

**Doctoral School in Molecular, Cellular and Environmental
Biology**
XXXII Cycle (A.A. 2018/2019)



**Investigating patterns and drivers of temporal changes
in taxonomic and functional diversity of coastal
habitats**

Dinamiche temporali nella diversità tassonomica e funzionale di
habitat costieri

Marta Gaia Sperandii

Tutor: Prof. Alicia Teresa Rosario Acosta



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A mio zio Claudio.

I died for Beauty — but was scarce
Adjusted in the Tomb
When One who died
for Truth, was lain
In an adjoining room

He questioned softly "Why I failed"?
"For Beauty", I replied
"And I — for Truth — Themself are One
We Brethren, are", He said

And so, as Kinsmen, met a Night
We talked between the Rooms
Until the Moss had reached our lips
And covered up — our names

Emily Dickinson (1830 -1886)

“Sono tempi difficili, lo so, ma non cedete alla rassegnazione, non abbandonate la speranza, mai! Neppure per un attimo. Anche quanto tutto sembra perduto, e i mali che affliggono l'uomo e la terra sembrano insormontabili, cercate di trovare la forza, e di infonderla nei vostri compagni.
E' proprio nei momenti più bui che la vostra luce serve. E ricordate che ogni tempesta comincia con una goccia. Cercate di essere voi quella goccia”.

Lorenzo “Orso” Orsetti (1986 - 2019)

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Abstract

We live in a time of global biodiversity crisis, with anthropogenic forces transforming the structure, functioning and productivity of natural systems. Quantifying the extent of temporal changes in ecological communities is therefore a shared priority of worldwide conservation agendas.

Due to their unique features, coastal dunes are contemplated among the most interesting ecosystems on earth. However, they are currently exposed to a number of threats globally affecting their conservation status. In the Mediterranean region, uncontrolled urbanization and population growth characterizing the last 70 years led to a progressive deterioration of coastal dune ecosystems and to a severe reduction in their extent. Several European coastal dune habitats have been recently assessed by the Red List of European Habitats as either endangered or vulnerable, and their conservation status in Italy largely reflects the European picture. Identifying the most endangered habitats and monitoring their dynamics are key research tasks that cannot be further procrastinated, if we want to avoid a complete disappearance of these ecosystems in the near future. In this study, I provide a comprehensive assessment of temporal changes characterizing Mediterranean coastal dune habitats in the last 10-15 years by using different approaches (a diachronic analysis of a random-plot database and a resurveying study), analyzing multiple dimensions of diversity (i.e. taxonomic and functional), and investigating multiple levels of biological organization (i.e. community and species).

I started by performing a diachronic analysis of a large database of random, standardized, georeferenced plots. Using linear and generalized linear models I explored temporal trends in species richness and cover of targeted sandy habitats, investigated trends in the cover of selected psammophilous native species and assessed temporal patterns of invasion. This diachronic analysis revealed concerning changes involving dune grasslands, where a negative trend in species richness and habitat cover emerged. At the same time, results hinted at “early warnings” of degradation processes in shifting dunes, where a decline in the cover of the sand-binding *Ammophila arenaria* subsp. *australis*, and a parallel increase in the cover of *Carpobrotus* sp. were recorded.

Then, I planned a large resurveying study which led me to revisit and resample 334 plots belonging to the first portion of coastal zonation (from the upper beach to coastal dune grasslands) in the course of two sampling seasons.

With the data collected during my first sampling season I tested the effectiveness of resurveying approaches based on quasi-permanent plots in revealing temporal changes in herbaceous communities of Mediterranean coastal dune systems. In particular, I quantified compositional shifts using Sørensen index of dissimilarity, I applied a partitioning method to determine whether observed change was driven by species turnover or by a “nestedness” effect, and I analyzed changes in the occurrence and cover of diagnostic species of the investigated habitats. Together with the disappearance of about 25% of historical plots, results revealed major transformations, mainly driven by species turnover, affecting most of the communities (especially upper beach, embryo and mobile dunes) and several of their diagnostic species.

After the second field season, I analyzed the complete set of resurveyed data to provide a comprehensive, habitat-based (*sensu* Annex I 92/43/EEC), multi-dimensional assessment of temporal changes spanning across multiple levels of biological organization (community and species). Specifically, I quantified taxonomic changes in community composition and dominance structure using two dissimilarity metrics reflecting local immigration and extinction processes known under the general term “species exchange ratio”. To assess functional shifts over time I used functional dissimilarity and community weighted mean (CWM) values. Taxonomic and functional dissimilarities were then compared among habitats and tested for significance using null models. Finally, I characterized changes at the level of single species by analyzing species-abundance distributions at both time points (T_0 and T_1) and by testing changes in occurrence frequency and cover by mean of non-parametric tests. I could observe considerable changes involving both the taxonomic and the functional spheres, varying among habitats but acting at most levels: from the community level to that of single species. This, together with the disappearance of 78 out of the 334 historical plots and with observed changes often exceeding “simulated changes”, confirmed preliminary results and highlighted an intense vulnerability of upper beach and shifting dunes.

Overall, this study provided a detailed, habitat-based quantification of the transformations experienced by coastal dune plant communities in the last 10-15 years. Along with enhancing the knowledge of recent dynamics affecting these vulnerable environments, it also proved that resurveying studies based on quasi-permanent random plots are effective tools for monitoring coastal dune ecosystems, even when based on short-to-medium time-spans. Finally, it allowed identifying specific EU Habitats that appear to be particularly at risk, thus supplying an important resource to direct future conservation efforts and management strategies.

Riassunto

In pochi secoli, l'azione di una sola specie, la nostra, ha prodotto devastanti trasformazioni sull'intera biosfera, scatenando una crisi ecologica di proporzioni globali. Le ripercussioni sono ormai visibili a differenti scale spaziali e livelli di organizzazione biologica: l'uomo sta modificando i sistemi naturali alterandone la struttura, il funzionamento e la produttività.

In questo contesto, quantificare il cambiamento ed indagarne le cause sono obiettivi specifici di una recente disciplina conosciuta con il nome di "ecologia temporale", e rappresentano al contempo priorità condivise dalla scienza della conservazione.

Sebbene la devastante azione dell'uomo sia ormai rintracciabile in tutti gli ambienti naturali, alcuni sono stati particolarmente colpiti. Tra questi troviamo le dune costiere, elementi di confine tra l'ambiente marino e quello terrestre, considerate tra gli ecosistemi naturali più interessanti in assoluto per via di una notevole eterogeneità in termini di habitat e per la presenza di una flora e fauna altamente specializzate. Nonostante l'elevato valore naturalistico e gli innumerevoli benefici (i.e. servizi ecosistemici) connessi alla presenza di questi ambienti, il loro stato di conservazione è praticamente ovunque molto critico. In area mediterranea, l'aumento di popolazione caratterizzante l'ultimo dopoguerra, unito ad una conseguente diffusa urbanizzazione, ha contribuito a causarne un progressivo deterioramento ed una grave riduzione in superficie. Conseguentemente, diversi habitat di duna costiera sono stati recentemente classificati come "minacciati" o "vulnerabili" dalla Lista Rossa Europea degli Habitat, ed il loro stato di conservazione in Italia riflette largamente la situazione europea. Pertanto, non solo il monitoraggio temporale delle dinamiche ecosistemiche, ma l'identificazione delle comunità le cui condizioni appaiono più critiche sono obiettivi urgenti, che non possiamo ulteriormente posticipare se vogliamo evitare la definitiva scomparsa di questi preziosi ambienti.

Con questo studio si propone un'analisi dei cambiamenti che hanno interessato le comunità vegetali di duna costiera dell'Italia centrale negli ultimi 10-15 anni, e si evidenziano in via preliminare alcuni dei potenziali fattori determinanti questi cambiamenti. A questo fine, si è deciso di lavorare a scala di comunità e di singole specie, esaminando i profili tassonomico e funzionale ed utilizzando due approcci: l'analisi diacronica di una grande banca dati vegetazionale e la realizzazione del primo studio di rivisitazione basato su rilievi georeferiti e campionati in modo non preferenziale ("random") in ambiente dunale. Quest'ultimo, in particolare, mi ha portata a rivisitare 334 rilievi, originariamente campionati tra il 2002 ed il 2007 in

diversi sistemi dunali dell'Italia Centrale (Lazio e del Molise), e rappresentativi della prima fascia della zonazione costiera (dalla spiaggia emersa fino ai pratelli dunali terofitici).

Il primo capitolo di questa tesi è dedicato all'analisi diacronica di "RanVegDunes", una corposa banca dati contenente, all'epoca di questo studio, circa mille rilievi floristici di dimensioni standard (4m²), georeferiti e campionati in maniera non-preferenziale. Ai fini di questa analisi sono stati utilizzati 858 rilievi rappresentativi della maggior parte degli habitat di duna costiera (dalla spiaggia emersa agli arbusteti mediterranei a *Cistus* sp.pl.) campionati, ciascuno una sola volta, nel periodo compreso tra il 2002 ed il 2015 in diversi sistemi dunali compresi in 5 regioni amministrative (Lazio, Campania, Abruzzo, Molise, Puglia). L'utilizzo di tecniche di regressione multipla (*linear model* e *generalized linear model*) ha permesso di estrarre tendenze temporali caratterizzanti numerose variabili oggetto d'indagine. Quest'analisi ha evidenziato, nella finestra temporale considerata, una significativa riduzione nella ricchezza specifica e nella copertura dei pratelli dunali terofitici (Habitat 2230 - Dune con prati dei Malcolmietalia), ulteriormente supportata dalla diminuzione in copertura di due specie diagnostiche di questa comunità: *Cutandia maritima* e *Medicago littoralis*. Diverse altre specie diagnostiche hanno mostrato, nel corso degli anni, una simile tendenza negativa, segnalando incipienti fenomeni di degrado ambientale. L'analisi dei *pattern* temporali di invasione ha fornito tuttavia i risultati più interessanti: la copertura di specie appartenenti al genere *Carpobrotus*, non-nativo e particolarmente dannoso in ambiente dunale, è risultata in aumento nelle comunità di avanduna, dove si è verificata una simultanea diminuzione nella copertura di *Ammophila arenaria* subsp. *australis*, specie diagnostica dell'habitat e fondamentale per via del suo ruolo nel processo di formazione e stabilizzazione delle dune. Quest'analisi ha confermato la validità, in ambiente dunale, del metodo diacronico basato su plot *random*, offrendo al contempo un panorama informativo, sebbene preliminare, delle principali tendenze temporali caratterizzanti gli ambienti di duna costiera nel periodo analizzato.

