seems to have characterized Castelporziano Estate in the last quarter century, conversely to the majority of world coastal areas, thanks also to the sediment influx from the Tiber River (Bazzichetto et al., 2020; Bonamano et al., 2024; Pang et al., 2023). This phenomenon is of pivotal importance because sand accretion could drive to more stable and resilient dune habitats, fundamental for the conservation of the typical coastal dune vegetation zonation (Johnston et al., 2023).

The accretion processes, combined with strict protection from anthropogenic disturbance, seem to facilitate directional ecological succession, promoting a shift toward later-stage dune communities. The replacement of early-stage vegetation (BPV) by more structured communities (HDV and WDV), and eventually inland forest elements (BMF), highlights a positive trajectory of habitat evolution. In this context, the removal of artificial structures (ART; Eldridge et al., 2011; Woods & Zinnert, 2024), have probably also enhanced these processes. Moreover, the observed encroachment in WDV could be interpreted as a positive successional trend related to shift from shrublands to more closed woodlands, which is supported by the increase in species less salt tolerant and more characteristic of inland forests (Maun, 2009).

These findings reinforce the central role of PAs in counteracting coastal degradation trends widely reported elsewhere (Gao et al., 2020; Jackson et al., 2019; Sperandii et al., 2018), and highlight how long-term conservation efforts can foster ecological resilience in coastal dune ecosystems.

4.2 | Vegetation compositional changes within habitat groups

At habitat group level, we observed differences between T_0 and T_1, in most cases likely attributable to the natural coastal dynamics, particularly in coastal shrubs.

In the HDV, the cover of *C. arenaria* subsp. *arundinacea* and *T. junceum* declined, while species typical of more stabilized dune grasslands—such as *O. variegata* and *Silene canescens*—increased. This suggests an early successional transition toward more inland grassland communities, likely favored by reduced anthropogenic pressure and ongoing conservation efforts (Acosta, 2021; Sarmati et al., 2025).

In WDV, the decline in *Cistus* species and the increased presence of other coastal shrubs such as *A. unedo* and *P. angustifolia* indicate a structural shift toward high maquis vegetation. This is further supported by the increased abundance of *Q. ilex* (Pedrotta et al., 2021). Such a trend likely reflects both successional progression and the effects of fire management practices, which—along with increasing canopy closure—may have contributed to the decline of *Cistus*, a genus well known for fire-stimulated germination (Moretti et al., 2006; Pausas, 2006).

In the BMF, we observed a further increase in the dominance of *Q. ilex*, accompanied by low overall compositional change. This trend, which contrasts with patterns reported in more disturbed Mediterranean sites (Acácio et al., 2021), may reflect the effects of protection policies facilitating the expansion of late-successional forest communities.

4.3 | Relationship between landscape and vegetation compositional changes

A key finding of our study is that the relationships between landscape metrics and vegetation compositional changes over the past 25 years follow remarkably similar patterns across all three habitat groups, reflecting the intrinsic mosaic structure of coastal dune ecosystems (Ciccarelli, 2014).

The RF model at the 25 m buffer size identified the change in habitat proportion (ΔPL) as the primary driver of vegetation compositional change. Specifically, habitat loss (negative ΔPL) was associated with higher Bray–Curtis values in our study, reflecting both the emergence of new patches and an increase in compositional change; this finding corroborates Fahrig's (2013) theory and aligns with documented patterns of natural ecological succession (Medina Machín et al., 2019; Shanmugam & Barnsley, 2002). Conversely, in areas where we registered a strong habitat gain (positive ΔPL), compositional change was limited, likely due to the inherent low species diversity of coastal dune ecosystems, where community composition had already stabilized (Acosta & Ercole, 2015; Peyrat & Fichtner, 2011). At around 40% habitat gain, unexpectedly high vegetation compositional change suggests a transitional phase in habitat development. This stage likely features a mosaic of established dune communities alongside colonizing pioneer species, creating conditions that intensify species change through increased structural heterogeneity and competitive interactions (Malavasi et al., 2018).

