









UN DECADE ON ECOSYSTEM RESTORATION

RESEARCH ARTICLE

Ecosystem state assessment after more than 100 years since planting for dune consolidation

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The assessment of the ecosystem state is fundamental to understand the success of ecological rehabilitation, especially in the long term. We aim to evaluate the rehabilitation success of a unique Mediterranean dune system site along the Tyrrhenian coast of Italy which underwent a dune consolidation intervention and species planting at the beginning of the twentieth century after the destruction of the natural ecosystem. We used three nearby non-rehabilitated protected coastal sites with different degrees of disturbance as reference sites encompassing different potential rehabilitation outcomes of the target site. To assess the overall result of the intervention, we used several plant characteristics and measured taxonomic and functional beta-diversity between all sites. We compared the proportions of typical and ruderal species of dune habitat types across sites. We further used the species–area relationship to examine if the number of observed species in our sites differed from the expected. Our analyses revealed that the rehabilitated site was taxonomically and functionally more similar to the least disturbed site. We suggest that plant characteristics arising from botanical inventories can be fruitfully used in rehabilitation assessment as they value the taxonomic and functional species diversity at the community scale. We conclude that plant characteristics compared across sites are useful tools in ecosystem state assessment if they reflect the ecological functions and conservation values of the natural ecosystems.

Key words: functional beta-diversity, Mediterranean, plant characteristics, protected areas, rehabilitation, taxonomic beta-diversity

Implications for practice

- Ecosystem state assessment can rely on different plant characteristics derived from botanical inventories;
- Ecosystem state can be evaluated by comparing plant characteristics across sites;
- Taxonomic and functional compositional dissimilarities inform on the ecosystem state.

Introduction

There has never been a more urgent need to restore damaged ecosystems than now (United Nations 2021). Accordingly, restoration ecology is likely to be one of the most important fields of this century given the rising environmental concerns at the global scale (Hobbs & Harris 2001; Ripple et al. 2017; Zerbe 2019). In this context, coastal dunes are among the most threatened habitat in Europe (Gigante et al. 2018; Marcenò et al. 2018; Prisco et al. 2020) and the related concerns span from abiotic to biotic aspects (Martínez et al. 2013; Fantinato 2019). Although dune rehabilitation studies seem to be not particularly abundant in the literature (but see, e.g. Fernández-Montblanc et al. 2020; Yang & Chu 2020), various actions have been carried out in dune systems

(Grootjans et al. 2002; Pickart 2013; Ellison 2018), for example, to mitigate degradation related to trampling (Santoro et al. 2012a) or to recreate the initial dune topography, considering hydrodynamic, and morphodynamic aspects (Rozé & Lemauviel 2004; Fernández-Montblanc et al. 2020).

To evaluate rehabilitation success with clearly established criteria, SER Society for Ecological Restoration International Science and Policy Working Group (2004) offers a list of attributes that can be used to measure rehabilitation success. Among

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them, Lithgow et al. (2013) and Gann et al. (2019) reported that one of the easily measurable ecosystem attributes that can be used to monitor ecosystem recovery is community composition. However, also other quantitative indices and qualitative surveys, that is, the use of semi-structured interviews and questionnaires, including information retrieved by the local people, have been proposed (Johnston & Ellison 2014; Lithgow et al. 2014, 2020). Further, the application in the evaluation of rehabilitation results of species traits is receiving growing attention worldwide since these assessments should be informed by species characteristics (Gann et al. 2019; Carlucci et al. 2020). Community properties have also been suggested as effective in describing the habitat quality (Del Vecchio et al. 2016).

Long-term monitoring is needed to evaluate the progress and success of rehabilitation actions in coastal dune ecosystems (Gann et al. 2019). From this perspective, we used a unique Mediterranean rehabilitated dune system site along the Tyrrhenian coast of Italy. Until the sixteenth century, the target site, called Feniglia dune, was covered by Mediterranean macchia, that is, by evergreen sclerophyllous formations (Bellarosa et al. 1989; Andreucci 2004). The deforestation of the Feniglia Dune began in the eighteenth century. After complete deforestation, at the beginning of the twentieth century (1912–1915), the site underwent dune consolidation interventions and revegetation actions. Interestingly, revegetation measures totally lacked experimental guidelines at that time, that is, the interventions had no conservation purpose and were done in favor of more practical reasons. A previous study identified a general rehabilitation success of this site using a random stratified sampling design that compared the composition and structure of vegetation plots with nearby sites (Landi et al. 2012). Apart from this study, there are likely no studies assessing similar rehabilitation interventions over such a long period in Europe (but see Kollmann & Rasmussen 2012 for a different ecological context). Compared to Landi et al. (2012), our study uses a different approach by making use of the entire pool of species derived from botanical inventories instead of random vegetation plots. We tried this approach because the rehabilitated site and other dune sites along the Tuscan Tyrrhenian coast were subjected to intensive botanical explorations in the last two decades leading to the accumulation of a big amount of botanical data that can be now used to evaluate the rehabilitation success in terms of plant characteristics (*sensu* Garnier et al. 2017).