Il secondo capitolo illustra i primi risultati ottenuti analizzando i dati raccolti durante la prima delle due stagioni di campo interessate dello studio di rivisitazione. In particolare, 188 rilievi ri-campionati sono stati confrontati con i loro corrispondenti storici: è stata condotta un'analisi di dissimilarità volta da un lato a quantificare il cambiamento, e dall'altro ad isolare il contributo relativo di due dei principali fenomeni determinanti la dissimilarità di comunità biologiche: lo "*species turnover*", ovvero la sostituzione di specie e la "*nestedness*", un fenomeno per cui una comunità

rappresenta un sottoinsieme di un'altra comunità. I risultati hanno tracciato un quadro molto negativo: più del 20% dei rilievi originali è scomparso, risultando completamente privo di vegetazione o addirittura sommerso. Le restanti comunità vegetali sono risultate molto trasformate e lo “*species turnover*” è risultato la forza motrice di questa trasformazione, che ha colpito particolarmente la vegetazione della spiaggia emersa ed il complesso dell'avanduna (dune embrionali e dune mobili). Ulteriori analisi condotte sulle specie diagnostiche hanno confermato questa tendenza, evidenziando una forte riduzione nella presenza di specie chiave come *Elymus farctus* ed *Ammophila arenaria* subsp. *australis*. Oltre a fornire stime preliminari di cambiamento inerenti la diversità tassonomica, questo lavoro ha permesso di testare l'appropriatezza dell'approccio di rivisitazione in ambienti dunali e su scale temporali considerate di breve-medio periodo.

Il terzo capitolo, infine, sintetizza i risultati dello studio di rivisitazione proponendo un quadro esauriente delle trasformazioni subite negli ultimi 10-15 anni dalle comunità vegetali di duna costiera, classificate in termini di Habitat di Direttiva (ex Allegato I della Direttiva 92/43/CEE). In particolare, si descrivono i cambiamenti nelle sfere tassonomica e funzionale, se ne testa la significatività simulando comunità fittizie attraverso l'uso di *null models*, e contemporaneamente si utilizzano indici e descrittori informativi del cambiamento in molteplici componenti ed a diversi livelli di organizzazione della diversità biologica. Nel confermare quanto accennato all'interno del Capitolo 2, i risultati dipingono una situazione particolarmente drammatica, caratterizzata da 78 (su 334) rilievi spariti e considerevoli trasformazioni nel profilo tassonomico e funzionale di molte comunità, spesso significativamente maggiori di quelle simulate dai modelli. Le diverse analisi condotte concordano nell'individuare gli habitat 1210 “Vegetazione annua delle linee di deposito marine” e 2120 “Dune mobili del cordone litorale con presenza di *Ammophila arenaria* (dune bianche)” come i più colpiti. Per quanto riguarda le comunità della spiaggia emersa (Habitat 1210), si perdono più del 60% dei plot originali. Nei superstiti, una forte diminuzione delle specie diagnostiche (cf. *Cakile maritima*, *Salsola kali*, *Chamaesyce peplis*), viene compensata da un aumento in specie perenni caratteristiche delle dune embrionali (cf. *Elymus farctus* and *Lotus cytisoides*), suggerendo l'azione di dinamiche successionali verificatesi in siti particolarmente conservati o meno esposti ai fattori di disturbo. Il quadro appare ancora più critico nelle dune mobili, dove sono evidenti fenomeni di degradazione dell'habitat efficacemente sintetizzati dall'analisi funzionale, che riscontra una significativa diminuzione nell'altezza media della vegetazione campionata nei rilievi, un aumento nell'area fogliare specifica, ed un crollo nella

proporzione di specie perenni. La conferma arriva dall'analisi tassonomica: *Ammophila arenaria* subsp. *australis* diminuisce, in termini di presenze, dell'80% e viene sostituita da *Elymus farctus*, si perdono diverse altre perenni caratteristiche dell'habitat (*Medicago marina*, *Eryngium maritimum*, *Anthemis maritima*) ed al loro posto compaiono terofite (cf. *Vulpia fasciculata*).

In conclusione, questo lavoro fornisce una valutazione dettagliata dei cambiamenti che nel corso degli ultimi 10-15 anni hanno interessato diversi habitat di duna costiera dell'Italia centrale. Seppur con qualche differenza, i diversi approcci hanno evidenziato forti trasformazioni attribuibili a fenomeni di degrado ambientale, particolarmente gravi negli ambienti della spiaggia emersa ed ancor più nelle dune mobili. Benché analisi dettagliate volte all'indagine dei fattori determinanti il cambiamento siano ancora in corso, osservazioni fatte in campo ed analisi preliminari hanno permesso di individuare quattro presunti responsabili: l'erosione, le attività connesse al turismo (pulizia meccanica, calpestio), l'urbanizzazione e la diffusione di specie invasive. In questo contesto, l'individuazione di alcuni habitat come maggiormente "a rischio" costituisce un'utile risorsa per indirizzare future strategie di conservazione, gestione e ripristino di questi ambienti.

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Sperandii M.G., Bazzichetto M., Gatti, F. & Acosta A.T.R. (2019). Back into the past: Resurveying random plots to track community changes in Italian coastal dunes. *Ecological Indicators*, 96: 572-578.

Sperandii M.G., Bazzichetto M., Acosta A.T.R. Barták V. & Malavasi M. (2019). Multiple drivers of plant diversity on coastal dunes: A Mediterranean experience. *Science of The Total Environment*, 652: 1435–1444.

Sperandii M.G., Barták V., Carboni M., Acosta A.T.R. Save the last stands: multi-dimensional assessment of temporal changes in Mediterranean sandy habitats. (in prep).

Sperandii M.G., Barták V., Acosta A.T.R. Are protected areas really doing their job? Effectiveness of the Natura 2000 network in conserving biodiversity of Mediterranean coastal dune ecosystems. (in prep).

Bazzichetto, M., **Sperandii**, M.G., Malavasi, M., Carranza M.L. & Acosta, A.T.R. Disentangling the effect of erosion and accretion on coastal dune plant communities. (in prep.)

GENERAL INTRODUCTION

Humans are transforming the biosphere at an alarming, unprecedented rate, up to the point of scientists renaming our current geological era as “Anthropocene”. Although official start dates of the Anthropocene are still debated (Zalasiewicz, 2015) a much more general agreement concerns its consequences. Anthropogenic forces, spanning across biological and spatial scales, are modifying our natural systems by altering their structure, their functioning and their productivity (Vitousek et al., 1997). In this context, quantifying such alteration and understanding its driving forces are crucial tasks in the protection and management of natural systems, and are therefore at the core of the emerging branch of temporal ecology (Wolkovich et al., 2014).

Assessing temporal changes in vegetation communities

Three broadly defined alternatives exist for quantifying temporal changes in plant communities, which are: a) extracting temporal trends out of large vegetation databases; b) installing and monitoring permanent plots; c) resurveying historical plots. All these methods have their pros and cons, and are highly different in terms of reliability and costs.

Extracting temporal trends out of large vegetation databases is a “low-cost” solution: it can yield relatively robust results, but precautions should be taken and results should be interpreted with care (Jandt et al., 2011; Chytrý et al., 2014). The main advantage of this method is that, as it doesn’t require additional fieldwork, it is particularly time- and resource-saving. Moreover, diachronic studies of this type can count on a vast amount of vegetation data (mostly, phytosociological) collected over the last century and readily available for many regions and many habitats (Chytrý et al., 2014). Such method, however, does not allow direct comparisons of old and new vegetation plots, as these were sampled in different locations. For the same reason, recorded transformations could be partially due to pseudo-turnover related to the different spatial position of the plots, making more difficult the detection of real change. Permanent plots, on the other hand, probably constitute the most precise tool to detect temporal changes at the local scale. In this case, direct comparisons between old and new plots are possible and, as their position is permanently marked on the field, the use of permanent plots allows to basically exclude the bias deriving from relocating the plot (i.e. relocation bias). Nevertheless, permanent plots can be highly resource-

intensive and, consequently, they are not so numerous and their coverage is in most cases spatially limited and not homogeneous (Bakker et al., 1996; Hédél et al., 2017). Moreover, most permanent plots were subjectively placed, with the aim of documenting vegetation succession, in sites where a change was expected to occur. Thus, if the aim is the assessment of medium-to-large scale vegetation change, analyzing a composite set of permanent plots could overestimate the general trend (Chytrý et al., 2014). For these reasons, resurveying studies (i.e. studies where historical plots are relocated and resurveyed by the same or by other authors) are considered in many contexts as the most appropriate and reliable method for detecting past vegetation change, also given the incredibly large availability of historical data, their extensive coverage (both geographically and in terms of habitats and community types), and their wide time-span due to the long tradition of vegetation-plot surveys (Chytrý et al., 2014; Hédél et al., 2017; Kapfer et al., 2017). Resurveying studies can be classified according to how detailed the information about original plot location is. To this regard, Kapfer et al. (2017) makes a distinction between “*non-traceable*” and “*quasi-permanent*” plots: non-traceable plots are those for which no specific information on the original location is available, and can thus only be relocated to physically and environmentally homogeneous areas. Quasi-permanent plots, on the other hand, are those with an approximate location, that can be relocated in the field using geographical coordinates.

Resurveying studies: how to cope with undesirable variability

Indeed, resurveying studies represent an effective compromise between the uncertainty related to the use of large databases for extracting temporal trends and the resources (time, financial costs) needed to install and monitor a network of permanent plots (which can be considered as a “special” type of resurveyed plots). However, they are also subject to some intrinsic error, which is basically related to their relocation (i.e. relocation bias), to the variability among surveyors (i.e. observer bias) and to temporal variability (i.e. seasonality). Except for permanent plots, a certain degree of relocation bias is always present within a resurveying study. This, however, has been shown to decrease with decreasing spatial heterogeneity of the studied vegetation (Kapfer et al., 2017), is obviously lower in quasi-permanent plots (in comparison to non-traceable plots) and decreases with increasing sample size. Unwanted variability in the form of “pseudo-turnover” can also arise when historical plots are not resurveyed by the original surveyors (which is

often the case). However, this observer bias is also known to decrease with decreasing spatial heterogeneity of the studied vegetation (Kapfer et al., 2017). Finally, changes in the phenological stage of the vegetation can also be a source of bias which can, however, be reduced by resurveying plots in a phenological period comparable to the historical survey. Although a complete removal of these biases is almost impossible to achieve, most of the times they can be estimated (e.g. Archaux et al., 2006; Ross et al., 2010) and some precautions and expedients can be adopted to successfully minimize them. Overall, whereas perfection is rarely attainable, the art of making vegetation resurveys is all about retaining an acceptable degree of error, as wisely pointed out by Hédél et al. (2017).

High-quality data always pays off

Much of the effectiveness of resurveying studies depends on the quality of historical data. In this regard, quasi-permanent plots probably feature the best trade-off, in terms of both costs and relocation bias, between permanent plots and non-traceable plots.

However, another important distinction should be made according to the original sampling strategy. Although phytosociological plots constitute an invaluable, incredibly rich source of information in vegetation science (especially in Europe, see Schaminée et al., 2009; Dengler et al., 2011), most of them were sampled preferentially and include inconsistencies in concepts and methods of sampling within single datasets (Chytrý, 2001), thus belonging to that kind of ecological data that does not fulfill statistical assumptions (e.g. independence of observations) necessary for valid statistical testing and inference (Botta-Dukát et al., 2007; Lájer, 2007). Moreover, as according to the Braun-Blanquet approach relevés were arbitrarily selected in the field to find the most “typical” example of a vegetation type, an assessment of change based on this kind of data would not be very representative of the overall trend of a particular vegetation type, but it would only highlight changes in sites that at the time of the original survey were particularly “typical” and “well-conserved”. These biases can be avoided using random plots, which appear as a much more statistically robust and representative source of information for resurveying studies. That being said, random plots are not a panacea. As plot location is “randomly” chosen, random plots will include, next to the “typical” aspect of a vegetation type, all its other shades. For this reason, resurveying studies based on random plots should count on relatively large sample sizes. Also, since vegetation

scientists started using random plots only in recent times, they still cover a relatively constrained time-span if compared to phytosociological plots.