Regarding changes in MPA (ΔMPA), the most pronounced vegetation compositional change occurred where patches slightly expanded, suggesting that patch stability fosters such process (Mestre et al., 2020). Conversely, a reduction in ΔMPA corresponded to more limited vegetation shift, likely due to the formation of isolated nuclei through the nucleation process (Durán & Moore, 2013). These nuclei likely host a subset of preexisting species, facilitated by dispersal mechanisms (Michaels et al., 2024; Toh et al., 1999). Areas with patch expansion exhibited reduced compositional changes, mirroring the trend observed for PL and reflecting the limited species pool in coastal environments (Acosta & Ercole, 2015; Peyrat & Fichtner, 2011).

The changes in artificial land cover (ΔPL_{ART}) showed exclusively negative trends, primarily driven by habitat encroachment (Figure 2). The strongest compositional change occurred where ΔPL_{ART} decreased, likely due to the occupation of newly available space and canopy closure (De Souza et al., 2022; Sender et al., 2021; Zheng et al., 2021). This phenomenon, particularly evident in WDV and BMF, indicates the progression of coastal dune zonation, contrasting with the mosaic structure of early successional stages. These findings underscore the effectiveness of Castelporziano's conservation measure strategies, which have facilitated these ecological transitions. The observed encroachment dynamics align with patterns reported in other stabilized European fixed dunes (Molina et al., 2020; Provoost et al., 2011).

Finally, changes in landscape connectivity (ΔED) and patch aggregation (ΔPD) influenced species dynamics similarly. The most significant shifts occurred where ΔED and ΔPD remained stable or slightly declined, particularly in patches with a modest increase in MPA, likely reflecting successional processes (Ajedegba et al., 2019). In contrast, areas with significant decreases in ΔED and ΔPD exhibited lower Bray–Curtis values, suggesting reduction in connectivity and aggregation due to habitat encroachment, accompanied by a minimal compositional change (Peyrat & Fichtner, 2011). Similarly, reduced compositional shift was observed where ΔED and ΔPD increased, likely linked to the nucleation process (Durán & Moore, 2013).

Over the past 25 years, the coastal dunes of the Castelporziano Estate have undergone significant changes in both landscape structure and species composition, likely driven primarily by natural succession. Unlike other Mediterranean dune systems affected by human disturbance (Acosta, 2021; Austrich et al., 2021; Gao et al., 2020; Malavasi et al., 2013, 2018; Salgado et al., 2022; Šilc et al., 2020), Castelporziano Estate has benefited from long-standing conservation measures—including restricted public access, cessation of mechanical beach cleaning, and active fire regime control—which have limited anthropogenic pressures and supported ecosystem recovery. These positive dynamics are consistent with recent findings showing that naturally evolving dune systems may support more structured and resilient vegetation compared to artificially restored ones (White et al., 2024), providing further insights into the potential benefits of these conservation strategies.

Furthermore, our integrated approach—combining resurveyed field data, satellite imagery, and landscape metrics—provided insights into ecological trends that would be difficult to detect through field monitoring alone. This methodology is particularly valuable for assessing both compositional and landscape changes over time and has clear applicability in other dynamic and spatially complex ecosystems.

5 | CONCLUSION

In this study, we propose a significant methodological advancement for monitoring both temporal and spatial ecosystem changes in coastal dune systems, through the integration of data at landscape and habitat scale by using satellite imagery and resurveyed field observations, respectively. This approach effectively captures the complex interplay of ecosystem dynamics and can be applied to other fragile and spatially heterogeneous ecosystems. When applied to the Castelporziano Presidential Estate—an exceptionally rare and protected site in the Mediterranean basin—it also allowed us to account for the variability in coastal dune zonation, offering valuable insights into long-term vegetation dynamics in a minimally disturbed context.

This integration of long-term vegetation resurveys with multitemporal RS and landscape metrics allowed us to detect patterns of change that would not have been identifiable through field-based observations alone—such as shifts in landscape dynamics and subtle successional processes. The approach provides a replicable framework that can be extended to other ecosystems where long-term data exist, offering valuable insights for conservation planning and ecosystem management. The findings from this long-term, minimally impacted protected coastal dune area further underscore the positive role of conservation strategies in enhancing ecosystem resilience.