In the view of the UN Decade on Ecosystem Restoration, our aim is to evaluate the success of the rehabilitation interventions and of the overall ecosystem state of the rehabilitated (target) site, using botanical inventories that systematically encompass typical, endemic, alien, and ruderal species, and understanding the suitability of using environmental associations (*sensu* Garnier et al. 2017). We used three reference sites with different degrees of disturbance to compare them with the target site. Further, our study uses taxonomic and functional beta-diversity across sites, and species–area relationship. Based on a previous study (Landi et al. 2012), we expect that the rehabilitated site will be more similar to the least disturbed site. Specifically, we asked if all plant characteristics are informative for assessing rehabilitation success when used to compare the sites.

Methods

Study Area

The studied rehabilitated site is the state nature reserve of Feniglia Dune (hereafter RH; 42.419022N, 11.242731E), a 474 ha dune system located in southern Tuscany (Grosseto, Italy) and protected since 1971. It is a 1 km wide Holocene isthmus that stretches west–east for about 6 km, connecting the Italian Peninsula with Monte Argentario. The RH has a maximum width of 1.050 m and reaches up to 14 m a.s.l. in the highest parts. The site falls in the Mediterranean macrobioclimatic region, in the Pluvioseasonal oceanic bioclimate. It is characterized by a weak Euoceanic continentality, a lower mesomediterranean thermotype, and an upper dry ombrotype (Pesaresi et al. 2017). The current dominant vegetation on the stabilized dunes is represented by *Pinus pinea* forests and *Pinus pinaster*. The dune ecosystem hosts annual vegetation on the drift line and perennial plant communities colonizing embryonic and foredunes. A more detailed description of the vegetation types present is reported in Supplement S1.

From the restoration ecology perspective, RH is an interesting site to study. At different moments of history, important vegetation changes succeeded due to human interventions (Fig. 1). The site, originally covered by Mediterranean macchia, was later on completely degraded by human interventions with macchia removal. Then, trees, shrubs, and herb species, both native and alien, were planted. This information is based on descriptions of past authors who studied the site (Sforzi et al. 1914; Liguori 1928; Bellarosa et al. 1989, 1996; Andreucci 2004). A detailed history of RH is available in Supplement S1. The site hosts forest and non-forest communities on dunes. The true rehabilitated part of RH, main object of this study, is the non-forest one, including annual vegetation of drift line of the embryonic shifting dunes, and the shifting dunes along the shoreline with *Calamagrostis arenaria* subsp. *arundinacea* and *Juniperus* scrub. The current forest is an old-established pine plantation that is physiognomically different from the original macchia (Bonari et al. 2017).

To compare botanical inventories, we used plant species characteristics in RH and in other three selected nearby Tuscan dune sites within protected areas that are very similar in terms of the environment, vegetation, coast erosion history, and protection. However, we selected sites that differed in degrees of disturbance, acknowledged as a relevant factor in sandy coastal ecosystems (Buffa et al. 2012; Farris et al. 2013). We thus selected lowly, medium, and highly disturbed sites to understand which was the overall ecosystem state of RH 100+ years after dune rehabilitation. The sites (Fig. 2) are: (1) a highly unassisted natural site (hereafter LD: lowly disturbed site) Special Area of Conservation (SAC) called “Burano Lake dunes” (code IT51A0032). It is the first Italian WWF Oasis, opened in 1967. Since 1980, it became a State Nature Reserve and includes one of the best-preserved sectors of the Tuscan coast (Angiolini et al. 2002), with innerdune *Juniperus phoenicea* scrub and remnants of sclerophyllous Mediterranean forest dominated by *Quercus ilex* subsp. *ilex* and *Q. suber* and with no coastal dune afforestation; (2) a highly disturbed site (hereafter HD: highly disturbed site) called “Tomboli di Follonica e Scarlino.” It is a Nature Reserve situated in the proximity of a city area and is