The importance of a comprehensive approach

An important aspect that should be considered when assessing temporal changes is that biodiversity is a complex and multi-dimensional construct composed of many components (e.g. richness, relative abundance, composition, occurrence of key species) differently affecting ecosystem properties (Hooper et al., 2005). Thus, no single indicator can exhaustively summarize its change. Although biodiversity assessments have been traditionally limited to taxonomic diversity (and, more specifically, to species richness), a number of studies in recent years highlighted the need of overcoming this approach by performing “multi-dimensional research” (i.e. research where two or more dimensions of biodiversity are simultaneously investigated, see Devictor et al., 2010; Magurran & Dornelas, 2010; Naeem et al., 2016). In this context, the functional aspect turned out to be essential, as it allows understanding community assembly processes as well as ecosystem functioning (Díaz et al., 2007; De Bello et al., 2010). Another important research challenge, especially relevant in temporal ecology, is the inclusion of several levels of biological organization when analyzing data, as they all contribute to community dynamics. In this regard, as individual species within a community exert varying impacts on different ecosystem functions and processes, many studies started using selected species, known as “key” or “diagnostic” species, for analyzing the quality of plant communities and detecting early warning of habitat disruption (Del Vecchio et al., 2016; Angiolini et al., 2018). Finally, a valuable though unfortunately often neglected approach consists of linking single components of biodiversity to landscape spatial patterns. By testing the influence of landscape metrics/processes (e.g. habitat fragmentation, changes in land use) on community changes, this method can provide an informative picture on the drivers of change.

Why coastal dunes?

Although 80% of the terrestrial biosphere shows more or less evident signs of human transformations (Ellis & Ramankutty, 2008), some regions have been affected more than others. This is the case for coastal areas, where

intense socio-economic development, coupled with population growth and migrations (Neumann et al., 2015), is imposing serious pressures on sandy beach and dune ecosystems, which are now trapped in a so called “coastal squeeze” between urbanization impacts on the terrestrial side and climate change effects on the marine side (Schlacher et al., 2007; Defeo et al., 2009). Although covering a relatively small portion of the earth’s surface, coastal dune ecosystems are largely recognized for their outstanding conservation value. In these dynamic environments, a severe gradient, produced by the simultaneous action of a set of environmental drivers, creates a precise sequence of ecologically distinct plant communities, ideally running perpendicular to the sea and commonly known as “coastal zonation” (Doing, 1985; Acosta et al., 2007). Along with a highly specialized and adapted flora, often including rare and endangered species (Acosta et al., 2009), these communities provide suitable habitats to an important fauna, mainly composed of invertebrates, amphibians and reptiles (Doody, 2012).

Beyond their conservation value, coastal dunes provide essential ecosystem services, ranging from protection against storms and floods up to climate regulation, groundwater storage and nutrient recycling (Everard et al., 2010; Arkema et al., 2013). Additionally, dunal landscapes offer recreation and therapeutic opportunities related to their aesthetic values (Nordstrom, 2004). Nevertheless, coastal dunes are currently listed among the most vulnerable ecosystems worldwide (Schlacher et al., 2007; Defeo et al., 2009), their main threats including sea level rise (Neumann et al., 2015), coastal erosion (Feagin et al., 2005), urbanization (Malavasi et al., 2013), pollution (Poeta et al., 2014) and other related human pressures (Calvão et al., 2013).

In the Mediterranean, uncontrolled urbanization and population growth characterizing the recovery from World War II led to a progressive deterioration of littoral landscapes, ultimately resulting in diffused fragmentation, biodiversity and habitat loss (Curr et al., 2000; Malavasi et al., 2013; Garcia-Lozano et al., 2018). It has been estimated that, during the previous century, European dune systems reduced their cover of about 70% (Brown & McLachlan, 2002). As a result, several coastal dune habitats have been recently classified by the Red List of Habitats as either endangered or vulnerable (Janssen et al., 2016). Widely reflecting the European situation, the conservation status of Italian dune habitats (referring to the years 2007-2012) based on the Third National Report under Article 17 of the Habitats Directive has been assessed as largely unfavorable. In particular, the conservation status of Mediterranean embryonic and shifting dunes was evaluated as “Unfavorable-Bad”, while that of coastal dune grasslands was assessed as “Unfavorable-Inadequate”, with all the habitats featuring a stable

trend since the previous Report (referring to the years 2001-2006). At the same time, future predictions of their status are also alarming, with shifting and fixed dunes projected to lose most of their distribution area in the near future (Prisco et al., 2013).

In this context, to reverse the negative trend and avoid a complete disappearance of coastal dune habitats, monitoring their changes and assessing the conservation status through time becomes a matter of utmost importance.

Multi-temporal studies in coastal dune habitats: where are we?

Until the beginning of this project, most multi-temporal studies in Mediterranean coastal dune environments had been performed at the landscape scale using remotely sensed data (Drius et al., 2013; Malavasi et al., 2013; Bertacchi & Lombardi, 2014). By analyzing large spatial extents, these studies are particularly effective for tracking changes in habitat cover, and are therefore able to identify processes such as fragmentation or habitat loss. However, they don't provide specific information about changes in the structure and composition of individual plant communities, which can only be obtained through field surveys. At the community scale, the most relevant contribution in this sense comes from Prisco et al. (2016a), who detected consistent temporal changes in the vegetation cover of sandy coastal habitats and of selected species through the analysis of a large phytosociological database. Resurveying studies, on the other hand, were mostly lacking. The only studies of this type had been either performed on small areas or analyzed short-term data, and they anyway mostly involved the revisitation of phytosociological plots (cf. Del Vecchio et al., 2015; Prisco et al., 2016b).

In this framework, extensive resurveying studies using high-quality historical data and investigating multiple facets of change across different organizational levels were actually lacking, and this is how this project came into being. Taking advantage of a large coastal vegetation database including almost 1000 georeferenced, randomly sampled 4m² plots surveyed since 2002 using a standardized methodology by members of the Vegetation Ecology Lab coordinated by Prof. A.T.R. Acosta, I planned a large resurveying study to quantify temporal changes experienced by coastal dune habitats of Central Italy in the last 10-15 years. Indeed, due to their highly dynamic nature, even short time-spans can be enough to track vegetation changes in coastal dune ecosystems (Prisco et al., 2016b). An extensive record of plant traits data, collected in the same areas covered by this

resurveying study by members of the lab over the years, further allowed me to analyze functional shifts in the communities.

Aims

This study intends to provide an exhaustive assessment of temporal changes characterizing coastal dune habitats in the last 10-15 years, while highlighting the role of some potential drivers. This should be attained by using different approaches (a diachronic analysis of a random plot database and a resurveying study), by analyzing multiple dimensions of diversity (i.e. taxonomic and functional), and by investigating multiple levels of biological organization (i.e. community and species). To accomplish such a challenging task, I proceeded through the following aims:

- 1) provide a first and preliminary assessment of changes in Italian coastal dune habitats by extracting temporal trends out of a large database of random, standardized, georeferenced plots (**Chapter 1**). Here, I focused on analyzing changes in species richness and cover of targeted sandy habitats, I investigated trends in the cover of selected psammophilous native species and, finally, I assessed temporal patterns of plant invasion.
- 2) test the effectiveness of resurveying studies based on quasi-permanent, random plots by using preliminary data obtained through the resurveying study. In particular, I quantified community changes in species composition, verified whether the change was driven by real “species turnover” or by a “nestedness effect”, and identified trends in diagnostic species (**Chapter 2**).
- 3) quantify patterns of temporal changes in taxonomic and functional diversity of EU coastal dune habitats (*sensu* Annex I 92/43/EEC) using the complete set of resurveyed data (**Chapter 3**). Specifically, to give a comprehensive picture of change I assessed compositional shifts and functional dissimilarity, and tested their significance using null models. Then, I investigated transformations in the dominance structure of the communities and in their species abundance distributions, and quantified shifts in their community weighted means. Finally, I assessed changes in occurrence frequency and cover of individual key species.

Chapter I

Hard times for Italian coastal dunes: insights from a diachronic analysis based on random plots

Hard times for Italian coastal dunes: insights from a diachronic analysis based on random plots

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Abstract Multi-year temporal studies are invaluable tools for monitoring changes in biodiversity through time. However, their applications in coastal ecosystems are still scarce. We investigated temporal trends in coastal dunes analyzing a set of 858 randomly-sampled georeferenced relevés performed between 2002 and 2015 along Central Italy’s sandy coastlines. Specifically, we explored changes in species richness and cover of targeted sandy habitats, we investigated trends in the cover of selected psammophilous native species and we assessed patterns of invasion by means of regression techniques. We observed a significant decrease in species richness and cover of the dune grasslands habitat. The species-level analysis confirmed a negative trend for two characteristic species of dune grasslands, *Cutandia maritima* and *Medicago littoralis*, while revealing a similar decline for *Crucianella maritima* and for *Ammophila arenaria* subsp. *australis*, key species of mobile dunes. The most striking trends emerged analyzing patterns in the cover of an invasive alien species, *Carpobrotus* sp., which showed a concerning increase in shifting dunes. In conclusion, our analyses reveal concerning changes involving dune grasslands, and at the same time hint at “early warnings” of degradation processes traceable in shifting dunes.

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Introduction

Although occupying a relatively small portion of the earth's surface, coastal dunes feature high ecological diversity, hosting a striking number of habitats considered to be relevant to international conservation goals (Janssen et al. 2016) along a well-described zonation running perpendicular to the coastline (Van der Maarel 2003; Acosta et al. 2009; Miller et al. 2010; Isermann 2011; Fenu et al. 2013; Ciccarelli 2015; Bazzichetto et al. 2016). Nevertheless, they appear to be threatened worldwide mainly due to coastal erosion (Feagin et al. 2005), urbanization, (Malavasi et al. 2013), pollution (Poeta et al. 2014, 2016) and other related human pressures. It has been estimated that, during the previous century, European dune systems reduced their cover of about 70% (McLachlan and Brown, 2006; Buffa et al. 2012). Additionally, a number of studies already reported on the vulnerability of coastal dune communities to biological invasions (Bruno et al. 2004; Vilà et al. 2006; Carboni et al. 2010; Del Vecchio et al. 2015a). In particular, it has been observed that in Mediterranean ecosystems species belonging to the genus *Carpobrotus* manifested an invasive behaviour (D'Antonio et al. 1993; Vilà et al. 2006; Traveset et al. 2008; Jucker et al. 2013; Novoa et al. 2013).