A promising future direction is the integration of landscape metrics and field data to refine the assessment of these interactions on coastal dunes across larger spatial scales, further strengthening conservation efforts and adaptive management strategies.

AUTHOR CONTRIBUTIONS

Writing—review and editing: **EC**, **ATRA**, **MM**, **SS**, **SDV**, **DC**, **FM**; Writing—original draft: **EC**, **ATRA**, **MM**, **SS**,

SDV, **DC**, **FM**; Visualization: **EC**, **ATRA**, **FM**; Methodology: **EC**, **ATRA**, **MM**, **FM**; Investigation: **EC**, **ATRA**, **FM**; Formal analysis: **EC**, **FM**; Data curation: **EC**, **SS**, **SDV**; Conceptualization: **EC**, **ATRA**, **MM**, **FM**; Supervision: **ATRA**, **MM**, **FM**; Data collection: **SS**, **SDV**, **ATRA**.

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CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

Data is available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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Resurveying Mediterranean coastal dunes: insights from the ReSarDu database*

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Abstract

The vegetation resurvey is considered a valid approach for assessing how species composition, abundance, and distribution have evolved in response to anthropogenic pressures, climate change, and habitat alterations over recent decades. ReSarDu – Resurvey Sardinian Dunes – is the first regional database compiled from resurveys of coastal dune systems across Sardinia (Italy). It includes 418 resurveys ranging in size from 1 to 400 m^2, collected between 2023 and 2025, based on 188 historical phytosociological relevés dating back to the 1970s.

ReSarDu has been created to understand long-term vegetation changes in Sardinian coastal dune systems. By integrating historical and newly collected phytosociological data, we provide a comprehensive tool for assessing biodiversity trends and supporting effective conservation and restoration strategies.

Keywords

Coastal dunes, Habitats Directive, Italy, old surveys, phytosociological relevés, resurvey, Sardinia, vegetation

Introduction

Assessing biodiversity change in the Anthropocene poses a significant challenge; therefore, the development of accessible databases is crucial to support ecological research and guide effective conservation strategies, addressing global biodiversity loss (Meyer et al. 2015; Dornelas et al. 2018).

A large amount of available vegetation data, encompassing extensive coverage in terms of space, habitats, and time, derive from phytosociological relevés (Chytrý et al. 2016). These data were collected over the past decades thanks to a long-standing tradition of botanists and represent an essential data source for fundamental research and nature conservation applications, including monitoring the occurrence and abundance of plant species in different habitats (Chytrý et al. 2016; Sabatini et al. 2021; Bagella et al. 2024; Gholizadeh et al. 2025). In this context, the development of specialised databases focused on temporal dynamics is particularly crucial, as they provide the empirical foundation for understanding long-term ecological shifts (Costello et al. 2013).

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A key methodological approach underpinning such databases is the resurvey of historical sites i.e. revisiting previously studied locations to resample historical relevés. This approach offers opportunities to study temporal vegetation changes with acceptable relocation accuracy and quantify long-term biodiversity dynamics (Kapfer et al. 2017; Knollová et al. 2024).

Vegetation resurvey is considered a valid approach for assessing how species composition, abundance, and distribution have evolved in response to anthropogenic pressures, climate change, and habitat alterations over recent decades (Kapfer et al. 2017; Dornelas et al. 2018). This approach not only highlights temporal trends but may also help identify drivers of change, thereby guiding targeted interventions to mitigate further declines (Perring et al. 2016). Nevertheless, even if it presents methodological shortcomings, such as relocation errors, it still represents one of the best methods currently available for monitoring vegetation changes (Verheyen et al. 2018; Douda et al. 2023).

In Europe, the ecological importance of coastal dune systems is formally recognized under the Habitats Directive (EEC 1992), which designates several dune habitats of Community interest. The Directive requires Member States to ensure their favourable conservation status through monitoring, protection, and restoration measures.

Sardinia, a Mediterranean hotspot of plant diversity (Médail and Quezél 1999), is internationally renowned for its coasts and beaches, many of which are in protected areas. In some northeastern and southeastern zones, access to approximately 20 beaches has been restricted; however, growing tourist flows urgently call for a regional plan to identify areas at risk of overtourism and promote sustainable tourism practices (Balletto et al. 2025).