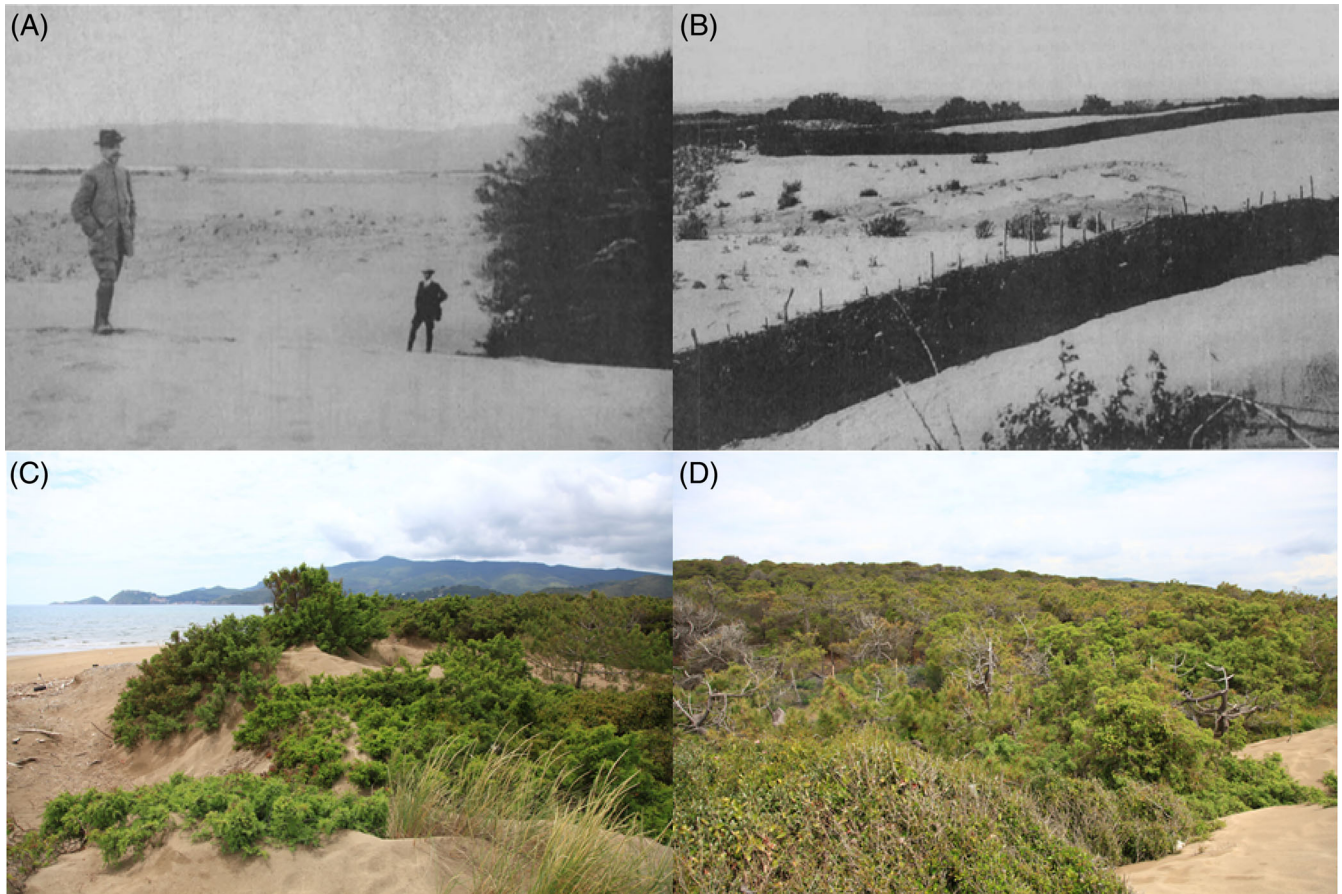


Figure 1. Dune rehabilitation works in 1911 (A, B) and a comparison with current vegetation (C, D). Photo A shows the Feniglia Dune before the tree planting; photo B shows the wind-break structures built within the Feniglia Dune; photo C *Calamagrostis arenaria* subsp. *arundinacea* in the foreground and *Juniperus macrocarpa* scrub and a part of the foredune in the background; photo D *Juniperus macrocarpa* scrub in the foreground and the old-established *Pinus pinea* forest in the background; photo credits: A and B from Liguori (1928), C and D by G. Bonari, April 2013.

heavily threatened by both human pressures, mainly tourism and urbanization, and coastal erosion (Sarmati et al. 2019). The demographic increase leads to the leveling of the dune reliefs, the burying of the wetlands behind the dunes, the enrichment of nutrients, the erosion for trampling, and mechanical cleaning of the beaches. As for RH, in this site (i.e. HD) pine afforestation occurred in the inner portion of the dunes since 1880; (3) a site with intermediate disturbance conditions (hereafter MD: medium-disturbed site) called “Coastal dunes of the Uccellina Park” (SAC code IT51A0015). The site is part of the Maremma Regional Nature Park since 1975. Here, the degree of disturbance is mainly natural and related to the natural floods (Arrigoni 2003), but also linked to the presence in the area nearby the park of intense agricultural activity and wild grazing. This site has also experienced pine afforestation in the inner portion of the dunes since the eighteenth century (Arrigoni 2003).

Data Preparation

The RH checklist resulted from surveys performed from 2014 to 2017 in all the seasons. For this site, we also prepared the list of

the species planted during the rehabilitation works (1912–1915) using several sources (Sforzi et al. 1914; Liguori 1928; Bellarosa et al. 1996), although for the reference sites LD and MD, we followed published checklists (Angiolini et al. 2002; Arrigoni 2003, respectively). The data from the site HD were our own unpublished botanical surveys from 2008 to 2013 and from 2018 to 2020.

We selected psammophytes defined by Ciccarelli et al. (2014) and checked the presence of the species in non-forest dune habitats at each site following Arrigoni (2003) and Angiolini et al. (2002), plus our field experience.

We obtained species life forms, chorological types and Ellenberg indicator values (EIVs) modified for Italy by Pignatti (2019). Concerning EIVs, we used light (L), temperature (T), moisture (M), reaction (R), nutrient (N), and salinity (S) expressed as integers. We did not retrieve EIVs for eight species and thus not used in particular analysis. Moreover, we discarded continentality EIVs as they are meaningless for peninsular Italy (Bonari et al. 2018). We prepared a list of typical dune and ruderal plant species at each site. Previous studies have demonstrated that these two groups of species are reliable