At present, it is known that habitat loss, land-use change and invasive species are causing a steady acceleration in the global rate of species extinction (Vellend et al. 2013), and there is growing consensus about biodiversity loss affecting ecosystem functioning, ecosystem services and generally, threatening human well-being (Díaz et al. 2006; Cardinale et al. 2012). In this context, diachronic studies are considered to be powerful tools for monitoring changes in biodiversity, exploring the causes beyond those changes and assessing the conservation status of particular habitats (Pignatti and Pignatti 2014; Del Vecchio et al. 2015b; Gigante et al. 2016; Prisco et al. 2016a). However, although recent years have witnessed a growing interest in the field of diachronic studies, such approaches appear to be still applied rather scarcely to highly dynamic ecosystems such as coastal dunes.

In Italy, multi-temporal analyses in coastal environments have been carried out at a landscape scale, mostly making use of remote sensing data (Drius et al. 2013; Bertacchi and Lombardi 2014; Malavasi et al. 2016). On the other hand, community-based approaches have been adopted within restoration projects (Landi et al. 2012), short-term monitoring and re-visitation studies conducted in relatively small study areas (Del Vecchio et al. 2015b; Prisco et al. 2016b). However, all these studies are either conducted at a local scale or focus on relatively short time-spans (but see Landi et al. 2012). In this context, to gain further understanding of temporal dynamics and to efficiently evaluate conservation measures, long-term monitoring studies performed at regional scale are urgently needed. A relevant contribution in this sense can be found in Prisco et al. (2016a) who detected consistent temporal changes in the vegetation cover of sandy coastal habitats and of selected species through the analysis of an extensive collection of phytosociological data. Nevertheless, caution is necessary when extracting temporal trends from vegetation databases since temporal analyses unfortunately fall outside the purposes for which phytosociological surveys were originally designed (Michalcová et al. 2011). This being said, potential sources of bias deriving from phytosociological data such as preferential

sampling, uneven sampling intensity and different plot sizes (Jandt et al. 2011), can all be avoided making use of random standardized plots.

Diachronic studies might also act as a valuable resource when assessing temporal trends in plant invasion. In fact, evaluating invasion levels of different habitats over time can provide a better understanding of invasion dynamics as well as deliver useful insights about risk levels faced by different plant communities in the long term (Medvecká et al. 2014; Del Vecchio et al. 2015a). Given the high dynamism characterizing these endangered environments, such information appears to be particularly significant in coastal dune systems. Nevertheless, except for a study conducted by Del Vecchio et al. (2015a, b), to our knowledge no specific effort has been dedicated to assessing temporal dynamics of invasion in coastal ecosystems until now.

Thus, the use of a diachronic approach providing a comprehensive understanding of both plant communities and invasion dynamics, can ultimately contribute to the achievement of conservation goals in coastal ecosystems. On this basis, this paper aims to investigate temporal trends in relatively recent Holocenic dunes of central Italy, by means of both a habitat- and a species-approach, through the use of a random georeferenced vegetation database consisting of data gathered between 2002 and 2015. In particular, we intend to (i) analyze changes in plant species richness and cover of the main sandy habitats (sensu Habitats Directive 92/43/CEE and EUNIS classification), (ii) identify trends in the cover of selected native target species, (iii) evaluate tendencies in the richness of alien taxa and in the cover of one of the most abundant exotic plants in coastal dune environments, *Carpobrotus* spp.

Materials and methods

Study area

In this study, we focused on sandy coastal ecosystems of Central Italy. In particular, sampling activities were carried out in sandy beaches located in 5 Italian administrative regions (Lazio, Campania, Abruzzo, Molise and Puglia). Throughout the study area, vegetation was recorded across the whole coastal zonation, thus including upper beach, embryo dunes, shifting dunes, dune grasslands, wooded dunes and Mediterranean forests.

Habitats and species data

The analyses performed within the present study were conducted using standardized randomly-sampled georeferenced relevés stored in the “RanVegDunes” database (Sperandii et al. 2017). This database includes georeferenced floristic relevés, each sampled once between 2002 and 2015 in different spatial locations along Central Italy’s sandy coastlines. It should be pointed out that relevés were not performed every year, but are only available for 10 years between 2002 and 2015. Vegetation data collected in the field were stored in Turboveg (Hennekens and Schaminée 2001) where, along with the list of recorded species and their relative abundances, additional information were entered for each plot such as geographical coordinates, a Habitat code assigned using the Interpretation Manual of the 92/43/EEC Habitats Directive (Biondi et al. 2009) and a level 3-EUNIS code (attributed according to a correspondence table developed by the Italian National

Institute for Environmental Protection and Research, ISPRA—http://www.isprambiente.gov.it/files/biodiversita/Tabella_Corrispondenze_181213.xls).

From “RanVegDunes” we extracted a set of 858 standardized, 4 m² relevés (hereafter, plots), available for ten years included in the previously mentioned 2002–2015 time-span, and referring to herbaceous and shrub formations. Selected plots were distributed across four EUNIS types (Table 1): B1.1—Sand beach drift lines, B1.3—Shifting coastal dunes, B1.4—Coastal stable dune grassland and B1.6—Coastal dune scrub. We chose to adopt level 3-EUNIS categories as reference units for conducting analyses at the community level as this system represents the standard classification for European habitats, and at the same time, by adopting a commonly accepted nomenclature, allows easier comparisons of the results between European countries (Medvecká et al. 2014). It is worth noting that some plots could not be assigned to a specific EUNIS type and were therefore labeled as “NOT CLASSIFIABLE” (hereafter, NC). NC plots included two different groups: (i) plots particularly rich in alien species ($\geq 20\%$ of alien cover, tagged as “invaded”) and (ii) plots performed in highly disturbed sites (tagged as “disturbed”), whose ascription to a single EUNIS type turned out to be unfeasible due to their hosting assemblages of species belonging to a mosaic of different habitats.

Table 1 EUNIS type, EU habitat category, description of the community and target species selected for this study

EUNIS type	EU habitat (ex Annex I 92/43/EEC)	Habitat description	Target species
B1.1 Sand beach drift lines	1210 Annual vegetation of drift line (upper beach)	Pioneer annual formations characterizing the strandline zone of the beach	<i>Cakile maritima</i> subsp. <i>maritima</i> , <i>Salsola kali</i>
B1.3 Shifting coastal dunes	2110 Embryonic shifting dunes (embryo dune)	Pioneer, perennial community of the low embryo-dunes dominated by <i>E. farctus</i>	<i>Elymus farctus</i> subsp. <i>farctus</i> , <i>Anthemis maritima</i> , <i>Medicago marina</i> , <i>Sporobolus virginicus</i> , <i>Cyperus capitatus</i>
	2120 Shifting dunes along the shoreline with <i>Ammophila arenaria</i> (mobile dune)	Seaward and semi-permanent cordons of dune systems dominated by <i>Ammophila arenaria</i> subsp. <i>australis</i>	<i>Ammophila arenaria</i> subsp. <i>australis</i> , <i>Echinophora spinosa</i> , <i>Anthemis maritima</i> , <i>Medicago marina</i>
B1.4 Coastal stable dune grassland	2210 <i>Crucianellion maritimae</i> fixed beach dunes	Chamaephytic community of the inland side of fixed dunes dominated by <i>Crucianella maritima</i>	<i>Crucianella maritima</i> , <i>Cutandia maritima</i> , <i>Medicago littoralis</i> , <i>Lotus cytisoides</i> , <i>Ononis variegata</i> , <i>Vulpia fasciculata</i>
	2230 <i>Malcolmietalia</i> dune grasslands	Annual, species-rich community colonized by small terophytes in dry, interdunal depressions of the coast	
B1.6 Coastal dune scrub	2250 Coastal dunes with <i>Juniperus</i> spp. (juniper scrub)	Shrub formations dominated by juniper on the fixed dunes	<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>
	2260 <i>Cisto-Lavanduletalia</i> dune sclerophyllous scrubs	Shrub formations dominated by sclerophyllous species	<i>Pistacia lentiscus</i> , <i>Phillyrea angustifolia</i>

To explore temporal trends in the cover of single species we selected 17 species among those regarded as diagnostic in each considered Annex I EU habitat, provided they were adequately represented in our database (see Supplementary material for details). Diagnostic species are considered to be playing a crucial role in supporting both the structuring and functioning of their reference habitat, and we identified them following Biondi et al. (2009). Concerning alien species, we decided to focus on *Carpobrotus acinaciformis* and *Carpobrotus edulis*, clonal South African succulents originally introduced as ornamentals and for preventing erosion (Castro-Díez et al. 2016), widely naturalized not only in Italian coasts (Carranza et al. 2010; Jucker et al. 2013) but also in other coastal habitats around the world (D'Antonio et al. 1993; Traveset et al. 2008; Vilà et al. 2006). Because of unresolved issues in the taxonomy of the species, in the present study they will be considered as a single taxon, namely *Carpobrotus* sp.. Plant nomenclature follows Conti et al. (2005).

Statistical analysis

Trends in species richness and cover over time, along with temporal patterns of invasion, were investigated by means of regression techniques (linear models and generalized linear models, but see next paragraphs for detailed explanations) chosen according to a number of response variables. In each of the models, EUNIS type was included as interaction term with sampling year in order to accommodate for patterns of species richness and vegetation cover characterizing different habitats of the coastal zonation. However, level 3-EUNIS types often include more than one vegetation unit, i.e. phytosociological syntaxa corresponding to Annex I EU Habitats (see Table 1). In order to assess which of the underlying psammophilous community was actually driving the change, new models including EU Habitat (see Table 1) as interaction term were fitted in case of statistically significant trends being detected at EUNIS level. Slope parameters (β values) were extracted from each model and used as a means to quantify temporal changes in target communities and species. All models were fitted in R (package: stats; R Core Team 2016). Overdispersion was calculated for each Poisson generalized linear model performing a dispersion test (package: AER; R Core Team 2016).

Model assumptions were evaluated by visually inspecting residual plots, which come as standard output of the models, and by checking for normality, homoscedasticity, and independence. Overall, model fit was assessed by means of an AIC-based approach. In particular, AIC values of each model (or QAIC in case of Quasi-Poisson models) were compared with those extracted from their corresponding intercept-only models, with the model showing the lowest AIC being the best (Burnham and Anderson 2003). Finally, correlograms were used to evaluate any remaining spatial dependencies among the residuals from the various models (R package “spdep”).

Habitat changes in richness and cover

Species richness was calculated for each plot as the total number of species recorded. Generalized linear models (GLMs) following a Poisson distribution and a log-link function (“glm” function; R Core Team 2016) were fitted, using species richness as response variable and sampling year as predictor. In case of overdispersion being detected, models were corrected using a quasi-Poisson error distribution.

Cover values were computed for each plot summing up the percentage cover of each species present in the plot. Note that, since this value can exceed 100% ground cover, we resolved to rescale cover values between 0 and 1 dividing each cover value by the maximum for each species. Then, on rescaled cover values we applied a logit-transformation to normalize model residuals. Linear models (“lm” function; R Core Team 2016) were then fitted using rescaled cover values as response variable and sampling year as predictor.