Despite their conservation and economic importance, most Sardinian dune systems, although supported by a considerable amount of historical data, have not been recently monitored to assess long-term changes in vegetation.

Resurveying Sardinian dunes is thus essential for tracking long-term temporal trends in plant biodiversity and supporting successful conservation and restoration measures.

This article introduces the first regional database, Resurvey Sardinian Dunes (ReSarDu), compiled from resurveys of coastal dune systems across Sardinia (Italy). The database includes data from historical surveys dating back to the 1970s and from resurveys carried out at the same sites in 2023–2025.

Specifically, this paper aims to: (i) fill the knowledge gap relative to biodiversity changes in Mediterranean dune vegetation through the last decades; (ii) provide a further contribution to ReSurveyDunes (Acosta et al. 2025), the database of resurveyed coastal dune vegetation in Italy.

Database structure and content

For the resurvey, we selected 188 historical phytosociological relevés (hereafter old surveys) mainly distributed along the northeastern and southwestern Sardinian coasts (Fig. 1) and conducted between 1975 and 2005 (Fig. 2a). These old surveys were mainly extracted from

Figure 1. Location of vegetation surveys (red dots) included in ReSarDu database (Sardinia, Italy).

VegDunes database (Prisco et al. 2012), which includes data from several studies on Sardinian dune vegetation (De Marco and Mossa 1975; Brambilla et al. 1982; Valsecchi and Bagella 1991; Filigheddu and Valsecchi 1992; Mossa 1992; Mossa and Biondi 1992; Bartolo et al. 1992; Arrigoni 1996; Biondi et al. 2001; Biondi et al. 2004) integrated with other old published (Farris et al. 2013) and unpublished surveys. Each old survey was provided with standard information, plot size, survey date and assigned to the corresponding Annex I habitat according to Habitats Directive (92/43/EEC).

The old plots to be resurveyed were selected based on several attributes, such as location, to ensure maximum spatial distribution, and the possibility of identifying their position as precisely as possible. To achieve this objective, for example, all past surveys carried out by the surveyors involved in the resurvey campaign were included.

Among the 188 selected old surveys, 73 exhibited low relocation uncertainty and were consequently considered as performed in quasi-permanent plots. The remaining 115, lacking detailed location information, were considered as performed in non-traceable plots (Kapfer et al. 2017). For identifying plot locations when coordinates were unavailable, we relied on alternative sources, including locality descriptions, reference points provided in the original publication, or support from the surveyor who conducted the initial sampling.

For each non-traceable plot, following Ross et al. (2010), we carried out three resurveys in three different plots (hereafter called new plots). In total, we conducted 418 resurveys: 73 in quasi-permanent plots and 345 in the new plots, all accurately georeferenced with a Garmin Montana 680.

Resurveying was conducted between 2023 and 2025 considering the same plot area and season of the old surveys. The shape was mainly rectangular, following the distribution of vegetation along transects. The occurrence of all vascular plant species was recorded, and species abundance was visually estimated using the Braun-Blanquet seven-degree scale (Braun-Blanquet 1964). Taxonomic nomenclature was standardized according to the Euro+Med PlantBase (Euro+Med PlantBase 2025). To each new survey, the following additional information were associated: elevation, exposure, and slope.

Each new survey was assigned to a specific habitat type according to the EU Habitats Directive (92/43/EEC), based on the presence/abundance of typical or characteristic species (Biondi et al. 2009). The following habitat types were identified: 1210 – annual vegetation of drift lines, 2110 – embryonic shifting dunes, 2120 – shifting dunes along the shoreline with *Ammophila arenaria*, 2210 – *Crucianellion maritimae* fixed beach dunes and 2230 – *Malcolmietalia* dune grasslands. The surveys not classifiable to any habitat type were labelled as NC (Not Classifiable as habitat). The most represented habitat is 2120 (122 surveys), followed by 2110 (108 surveys). The largest share of old surveys derive from the 1981–1990 period (Fig. 2a). The most frequent survey sizes range from 11 to 50 m² (Fig. 2b).