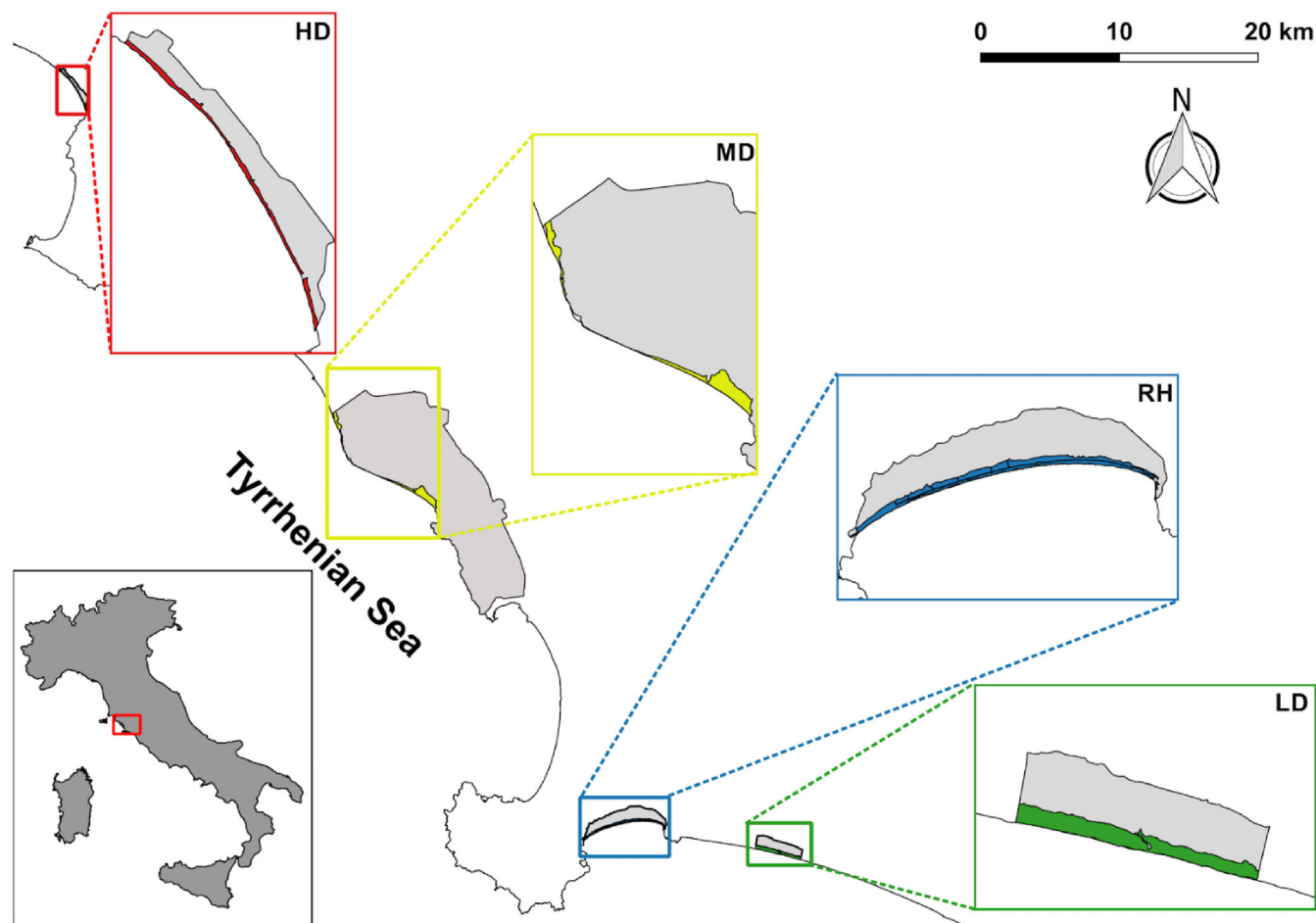


Figure 2. Target site (RH) and comparison sites (HD, MD, LD) along the coastline of Tuscany, with the location of the sites in Italy. The four boxes highlight the non-forest dune environments under study within the four protected areas (in gray). HD, highly disturbed site Tomboli di Follonica e Scarlino Nature Reserve (red); MD, medium-disturbed site Coastal dunes of the Uccellina Park (yellow); LD, lowly disturbed site Burano Lake Nature Reserve (green); RH, rehabilitated site Feniglia Dune (blue).

indicators for conservation and monitoring goals (Santoro et al. 2012b; Del Vecchio et al. 2013, 2015a; Prisco et al. 2016a; Angiolini et al. 2018). As typical species, we considered the diagnostic and characteristic species listed by the Interpretation Manual of Habitats Directive and further studies on dune habitat types (Biondi et al. 2009; Biondi & Blasi 2015; Angiolini et al. 2018; Sarmati et al. 2019; Sperandii et al. 2019). Ruderal species were identified based on previous studies on the Italian dune environments (Biondi et al. 2012c; Del Vecchio et al. 2016; Prisco et al. 2016a; Prisco et al. 2017). They are typically dominating a disturbed site (Biondi et al. 2012b; Prisco et al. 2016b).

Given their high conservation value, we also detected endemic taxa, according to Bartolucci et al. (2018). Conversely, as an indicator for a low conservation status of dune habitats (Del Vecchio et al. 2015a; Lazzaro et al. 2020; Prisco et al. 2020), along with ruderal species, we also used alien species, with their naturalization status (locally and in Italy) according to Galasso et al. (2018). Finally, we retrieved the known

introduction time at RH for native and alien species from Bellarosa et al. (1996).

Data Analysis

As the first step, we assessed the success of planting actions in RH at the site level, that is, considering forest and non-forest areas. To do so, we evaluated in our recent surveys whether native, especially psammophytes, and alien species were still present at the site after they were planted in 1912–1915.