Cover changes of native target species

Temporal changes in the cover of native target species were explored using a subset of 754 relevés (excluding NC plots). For each species we rescaled cover values over the years between 0 and 1. Then, in order to investigate if and how their abundance changed over time, for each target species we fitted linear models (“lm” function; R Core Team 2016) using rescaled logit-transformed cover values as response variable and sampling year as predictor.

Temporal patterns of invasion

We investigated temporal patterns of invasion examining changes both in the richness of alien species and in the cover of the most abundant exotic species in our database, *Carpobrotus* sp.. After identifying alien species according to Celesti-Grapow et al. (2009), alien species richness (calculated as the total number of alien taxa) and *Carpobrotus* sp. cover values were computed for each plot. Then, following the same approach we described above, we applied generalized linear models (“glm” function; R Core Team 2016) to alien species richness and linear models (“lm” function; R Core Team 2016) to *Carpobrotus* cover values.

Finally, it should be noted that as “NC” relevés consisted of both “invaded” and generically “disturbed” plots, temporal trends of invasion were further explored within this category. In particular new models where “plot status” (i.e. disturbed or invaded) was included as interaction term were ran on “NC relevés” for both alien species richness and *Carpobrotus* sp. cover.

Results

Habitat changes in richness and cover

Between 2002 and 2015, a significant decrease in species richness could be identified in EUNIS type B1.4 only, while no relevant trend could be otherwise detected (Table 2; Fig. 1a). As EUNIS type B1.4 includes plots belonging to EU Habitat 2210 (*Crucianellion maritima* fixed beach dunes) and EU Habitat 2230 (*Malcolmietalia* dune grassland), a second GLM was run only on EUNIS B1.4 plots. The use of EU Habitat as a covariate allowed us to identify EU Habitat 2230 as being responsible for the decreasing trend observed at EUNIS level (estimate: -0.028 ± 0.010 ; $p: 0.006$; Fig. 1b).

Temporal trends in habitat cover highlighted no significant change except for EUNIS type B1.4 (Table 3; Fig. 2a). As in the previous case, in order to find out to which community was actually driving the trend, we fitted a second linear model (only selecting

Table 2 Changes in the richness of selected EUNIS types over time

GLM quasipoisson (eunis/anno -1)	Trend	Estimate	SE	<i>p</i> value
eunisB1.1:year	↑	0.032	0.017	0.064
eunisB1.3:year	↓	− 0.006	0.007	0.379
eunisB1.4:year	↓	− 0.024	0.009	0.008
eunisB1.6:year	↑	0.018	0.010	0.063
NC:year	↓	− 0.002	0.014	0.863

Statistically significant changes are reported in bold
 NC not classifiable plots

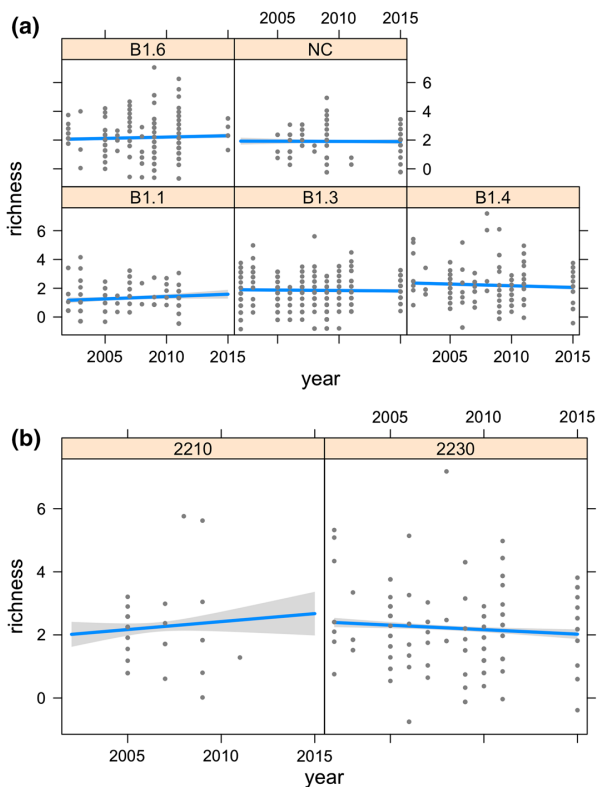
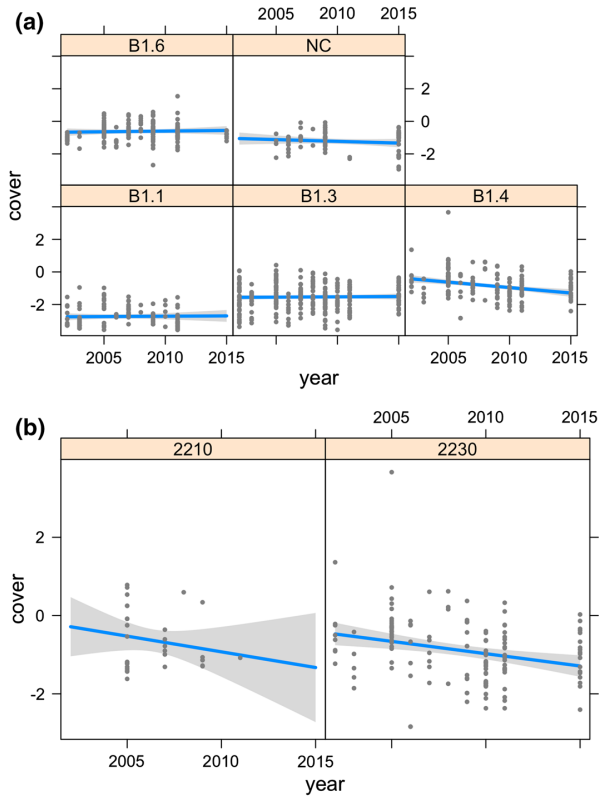


Fig. 1 Changes in the richness of EUNIS types over time (a) and in the two EU habitats included in EUNIS type B1.4 (b)

Table 3 Changes in the cover of selected EUNIS types over time

	LM (eunis/year – 1)	Trend	Estimate	SE	<i>p</i> value
	eunisB1.1: year	↑	0.004	0.020	0.841
	eunisB1.3: year	↑	0.004	0.011	0.722
	eunisB1.4: year	↓	– 0.067	0.016	< 0.001
Statistically significant changes are reported in bold	eunisB1.6: year	↑	0.008	0.017	0.64
NC not classifiable plots	NC: year	↓	– 0.021	0.021	0.312

**Fig. 2** Cover changes in EUNIS types over time (a) and in the two EU habitats included in EUNIS type B1.4 (b)

EUNIS B1.4 plots) including EU Habitat as interaction term. This second model indicated *Malcolmietalia* dune grasslands as driving the previously detected negative trend (estimate: -0.0673 ± 0.019 ; p : 0.001; Fig. 2b).

Table 4 Changes in the cover of target species over time (only significant trends are showed)

Species name	Annex I EU habitat	Level 3—EUNIS type	Estimate	Trend	<i>p</i> value
<i>Ammophila arenaria</i> subsp. <i>australis</i>	2120	B1.3	− 0.068	↓	< 0.001
<i>Anthemis maritima</i>	2110, 2120	B1.3	0.038	↑	0.041
<i>Medicago marina</i>	2110, 2120	B1.3	− 0.028	↓	0.015
<i>Crucianella maritima</i>	2210	B1.4	− 0.126	↓	< 0.001
<i>Lotus cytisoides</i>	2110, 2120	B1.3	0.053	↑	< 0.001
<i>Vulpia fasciculata</i>	2230	B1.4	0.066	↑	< 0.001
<i>Cutandia maritima</i>	2230	B1.4	− 0.099	↓	< 0.001
<i>Medicago littoralis</i>	2230	B1.4	− 0.073	↓	< 0.001
<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	2250	B1.6	− 0.083	↓	< 0.001

Cover changes of native target species

During the time-span considered, 9 out of the 17 selected species showed a significant change in their cover (Table 4, Supplementary material 1). In particular, 6 out of 9 species featured a negative trend, the greatest loss being encountered by *Crucianella maritima*, an endangered chamaephyte characterizing transition dunes. A similar pattern could be detected for *Ammophila arenaria* subsp. *australis*, key species of mobile dunes, for *Medicago marina* and for therophytes belonging to dune grassland habitats such as *Cutandia maritima* and *Medicago littoralis*. A marked decline over time was also observed for *Juniperus oxycedrus* ssp. *macrocarpa*, an evergreen shrub which dominates the landscape of wooded dunes, while no peculiar change could be noticed among the species characterizing the upper beach (*Cakile maritima*, *Salsola kali*). As for species featuring a positive trend, *Lotus cytisoides* and *Anthemis maritima* are perennial forbs of shifting coastal dunes habitats, while *Vulpia fasciculata* is an annual herb growing in dune grasslands.

Temporal patterns of invasion

During the time-span considered, alien species showed a significant decrease only in NC plots (estimate: − 0.198 ± 0.041; *p*: 0.000). Another GLM built up using “plot status” as covariate suggested “disturbed” plots as driving the negative trend (Table 5).

Table 5 Temporal changes in the richness of alien species, according to “plot status” (disturbed –DIST-, or invaded –INV-)

GLM poisson (status/year − 1)	Trend	Estimate	SE	<i>p</i> value
Statusdist: year	↓	− 0.219	0.052	< 0.001
Statusinv: year	↓	− 0.059	0.108	0.582

Statistically significant changes are reported in bold

Table 6 Temporal changes in the cover of *Carpobrotus* sp., according to EUNIS type

	LM (eunis/year – 1)	Trend	Estimate	SE	<i>p</i> value
	eunisB1.1: year	↑	0.000	0.019	1.000
	eunisB1.3: year	↑	0.051	0.010	< 0.001
	eunisB1.4: year	↑	0.004	0.015	0.776
Statistically significant changes are reported in bold	eunisB1.6: year	↑	0.014	0.017	0.401
NC not classifiable plots	NC: year	↓	– 0.359	0.020	< 0.001

Table 7 Temporal changes in the cover of *Carpobrotus* sp. according to “plot status” (disturbed –DIST-, or invaded –INV-) in NC (not classifiable) plots

LM (status/year – 1)	trend	Estimate	SE	<i>p</i> value
Statusdist: year	↓	– 0.210	0.033	< 0.001
Statusinv: year	↑	0.381	0.113	0.001

Statistically significant changes are reported in bold

The analysis of changes in the abundance of *Carpobrotus* sp. over time produced two significant results (Table 6). In particular, its cover underwent a positive change in shifting coastal dunes (EUNIS type B1.3), while encountering a decline in “NC” category. Finally, running a second model including “plot status” as interaction term resulted in two significant patterns: a decreasing trend in highly “disturbed” plots, and an increasing one in “invaded” plots (Table 7).

Correlograms highlighted limited spatial autocorrelation in the residuals of the models, but only when considering first lag neighbors (data not shown). Nevertheless, it is worth noting that AIC values of intercept-only models were always found to be consistently higher than those computed on the corresponding full models, therefore indicating predictor terms to explain significant variation in response variables.