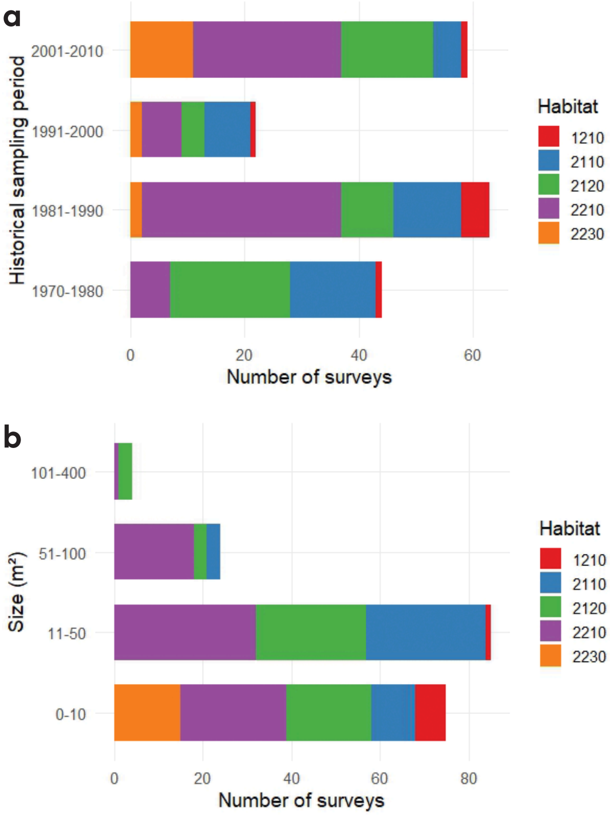

Figure 2. Number of old surveys in Sardinia (Italy) grouped by (a) sampling periods and (b) size (m²), and habitat types as defined in the Annex I of Habitats Directive (92/43/EEC): 1210 – annual vegetation of drift lines, 2110 – embryonic shifting dunes, 2120 – shifting dunes along the shoreline with *Ammophila arenaria*, 2210 – *Crucianellion maritimae* fixed beach dunes, and 2230 – *Malcolmietalia* dune grasslands.

Future perspectives

The ReSarDu database serves as a valuable resource for understanding long-term vegetation changes in Mediterranean coastal dune systems. By integrating historical and newly collected phytosociological data, we provide a comprehensive tool for assessing biodiversity trends and supporting effective conservation and restoration strategies. Being composed of georeferenced data, ReSarDu has the potential to help address existing knowledge biases regarding the flora of Sardinia (Bagella et al. 2020; Melis et al. 2025).

The database constitutes a reservoir of georeferenced plots that can be repeatedly monitored in the coming years, offering unique opportunities to investigate temporal trajectories of plant communities, assess the impacts of anthropogenic pressures and climate change, and evaluate the success of management actions.

The standardized structure of ReSarDu ensures compatibility and interoperability with national and international vegetation databases, such as ReSurveyDunes and ReSurveyEurope, thereby promoting data sharing and facilitating large-scale ecological analyses across Mediterranean coastal systems.

Authorship contribution

Bagella S., Caria M.C., Denaro A., Malavasi M.: Conceptualization. Bagella S., Caria M.C., Denaro A., Farris E., Malavasi M.: Methodology. Denaro A., Rivieccio G., Maccioni A., Farris E., Bagella S., Caria M.C., Fadda M., Bruno A., Malavasi M.: Investigation. Denaro A., Sperandii M.G., Malavasi M.: Data Curation. Bagella S., Denaro A.: Writing – Original Draft. All authors: Writing – Review & Editing. Farris E., Bagella S.: Funding Acquisition.

Competing interest

The authors declare that they have no conflict of interest. Simonetta Bagella is an Associate Editor, Alicia Teresa Rosario Acosta, Emmanuele Farris, and Maria Carmela Caria are part of the Editorial Review Board in Vegetation Ecology and Diversity but took no part in the peer review or decision-making process for this manuscript.

Data availability

By the end of the project, we plan to integrate ReSarDu into VegItaly database (GIVD: EU-IT-001). The data sharing will be fully accessible upon specific request to the database custodians (Agnese Denaro adenaro@uniss.it; Simonetta Bagella sbagella@uniss.it).

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