Then, we focused only on the non-forest parts of the dunes. We calculated the positive and negative deviation in the percentage of expected versus observed number of species at each site and compared them. To do so, we used a formula proposed by D'Antraccoli et al. (2019). This formula is derived by a species–area relationship and provides constants for Tuscany that allow calculating the expected species numbers in any given area of Tuscany. We calculated the positive and negative deviation in the percentage of expected versus observed number of

Table 1. List of the species planted during the rehabilitation works according to Bellarosa et al. (1996), their alien status in the studied area according to Galasso et al. (2018) and their current presence in the study area. (*) = Strictly psammophyte species according to Pignatti (2019).

Species planted in rehabilitation works	Year(s) of introduction	Current presence
Native species		
<i>Cakile maritima</i> subsp. <i>maritima</i> (*)	1912	Yes
<i>Calamagrostis arenaria</i> subsp. <i>arundinacea</i> (*)	1912; 1914; 1930s	Yes
<i>Euphorbia paralias</i> (*)	1912	Yes
<i>Juniperus macrocarpa</i> (*)	1912–1915	Yes
<i>Medicago marina</i> (*)	1912	Yes
<i>Populus</i> spp.	Before 1915	Yes
<i>Tamarix africana</i>	1912–1915	Yes
Locally alien species		
<i>Eucalyptus</i> spp.	1912–1915	Yes
<i>Euonymus japonicus</i>	1912–1915	No
<i>Hesperocyparis arizonica</i>	Unknown	Yes
<i>Hesperocyparis macrocarpa</i>	Before 1915	Yes
<i>Juniperus virginiana</i>	Unknown	No
<i>Morus nigra</i>	1912–1915	No
<i>Myoporum insulare</i>	Unknown	No
<i>Myoporum</i> cfr. <i>tetrandum</i>	1912–1915	No
<i>Nerium oleander</i> subsp. <i>oleander</i>	1912–1915	No
<i>Olea europaea</i> subsp. <i>europaea</i>	1912–1915	Yes
<i>Pinus halepensis</i> subsp. <i>halepensis</i>	Before 1915	Yes
<i>Pinus pinaster</i>	1912	Yes
<i>Pinus pinea</i>	1912	Yes
<i>Pinus radiata</i>	Before 1915	No
<i>Robinia pseudoacacia</i>	1912–1915	Yes
<i>Sequoiadendron giganteum</i>	Unknown	No
<i>Ulex europaeus</i> subsp. <i>europaeus</i>	1912	Yes

species for all species, native species, and alien species using the extent of the non-forest dune area of each site.

To analyze the taxonomic and functional dissimilarities between RH and the other sites, we compared different plant characteristics (Garnier et al. 2017), such as life-form and chorological spectra, plant family, and EIVs, across sites. To quantify compositional differences between sites (i.e. RH, LD, MD, and HD), we calculated taxonomic ($\beta_{\text{sor-tax}}$) and functional ($\beta_{\text{sor-fun}}$) beta-diversity as pairwise dissimilarities between each pair of sites using Sørensen's dissimilarity index (Sørensen 1948). Both $\beta_{\text{sor-tax}}$ and $\beta_{\text{sor-fun}}$ were partitioned into two components: the turnover component ($\beta_{\text{sim-tax}}$ and $\beta_{\text{sim-fun}}$) and the nestedness component ($\beta_{\text{nes-tax}}$ and $\beta_{\text{nes-fun}}$) (see formulas in Baselga 2010; Leprieur et al. 2012). Although β_{sim} represents the true spatial replacement of species between sites without the influence of taxonomic and functional richness gradients, β_{nes} represents the differences in species and functional richness between sites that occur when species- and functional-poor sites are subsets of species- and functional-rich

sites. $\beta_{\text{sim-tax}}$ and $\beta_{\text{sim-fun}}$ are equal to 0 when two compared sites are identical in terms of shared species and functions, respectively, and values near 1 when two sites are completely distinct in terms of shared species or functions, respectively. In contrast, $\beta_{\text{nes-tax}}$ and $\beta_{\text{nes-fun}}$ are equal to 0 when the species and functions in the two sites are not a subset of each other, respectively, and values are near to 1 when the species and functions in the species- and function-poor site are a complete subset of the species- and function-rich site, respectively.

We calculated $\beta_{\text{sim-tax}}$ and $\beta_{\text{nes-tax}}$ using a site-by-species matrix and the beta.pair function in the R package “betapart” (Baselga & Orme 2012). For $\beta_{\text{sim-fun}}$ and $\beta_{\text{nes-fun}}$, we first constructed a functional dendrogram that estimates species functional differences in the trait space (Petchey & Gaston 2007). For this, we used species' EIVs as environmental association and computed Gower pairwise distances between species. The resulting functional dendrogram represents a continuous measure of functional dissimilarity, where species located at a greater distance in the dendrogram are more functionally dissimilar, whereas species located at a closer distance in the dendrogram are more functionally similar. Subsequently, we used the functional dendrogram and the site-by-species matrix to calculate $\beta_{\text{sim-fun}}$ and $\beta_{\text{nes-fun}}$ with the phylo.beta.pair function in R package “betapart” (Baselga & Orme 2012). Further, we also explored by means of linear regression if $\beta_{\text{sim-tax}}$ and $\beta_{\text{sim-fun}}$ varied as a function of geographical distances between sites. We generated all graphs with the R package “ggplot2” (Wickham 2009). All analyses were performed in R v.3.5.3 (R Core Team 2019).