Discussion

Habitat changes in richness and cover

As highlighted by the models, between 2002 and 2015 EUNIS B1.4 type suffered negative changes in both species richness and cover. A further exploration of this trend allowed us to specifically identify dune grasslands (EU Habitat 2230) as driving the decreasing pattern, in line with observations made by Prisco et al. (2016a) and with those of Janssen et al. (2016), who recently classified it as the most “endangered” among coastal dune habitats. This raises fresh concerns about the fate of one of the Mediterranean most biodiverse habitats, its hosting several species of insects, nesting birds and rabbits, along with a number of endemic and highly specialized taxa (McLachlan and Brown 2006; Fattorini et al. 2012).

Cover changes in native target species

Consistent with our findings at the habitat scale, the species-level analysis showed a decline in two diagnostic species of dune grasslands, *Cutandia maritima* and *Medicago littoralis*. A similar trend was encountered by *Ammophila arenaria* subsp. *australis*, key species of shifting dune habitats. Even though no significant change over time could be detected in the habitat where this species is considered to be diagnostic (EUNIS type B1.3), the decrease in the cover of this perennial grass appears somehow connected with the positive trends recorded by the perennial forbs *Lotus cytisoides* and *Anthemis maritima*, both often indicated as being capable of forming replacement communities in degraded shifting dunes (Géhu and Biondi 1994; Acosta et al. 2007), and with the increase in the cover of the invasive *Carpobrotus* sp. (see next paragraph). Similarly, the sharp decrease encountered by *Crucianella maritima*, a perennial entity dominating stable dune grasslands, can be related to the widespread presence of species such as *Ononis variegata* and *Pycnocomon rutifolium*, which become abundant in *Crucianella* communities affected by disturbance (Géhu and Biondi 1994). Finally, a marked decline over time could be also observed in the cover of *Juniperus oxycedrus* ssp. *macrocarpa*. Even though not supported by a parallel loss in the corresponding EUNIS type, this tendency should not be underestimated given that in recent decades fixed dunes belonging to EU habitat 2250 have undergone a serious contraction due to anthropogenic disturbance (Malavasi et al. 2013; Genovesi et al. 2014). Increasing temporal patterns observed by Prisco et al. (2016a) in the cover of both EU Habitat 2250 and *Juniperus oxycedrus* ssp. *macrocarpa* seem to contradict our results, though ascribed by the authors to the positive role of Natura 2000 Network. However, the expansion of artificial and agricultural surfaces linked to human activities (Salvati et al. 2014; Sytnik and Stecchi 2015), together with a predicted reduction of this habitat under climate change scenarios (Prisco et al. 2013; Seabloom et al. 2013), could make this habitat vulnerable to land degradation in the near future, also within protected areas (Tsiafouli et al. 2013; Kallimanis et al. 2014; Salvati et al. 2014; Pinna et al. 2015).

Temporal patterns of invasion

Our analyses provide strong evidence that in “NC” plots the number of alien species has declined over the years. Such a finding appears even more surprising when taking into consideration the fact that the decrease actually took place in highly “disturbed” plots. Indeed, though a number of studies have already reported on high levels of anthropogenic disturbance in coastal environments, our results suggest that, besides affecting native communities, such conditions might also impact upon alien species, as shown by the declining pattern observed for *Carpobrotus* sp. in highly “disturbed” plots. Nevertheless, however positive, the decrease of *Carpobrotus* sp. in such plots is strongly counterbalanced by its significant growth in shifting dunes, coastal dune vegetation’s most characteristic habitat (EUNIS B1.3). Here, the increasing trend recorded by *Carpobrotus* sp., mirrored by a complementary decrease in the cover of *Ammophila arenaria* subsp. *australis*, appears to be particularly worrying since, despite the already documented presence of *Carpobrotus* in shifting dunes, invasion processes hitherto headed by this exotic plant have mainly affected dune grasslands and *Crucianella*-dominated communities.

Conclusions

In the present study, we have set out to unravel temporal trends in selected psammophilous communities through the use of a diachronic approach entirely based on random, standardized and unpreferentially collected data.

Our analyses revealed changes at a habitat level and raise concerns over the fate of dune grasslands, which during the considered period experienced a significant decline in both species richness and cover. However, it should be noted that as Mediterranean dune grasslands are mainly composed of annual therophytes, changes in their dynamics can be traced in the course of a few years, while the detection of similar trends in perennial communities might require longer-term observations. This being said, individual species might predict community trends through changes in their cover, with negative patterns serving as “early warnings” about the fate of the whole habitat. This could be the case in shifting dunes, where no statistically significant change was observed at habitat level, whereas a negative pattern was identified in the cover of key species *Ammophila arenaria* subsp. *australis*. Nevertheless, the most striking results emerged from the analysis of temporal patterns in the cover of *Carpobrotus* sp, which underwent a decrease in disturbed plots while, on the other hand, displaying a significant growth in shifting dunes.

Diachronic analyses in coastal dune ecosystems are both useful and highly versatile. As well as expanding current knowledge on temporal dynamics, they can contribute significantly to the development of conservation activities and of species-dedicated measures. In particular, our results highlight that priority should be given to the implementation of recovery processes in dune grasslands, while monitoring activities of invasion levels should mainly focus on well-preserved habitats experiencing recent alien invasion, such as shifting dunes.

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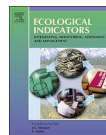
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Chapter II

Back into the past: Resurveying random plots to track community changes in Italian coastal dunes



Back into the past: Resurveying random plots to track community changes in Italian coastal dunes



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ABSTRACT

Resurveying studies are commonly appreciated as a means to monitoring temporal changes in plant diversity. However, most of them still rely on phytosociological plots, which, although representing an invaluable source of data, can lead to biased estimates of vegetation changes. At the community-level, temporal changes can be quantified by means of beta-diversity measures. However, compositional variation can be the result of two different, often contrasting, processes: turnover and nestedness. In this context we test the effectiveness of resurveying approaches based on quasi-permanent plots in revealing temporal changes in herbaceous communities of Mediterranean coastal dune systems. Indeed, due to their being highly dynamic, coastal dunes can be considered ideal habitats for implementing such tools. In particular, we quantified temporal changes in species composition occurred over 10–15 years by calculating Sørensen index of dissimilarity and, in order to determine whether the change was really driven by species turnover, we partitioned Sørensen index into its two components of turnover and nestedness. At the same time, since diagnostic species are considered to be particularly sensitive to habitat modifications and helpful in assessing changes in the ecological structure of a community, we analyzed temporal changes in the occurrence and cover of diagnostic species of the investigated habitats. Results show that coastal dune communities of our study area underwent consistent changes during the analyzed time-span. Almost 25% of the historical plots disappeared. Major transformations, mainly driven by species turnover, involved upper beach communities, embryonic and mobile dunes, as revealed by the parallel analysis of beta diversity and diagnostic species. This work shows how resurveying approaches can efficiently reveal useful insights on vegetation dynamics, therefore providing a solid basis for the implementation of effective conservation strategies, especially in endangered habitats.

1. Introduction

In the last decades, global changes and anthropogenic pressures seriously affected the structure and functioning of ecosystems across the globe, eventually becoming major drivers of alteration in their composition and diversity (Walther et al., 2005; Verheyen et al., 2016; Hédl et al., 2017). Quantifying such alteration, along with identifying main trends, is a crucial task in the protection and management of natural systems (Kapfer et al., 2017) and is therefore considered a priority issue in conservation ecology.

Resurveying studies, consisting in the re-sampling of vegetation plots historically surveyed by other authors, are being increasingly used as a means to detect temporal changes in the vegetation of many ecosystems. In order to maximize reliability and robustness of subsequent

analyses, resurveying studies should be able to accurately retrieve original plot location and, to this regard, permanent plots currently represent the most precise tools. However, permanent plots can be highly resource-intensive and their coverage is in most cases spatially limited (Hédl et al., 2017). On the other hand, quasi-permanent plots, i.e. plots that can be relocated using a plot-specific geographic position (*sensu* Kapfer et al., 2017), despite retaining a certain degree of relocation error, stand for a valid, cost-effective alternative. Although such tools are starting to gain popularity, they still mostly rely on phytosociological data, mainly because of the long tradition of phytosociological relevés providing an invaluable source of data in a variety of habitats (Bakker et al., 1996; Ross et al., 2010). However, as phytosociological relevés are traditionally based on preferential sampling, their use in revisitation studies and associated analyses violates the statistical

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assumptions of randomness and independence of observations (Lájer, 2007; Michalčová et al., 2011) which, together with the frequent lack of geographical coordinates, can result in biased estimates of vegetation change (Jandt et al., 2011; Chytrý et al., 2014).

Whittaker (1960, 1972) introduced the concept of beta diversity (the amount of variation in species composition among a set of sampling units) for linking local-scale diversity (or alpha diversity) to regional-scale diversity (gamma diversity). Since then, beta diversity has become a primary tool for examining changes in the composition of species assemblages, not only along spatial or environmental gradients, but also along temporal gradients. In this context, Baselga (2010) and Baselga (2012) suggested how the concept of beta diversity actually involves two distinct processes, one (temporal turnover) being the real temporal variation of species assemblages from one time to another, and the other (nestedness resultant-dissimilarity) being an effect of the poorest site being a strict subset of the richest site. As these two components may show contrasting patterns, their separation is crucial in order to assess actual temporal trends in biodiversity (see Baselga 2012 and references therein).

While beta diversity measures focus on quantifying changes between communities, they give no insights about temporal trends experienced by single species. In this sense, diagnostic species (i.e. species that, guaranteeing both existence and functionality of their habitats, can be considered representative of different vegetation types and are particularly sensitive to a range of threats and habitat modifications) are being increasingly used by researchers as crucial units for monitoring biodiversity (Santoro et al., 2012b; Del Vecchio et al., 2016; Angiolini et al., 2017). Providing information about underlying abiotic components, diagnostic species can help evaluate changes in the ecological structure of a community (Lambeck, 1997; Kimball et al., 2010; Del Vecchio et al., 2016), and are therefore of great use in the assessment of temporal changes.

In this framework, taking advantage of a large coastal vegetation database comprising standardized random plots originally sampled since 2002 (Sperandii et al., 2017), we tested the effectiveness of resurveying approaches based on quasi-permanent random plots for assessing temporal changes in Mediterranean coastal dunes. Indeed, despite their being highly suitable systems for implementing such approaches, up to our knowledge revisitation studies focusing on Mediterranean sandy habitats and making use of quasi-permanent random plots haven't been implemented yet.

Being transitional ecosystems located at the boundary between land and sea, coastal dunes are unique habitats characterized by constraining environmental conditions that limit survival and successful reproduction to a relatively small set of highly specialized plant species (Maun, 2009; Fenu et al., 2013; Marcenò et al., 2018). Such environmental constraints, together with their ecotonal nature, make coastal dunes highly dynamic ecosystems where even short time-spans can be enough to track vegetation changes (Sperandii et al., 2018). At the same time, in spite of a prominent conservation value (Van der Maarel 2003; Martínez et al. 2008; Acosta et al., 2009) and a wide range of socio-economic services provided (Defeo et al., 2009), coastal dunes appear among the most threatened ecosystems on earth (Schlachter et al., 2007; Janssen et al., 2016).