Results

All the five strictly psammophytes planted in RH during the rehabilitation works were still present (Table 1).

The RH non-forest dune checklist included 90 plant taxa and 72 genera, whereas LD had 208 taxa, HD 131 taxa, and MD 142 taxa. Endemics were 1 in RH, 3 in LD, 0 in HD, and 3 in MD.

We compared the proportion of life forms, chorological types, main families, typical, and ruderal species, across sites (Fig. 3). We found that RH was most similar to HD in terms of representation of life forms. These two sites basically differed in the proportion of hemicryptophytes (Fig. 3A). LD was differentiated by the greatest proportion of therophytes (50%) and the lowest of chamaephytes (6%) (Fig. 3A).

The chorological spectrum showed that RH, together with LD, had the lowest proportion of species linked to anthropogenic disturbance as alien and widely distributed species (13 and 14%, respectively; Fig. 3B). Considering the taxonomic spectrum of families, Poaceae showed similar values across all sites. Poaceae, Asteraceae, and Fabaceae were the most represented families at all sites except for RH, where Brassicaceae replaced Fabaceae (Fig. 3C).

Furthermore, RH exhibited the lowest proportion of ruderal species (9% of the RH flora), whereas the maximum was in HD sites (31% of the HD flora). Typical species represented 52% of the RH flora, whereas in the LD, HD and MD they

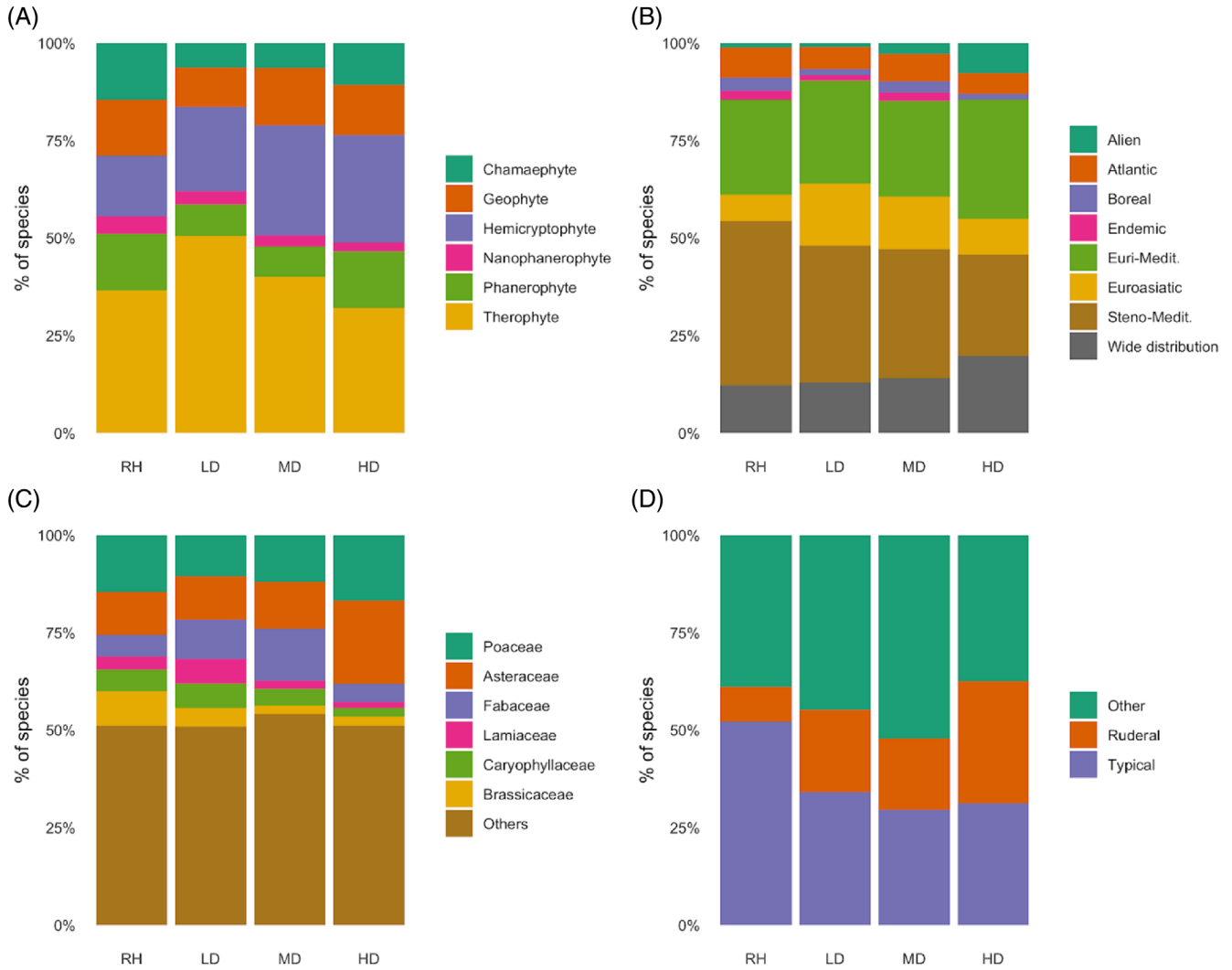


Figure 3. Percentages of life forms (A), chorological types (B), the main six families (C), and ruderal-typical ratio (D) across the sites. Different tones show different categories.

reached very similar percentages (34, 31, and 30%, respectively; Fig. 3D).