In consideration of the above, we endeavor to answer the following research questions:

- i) To what extent have coastal dune habitats of Central Italy changed over the last 10–15 years?
- ii) Can we relate this change to a real “species turnover” or rather to a “nestedness effect”?
- iii) Can we identify trends for diagnostic species of the involved habitats?

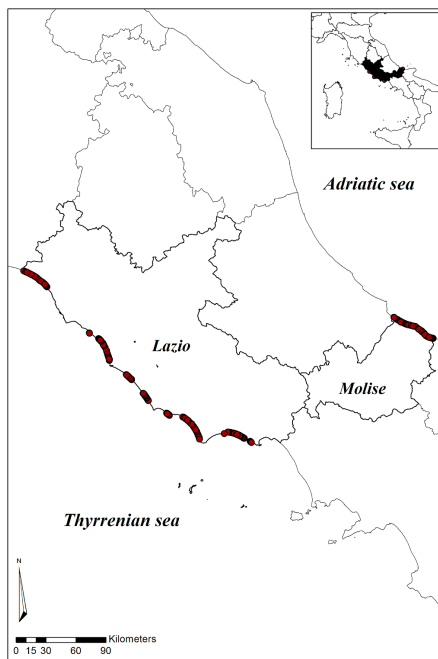


Fig. 1. Main dune systems of Lazio and Molise (Central Italy).

2. Materials & methods

This resurveying study was performed on coastal dune systems located in Central Italy along the Tyrrhenian and Adriatic coasts (Fig. 1). Throughout the study area, climate is Mediterranean (Carranza et al., 2008) and holocene dune systems occupy a narrow stripe along the seashore.

2.1. Historical data

A total of 188 historical relevés were extracted from an existing database of Italian coastal dunes (“RanVegDunes”; Sperandii et al., 2017). This database consists of original georeferenced relevés collected since 2002, for which sandy vegetation was recorded in standardized 4-m² random quadrats (i.e. plots). For each plot, a species list was available with abundance values estimated using a percentage cover scale. Additional information, for each plot, includes a level 3-EUNIS code assigned according to the EUNIS habitat classification system (Davies et al., 2004; Table 1). The selected 188 plots were originally sampled between 2002 and 2007 (hereafter T_0) throughout the first portion of the coastal zonation, therefore including annual pioneer communities of the upper beach, embryonic dunes, mobile dunes and coastal stable dune grasslands. Specifically, 63 plots were sampled in 2002, 56 were sampled in 2005 and 59 in 2007. As in this paper we will consider plant communities in terms of level-3 EUNIS habitats, it is necessary to clarify that the above-mentioned investigated communities correspond to EUNIS categories B1.1, B1.3 and B1.4 (see Table 1 for description of the communities and distribution of the plots among

Table 1
Level 3-EUNIS type, description of the community and diagnostic species selected for this study.

Level 3-EUNIS type	Description and correspondence with EU habitats (ex Annex I 92/43/EEC)	Diagnostic species	Number of observations
B1.1 Sand beach drift lines	Pioneer annual formations characterizing the strandline zone of the beach (EU hab 1210 – Annual vegetation of drift lines)	<i>Cakile maritima</i> Scop. subsp. <i>maritima</i> , <i>Chamaesyce pepilis</i> (L.) Prokh., <i>Polygonum maritimum</i> L. <i>Salsola kali</i> L.	37
B1.3 Shifting coastal dunes	Mobile coastal sand ridges which include embryonic dunes characterized by <i>Elymus farctus</i> (EU hab 2110 – Embryonic shifting dunes) and semi-permanent dune systems dominated by <i>Ammophila arenaria</i> subsp. <i>Australis</i> (EU hab 2120 – Shifting dunes along the shoreline with <i>Ammophila arenaria</i>)	<i>Ammophila arenaria</i> (L.) Link subsp. <i>Australis</i> (Mabille) Laínz <i>Anthemis maritima</i> L. <i>Calystegia soldanella</i> (L.) Roem. & Schult., <i>Cyperus capitatus</i> Vand. <i>Echinophora spinosa</i> L., <i>Elymus farctus</i> (Viv.) Runemark ex Melderis subsp. <i>farctus</i> , <i>Eryngium maritimum</i> L., <i>Euphorbia paralias</i> L., <i>Lotus cytisoides</i> L. <i>Medicago marina</i> L. <i>Otanthus maritimus</i> (L.) Hoffmanns. & Link subsp. <i>Maritimus</i> <i>Pancretrium maritimum</i> L. <i>Sporobolus virginicus</i> Kunth, <i>Bromus diandrus</i> Roth subsp. <i>Maximus</i> (Desf.) Soó <i>Crucianella maritima</i> L. <i>Catantha maritima</i> (L.) Barbey <i>Lagurus ovatus</i> L. <i>Medicago littoralis</i> Loisels. <i>Ononis variegata</i> L. <i>Phleum arenarium</i> L. subsp. <i>caesium</i> H. Scholz <i>Pseudorhiza pumila</i> (L.) Grande <i>Pycnocomon rufifolium</i> (Vahl) Hoffmanns & Link <i>Silene caescens</i> Ten. <i>Sixalix atropurpurea</i> (L.) Greuter & Burdet <i>Vulpia fasciculata</i> (Forssk.) Fritsch	95
B1.4 Coastal stable dune grassland	Stable dune grasslands including chamaephytic communities of the inland dunes dominated by <i>Crucianella maritima</i> (EU hab 2210 – <i>Crucianellon maritima</i> fixed beach dunes) and annual, species-rich communities colonizing dry interdunal depressions (EU hab 2230 – <i>Malcolmietalia</i> dune grasslands)	<i>Crucianella maritima</i> L. <i>Catantha maritima</i> (L.) Barbey <i>Lagurus ovatus</i> L. <i>Medicago littoralis</i> Loisels. <i>Ononis variegata</i> L. <i>Phleum arenarium</i> L. subsp. <i>caesium</i> H. Scholz <i>Pseudorhiza pumila</i> (L.) Grande <i>Pycnocomon rufifolium</i> (Vahl) Hoffmanns & Link <i>Silene caescens</i> Ten. <i>Sixalix atropurpurea</i> (L.) Greuter & Burdet <i>Vulpia fasciculata</i> (Forssk.) Fritsch	44

EUNIS types). However, it should be noted that, as 12 plots could not be associated to any EUNIS category because they were highly degraded or highly invaded by alien species, they were labeled as “not classifiable” (NC).

2.2. Revisitation study

Historical plots were revisited and resampled in 2017 (hereafter T_1), following the same methods used by the original surveyors. This allowed us to evaluate changes occurred over 10–15 years. During the resurvey, special care was taken to perform the resampling during the same months in which the original sampling was done (April–May). Plot positions were relocated using a GPS unit on which historical geographic coordinates were stored (quasi-permanent plots *sensu* Kapfer et al., 2017).

2.3. Data analysis

2.3.1. Beta-diversity analysis

To assess variation in species composition over time, presence-absence matrices were used. Specifically, pairwise dissimilarity values between matched sites (old vs new) were computed using Sørensen index of dissimilarity (β_{SOR}):

$$\beta_{\text{SOR}} = (b + c) / (2a + b + c)$$

where a is the number of species present at both T_0 and T_1 , b is the number of species exclusive to T_0 and c is the number of species exclusive to T_1 . Values of the index range from 0 to 1, with 0 indicating a null dissimilarity (the communities have the same species composition)

and 1 indicating total dissimilarity (the communities do not share any species). This was done using R package betapart (function *beta.temp*, Baselga and Orme, 2012), which at the same time allows partitioning beta-diversity into the two components of turnover and nestedness (Baselga, 2012). To determine whether temporal change occurred similarly across the investigated portion of coastal zonation, differences in Sørensen values among different communities (identified through EUNIS categories) were tested using Kruskal-Wallis rank-based non-parametric test. Additionally, in order to find out which was the prevailing process behind the change, turnover and nestedness values were compared for each plot and also among different communities.

2.3.2. Variation in occurrence frequency and cover of diagnostic species

Diagnostic species (see Table 1) were identified using the Italian Interpretation Manual of the 92/43/EEC Habitats Directive (Biondi et al. 2009). Specifically, we selected a total of 29 diagnostic species, choosing those that, for each plant community, were most abundant in our study area. For each species and time point separately, occurrence frequencies (i.e. the number of plots in which a species occurs) and cover were calculated as follows.

First, standardized occurrence frequencies and cover values were calculated, for each species and time point separately, following Kapfer and Grytnes (2017). In particular, occurrence frequencies were standardized, for each diagnostic species, dividing the number of species occurrences recorded during a specific survey by the total number of plots sampled during that survey. Similarly, cover values for each time period were standardized dividing the total cover of a species recorded during a survey by the number of species occurrences in that survey. Standardized changes were then calculated for both occurrence and

cover values by subtracting old values from new values, with positive changes indicating an increase in the occurrence frequency/cover of the species and negative values indicating a decrease in the occurrence frequency/cover of the species. In order to assess whether changes in occurrence frequencies between the two time points were significant, we used McNemar's non-parametric test for dependent data (Agresti, 2003). By comparing changes in the proportion of occurrences of a certain species at T_0 and T_1 , this test assesses whether the probability of the species not being present in the first survey and appearing in the second survey is equal to the probability of the species being present in the first survey and disappearing in the second survey.

To test for statistically significant cover changes between old and new relevés, exact Wilcoxon-Pratt signed rank tests for paired samples were performed for each diagnostic species in its reference habitat. This was done using R package "coin" (function: wilcoxon_test; Hothorn et al., 2008), which allows obtaining exact p-values of the test statistic by specifying an argument of the function (distribution = "exact") and at the same time, by default, implements Pratt's method of handling zeros (Pratt, 1959). It should be noted that, in order to satisfy assumptions about independence of observations when performing statistical tests, each of the above-cited analyses was carried out on three different subsets ($N_{subset1} = 121$; $N_{subset2} = 121$; $N_{subset3} = 118$) randomly extracted from the original 188 points dataset. These subsets were created performing three random selections of points so that the minimum distance between historical observations would be at least 100 m. (ArcGis 10.1, ESRI). All statistical analyses were performed using R (R Core Team, 2017).

3. Results

3.1. Temporal changes in coastal dune communities

During the resurvey we could ascertain that 44 out of the 188 historical plots actually disappeared. Upper beach and foredune plant communities were most affected by this phenomenon, with EUNIS categories B1.1 and B1.3 respectively losing 21–25% and 58–60% of the historical plots (Appendix A).

Sørensen index of dissimilarity unveiled substantial changes, as shown in Fig. 2. Two peaks can be particularly identified, the first including values around 0.9–1 and the second covering values around 0.4–0.6. With regard to the first peak, it should be noted that values of 1 (which identify a total dissimilarity between matched sites) together with relevés that completely changed in their species composition also incorporate disappeared plots.