Most of the percentages of variation in expected versus observed number of species, both native and alien, were negative across species categories, with RH showing the highest negative values. The only exception was in HD, which showed a positive variation in the number of alien species (Fig. 4).

The lowest taxonomic ($\beta_{sim-tax}$) and functional ($\beta_{sim-fun}$) turnover occurred between RH and LD. These two sites also presented the highest taxonomic ($\beta_{nes-tax}$) and functional ($\beta_{nes-fun}$) levels of nestedness. The contribution of each EIV trait on the functional turnover ($\beta_{sim-fun}$) and nestedness ($\beta_{nes-fun}$) between RH and all other sites is reported in Supplement S1, Table S1.

The $\beta_{sim-tax}$ and $\beta_{sim-fun}$ as a function of geographical distances between sites were not significant and are reported in Supplement S1, Figure S1.

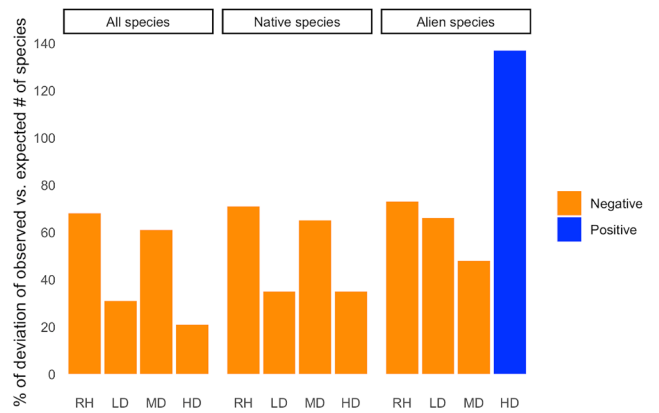


Figure 4. Positive or negative percentage of deviation in expected vs. observed species number per site considering all species, native species and alien species.

Discussion

The first result that emerges from our study when examining if planted species in 1912–1915 still occur in the rehabilitated site is that all psammophytes originally planted are still present. However, this result should also be interpreted considering that native species such as *Cakile maritima*, *Euphorbia paralias*, and *Medicago marina* are very pioneer species, mainly spread by the sea current and are able to colonize degraded dune systems. On the other hand, the survival of shrubs and trees, including alien species, had a less clear pattern. The low survival of alien species might depend also on other determinants than species origin, for example, harsh environmental conditions. However, the use of alien species for rehabilitation actions is not recommended (Funk et al. 2008). Our findings suggest that the selection of the species for rehabilitation purposes should take into account the ecology and biology of the taxa, especially to prevent the spread of alien species in threatened habitats with high conservation value such as dunes.

Our results provide evidence that the rehabilitation works of the target site were useful in terms of ecosystem recovery and the current ecosystem state of the non-forest dune part is overall good. Our study corroborates the strategy of comparing multiple reference sites to evaluate rehabilitation success and ecosystems state (Gallego-Fernández et al. 2011; Jaouadi et al. 2017). Although, few studies in coastal environments have used more than one site, likely because suitable reference sites are difficult to find (Lithgow et al. 2013; Gerwing & Hawkes 2021). As expected, our results using different ecological indicators at the site level brought us to similar conclusions of a previous study in the same rehabilitated site using vegetation-plot data (Landi et al. 2012), namely that the rehabilitated site was the most similar to the least disturbed one. This might also be linked to the fact that the rehabilitated site shows natural dune vegetation succession (Angiolini et al. 2013).

Our study shows that the use of botanical inventories, although not always fully available for all sites, is generally appropriate to assess the success of ecosystem rehabilitation. However, these data, unless they are for example protected areas with recurrent plant surveys and samplings, might be lacking. Despite that, when available, the use of several plant characteristics derived from botanical inventories allows objective number-based comparisons among sites offering a framework for a detailed assessment of the rehabilitation success. Having at disposal the list of species permits a comprehensive assessment of its community composition and diversity, which in turn allows a robust inference on its ecological integrity. Starting from the botanical inventory of species it is possible to generate a series of additional key information. Thus, this tool results fundamental for ecosystem state assessment. For example, the checklist of plant species warrants to work not only with the dominant species but also with the most common species. This translates into obtaining important ecological indications also from non-dominant scarcely present species, which, however, may be functionally relevant and powerful site indicators, for example, typical, diagnostic, or even flagship species. To some extent, these categories of species can be recorded also with

vegetation plots, but the probability of not recording them during the sampling is higher, especially because not always the sampling effort (and design) is adequate due to time/resource constraints (Zhang et al. 2014; Hoffmann et al. 2019; Ståhl et al. 2020).

Notably, not all the plant characteristics well differentiated the sites. Overall, our study highlights that some environmental associations, such as chorological forms, EIVs, or the presence of typical dune and alien species, provide valuable insights for the rehabilitation assessment, whereas some others, such as the most represented families or life forms, are less informative. In particular, the proportion of families and life forms across sites did not accurately discriminate the sites along the gradient of disturbance. Nevertheless, on the one hand, main families agreed with the whole Italian dune flora, whereas, on the other hand, life forms informed on the structure of the vegetation but they were not necessarily linked to the rehabilitation process, but more likely, to localized site conditions, for example, presence of the grassland in the semi-fixed dune (Ciccarelli et al. 2014; Croce et al. 2019; Muñoz-Reinoso 2021). Moreover, differences in endemics were also rather uninformative. This can be related to the fact that endemic species of the Tyrrhenian dunes are relatively low in number (Ciccarelli et al. 2014; Pignatti 2019).

We found that the number of observed species was generally lower than that of expected species across all sites of our study. Dune environments are stressful habitats and the number of occurring species on dune might be intrinsically low (Angiolini et al. 2018). All the Tuscan coast holds 704 species in the coastal dune ecosystem (Ciccarelli et al. 2014). As elsewhere in the Mediterranean region, also the Tuscan coast is eroding (Ciccarelli 2015; Garcia-Lozano et al. 2018), and this constantly contributes to reducing the available physical space for dune plant species. Optimally, a rehabilitation that engages natural processes can improve beach resilience to erosion and reduce or prevent further erosion (Ellison 2018). However, the higher negative value of the HD site across all species categories, that is, all taxa, native taxa, and alien taxa, when compared to RH, provide further support that rehabilitation worked well in the target site, although there can still be ecological niches for more species. However, we speculate that this might also be due to an impoverished seed bank. In addition, some species could be missing from RH because of the pine afforestation, which occupied the physical space of some psammophilous species (Leege & Kilgore 2014; Muñoz-Reinoso 2021). In support of this hypothesis, the LD site, which was not subjected to pine afforestation in the back dune, showed a lower deviation in the number of expected versus observed number of native species. By contrast, the HD site showed more aliens than expected due to the high level of disturbance.

Our study demonstrates that an assessment of the rehabilitation success can be carried out by comparing the taxonomic and functional composition of the different sites. In particular, our results showed that the target site is generally taxonomically and functionally more closely related to the least disturbed site. In most cases, the lowest taxonomic turnover and the highest levels of taxonomic nestedness occurred between the target site

and the LD site, suggesting that the two sites have similar nested species composition, especially in terms of typical and alien species, as also partially confirmed by other analyses. This key result highlights that since rehabilitation, the ecological level reached by the target site is at least as good as the most natural site we used for comparison. Previous studies suggested that the functional composition of the native community is likely to be more important than community diversity (e.g. species richness; Funk et al. 2008). In our study, we found congruent patterns between taxonomic composition (both the turnover and nestedness components) and functional composition between the target site and the LD site, suggesting that on these two sites the replacement of species is also accompanied by changes in their functions. In turn, this also suggests that the target site can be less susceptible to invasions, as there is likely lower functional space available for incoming aliens (Funk et al. 2008) and it is, therefore, less prone to functional homogenization (Tordoni et al. 2019). However, it is reasonable to believe that the rehabilitated site has had enough time to recover from its degradation. There are cases in the literature that report 10 years of establishment as not enough for a successful rehabilitation evaluation (Wilkins et al. 2003). Here, more than 100 years seemed a realistic time to regain the original ecological quality as a result of rehabilitation activity. Importantly, these efforts were coupled with effective conservation strategies. The presence of the nature reserve also played an undoubtedly important positive role for rehabilitation success and for the ecosystem maintenance.

The main limitation of our study is represented by the fact that we cannot be sure that the reference sites have the same abiotic environments. Although this is a common drawback of field studies, we cannot be sure whether the differences between the target site and the reference sites are due to different management. In addition, we are aware that we cannot be fully sure that our findings are entirely caused or triggered by the interventions. It is complicated, if not impossible, to disentangle the active effect of the rehabilitation and that of the shift of species composition due to vegetation succession, intended as a passive process (Acosta et al. 2013). It is worth mentioning that dune systems can exhibit shifts in plant species composition within 20 years (Del Vecchio et al. 2015b). Additionally, the effect of coastal sea currents and subsequent distribution of the sediments or even historical processes or dispersal may have acted in shaping the checklists we analyzed. After so many years, a protected site might have potentially become taxonomically and functionally good also if unassisted. Further, the calculation of expected species number across all sites has to be interpreted carefully, because the constant parameters we have used to produce these results are calculated from a number of Tuscan floras that span over different environments and are therefore not specifically calibrated for dune environments. Lastly, the fact that the target site is generally taxonomically and functionally similar to the least disturbed site could partially be explained by their spatial proximity, although we found no overall direct relationship between spatial distance and taxonomic and functional similarities. Accordingly, the above discussion has to be interpreted carefully taking into consideration such precautions.

Our findings provide insights into the possibilities of implementing rehabilitation assessments based on plant characteristics derived from botanical inventories. We suggest that plant characteristics can be fruitfully used in rehabilitation assessment as they value the taxonomic and functional species diversity at the community scale. Yet, we stress the importance of an accurate selection of the comparison sites, possibly encompassing different potential rehabilitation outcomes of the target site (Gerwing & Hawkes 2021).

In summary, using different taxonomic and functional components can open new scenarios that permit quantifying the repair of a site or of a habitat, thus assessing the recovery of ecosystem functioning. Lastly, we suggest that the ecosystem state of a site can be evaluated by comparing plant characteristics, including their environmental associations, across sites, if they reflect the ecological functions and conservation values of the natural ecosystems.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1: Main vegetation types present in the target site (RH)

Table S1: Functional turnover ($\beta_{sim-fun}$) and nestedness ($\beta_{nes-fun}$) between RH and all other sites.

Figure S1: Pairwise geographic distances between sites against taxonomic (A) and functional (B) dissimilarities.

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