Although the distribution of Sørensen index values seems to follow coastal zonation (Fig. 3), with high values characterizing upper beach

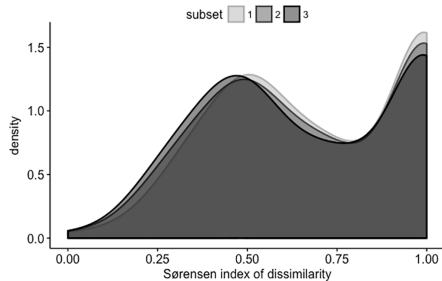


Fig. 2. Density plot reporting the values of Sørensen index of dissimilarity for the three randomly selected subsets ($N_{subset1} = 121$; $N_{subset2} = 121$; $N_{subset3} = 118$) of 188 survey plots.

communities and lower values associated to more inland communities, no statistical differences were found when testing values of the index against EUNIS categories in all three subsets (Kruskal-Wallis $p > 0.05$).

Partitioning beta diversity into its two related components revealed similar results in all subsets (Table 2). In particular, turnover turned out to be the prevailing process in most cases (83–85% of the plots), while nestedness drove the change in only 12–16% of the plots. This holds for all EUNIS categories, where turnover prevailed in 78–100% of the plots (see Appendix B).

3.2. Changes in occurrence frequency and cover of diagnostic species over time

During the considered time-span, 25 out of the 29 investigated diagnostic species decreased in their occurrence frequency while the rest showed a positive trend (Appendix C). However, McNemar's tests indicated significant changes for just 8 species belonging to EUNIS categories B1.1 and B1.3, which all decreased in their occurrence. The species that underwent the most substantial decline are *Cakile maritima* and *Salsola kali*, followed by *Chamaesyce pepilis*, *Echinophora spinosa*, *Elymus farctus* and *Ammophila arenaria* (Fig. 4).

As for cover changes, 12 out of 29 species experienced a decrease, while the rest experienced an increase during the considered time-span (Appendix D). However, such changes resulted to be significant for just 6 species (Fig. 5) belonging to EUNIS categories B1.1 and B1.3. The most important decrease was observed for *Ammophila arenaria*, *Salsola kali* and *Chamaesyce pepilis*, while the most important increase (although relatively low) was found for *Echinophora spinosa*.

4. Discussion

During the last 10–15 years, coastal dune communities of Central Italy underwent substantial changes that can be summarized in the disappearance of almost 25% of the historical plots and in major transformations affecting most investigated communities, not only in their species composition but also in the occurrence frequency and cover of their diagnostic species. Concerning disappeared plots, some turned out to be submerged due to local erosion processes leading to a retreat of the coastline, while others, mainly in areas associated with seasonal tourism, were found to be completely unvegetated.

For all communities investigated, turnover was found to be mostly responsible for compositional changes between old and new plots, thus supporting the dynamic nature of coastal dune ecosystems (Martínez et al., 2008; Agardý et al., 2005; Buffa et al., 2012; Calvão et al., 2013). The fact that species replacement prevailed over nestedness might point to ongoing transformation processes, as also suggested by recent diachronic studies based on permanent plots (Prisco et al., 2015; Prisco et al., 2016). This seems to be supported by the analysis of diagnostic species, which revealed how all the species experiencing a statistically significant change during the considered time-span decreased in their occurrence frequency and/or in their cover, except for a slight increase in the cover of two of them.

The most considerable variation seems to have affected pioneer communities of the upper beach and foredunes (corresponding to Eunis cat. B1.1 and B1.3), which also harboured the vast majority of disappeared plots. Here, values of Sørensen index of dissimilarity turned out to be, on average, higher than in coastal dune grasslands. Indeed, although formal testing rejected statistical differences among the investigated communities, results from the analysis of temporal changes in occurrence and cover of diagnostic species support the hypothesis of the seaward portion of coastal zonation having experienced the greatest change, as also found by Prisco et al. (2015, 2016). In particular, 3 out of the 5 species tested for the upper beach sector (*Salsola kali*, *Cakile maritima* and *Chamaesyce pepilis*) strongly decreased in their occurrence frequency during the time considered. However, *Salsola kali* and *Chamaesyce pepilis* also decreased in their cover, while *Cakile maritima*

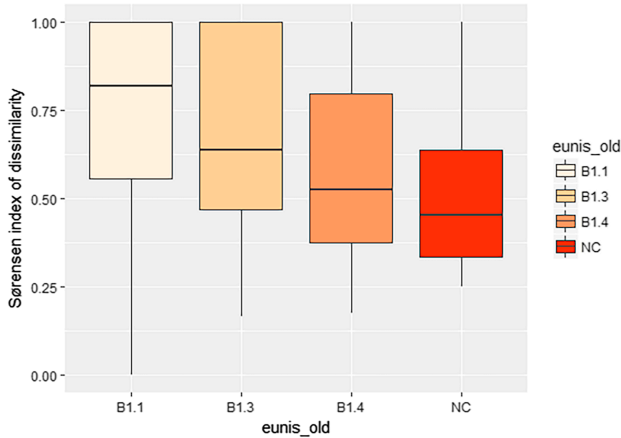


Fig. 3. Boxplot showing values of Sørensen index of dissimilarity among the considered EUNIS categories. NB. All three subsets are shown together.

Table 2

Partition of Sørensen index of dissimilarity. *prevalence*: % of plots in which the specified component was found to be prevailing (averaged over subsets); *sd*: standard deviation. NB: disappeared plots and plots that didn't change at all (Sørensen index value = 0) were excluded from this calculation.

component	prevalence	sd
nestedness	15.03	1.94
turn/nest	0.40	0.69
turnover	84.57	1.30
tot	100	-

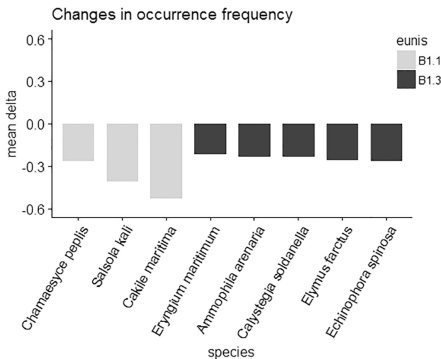


Fig. 4. Mean temporal changes in occurrence frequency calculated, over the three subsets, for diagnostic species that underwent significant changes ($p < 0.05$ in at least 2 out of the 3 subsets).

slightly increased in its cover from T_0 to T_1 . This divergence might be due to the fact that, as the species' reference habitat is the most subject to natural (occasional inundation, erosion) and anthropogenic (mechanical cleaning) disturbance, and at the same time dispersal for this

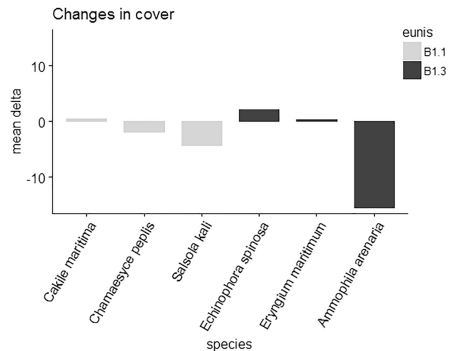


Fig. 5. Mean temporal changes in cover calculated, over the three subsets, for diagnostic species that underwent significant changes ($p < 0.05$ in at least 2 out of the 3 subsets).

species mainly depends on tides and winds (Davy et al., 2006), populations of *C. maritima* may randomly germinate and develop more backward, in neighboring communities. However, considerations on temporal changes affecting drift line communities should be made with utmost care. Indeed, as these communities are mostly formed by annual species, whose occurrence and prevalence can be considerably dependent on climatic variations over the years, and at the same time are prone to high disturbance, they tend to be inherently ephemeral and shifting (Doing, 1985; Acosta et al., 2009; Landi et al., 2012). Together with drift line communities, foredunes turned out to experience important changes during the considered time-span. Here, the vast majority of the investigated diagnostic species showed a decreasing trend in their occurrence frequency. In particular, the disappearance of diagnostic species such as *Eryngium maritimum*, *Calystegia soldanella* and *Echinophora spinosa* might indicate ongoing degradation processes occurring in this sector. At the same time, the substantial loss in the occurrence of *Ammophila arenaria* and *Elymus farctus* raises considerable

environmental concerns, as the two rhizomatous species play a key role in dune formation and stabilization. Similar results are reported by Del Vecchio et al. (2015), who found significant changes affecting foredune habitats in the context of a 20-years revisitation study based on phytosociological relevés. However, together with an increase in the cover of *Elymus farctus* over the years, Del Vecchio et al. (2015) identified an increase in the cover of *Ammophila arenaria*, whereas we found a parallel decrease in both occurrence and cover of this species over the years.

Our results confirm the vulnerability of three important sectors of the coastal zonation: upper beach, embryo dunes and shifting dunes. By representing the first elements of coastal zonation, these communities are certainly most exposed to both natural and anthropogenic sources of disturbance such as coastal erosion and seaside mass tourism (Acosta et al., 2006; Buffa et al., 2012), which are regarded among the most important threats affecting coastal dune ecosystems. In particular, many studies already evidenced the negative impacts exerted by trampling, mechanical cleaning of the beach and other tourism-related activities on sand dune habitats (Santoro et al., 2012a; Farris et al., 2013). At the same time, it has been shown how erosion, either caused by natural phenomena or by the development of artificial infrastructures such as harbors, strongly modifies coastal zonation, often truncating its first elements (Buffa et al., 2012; Ciccarelli, 2014; Prisco et al., 2015).

As long-term perspectives are increasingly needed to study compositional changes in many ecosystems, resurveying studies represent a valuable and cost-effective solution. Although it is very difficult to avoid some of the bias they are naturally prone to (e.g. relocation bias, observer bias), efforts can be made to minimize them and much depends on the analyzed ecosystem. In this context, revisitation approaches based on georeferenced and standardized random plots, reducing relocation inaccuracy and avoiding biases deriving from both scale-dependence of inter-specific correlations and violation of statistical assumptions about randomness (Chytrý and Otyčková, 2003; Jandt et al., 2011; Michalčová et al., 2011), provide reliable estimates of change while at the same time allowing wide spatial coverage. Being highly dynamic ecosystems, coastal dunes can be considered a useful testing system for resurveying approaches based on standardized, georeferenced random plots, even when considering short- to medium time-spans. However, with this work we intend to highlight that also other ecosystems could actually benefit from the use of such approaches, especially when based on standardized, georeferenced random plots instead of phytosociological plots.

5. Conclusion

Despite being challenging, revisitation studies are highly recommendable tools for analyzing temporal dynamics in plant communities (Hédl et al., 2017; Kapfer et al., 2017). This study, based on georeferenced random plots, revealed substantial changes affecting coastal dunes of Central Italy in the last 10–15 years. In particular, by conducting analyses at both the community- and species-level, we provide evidences of upper beach and foredunes communities having experienced major transformations during the considered time-span. At the same time, partitioning beta diversity allowed to identify species turnover as the main driver of change. Whereas further research will be needed to confirm such trends and investigate possible causes, we stress the value of resurveying approaches in incrementing knowledge of vegetation dynamics and, to this regard, we highlight their usefulness in providing a good basis for the implementation of effective conservation strategies, especially in endangered habitats.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2018.09.039>.

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Chapter III

Save the last stands: multi-dimensional assessment of temporal changes of Mediterranean sandy habitats

Save the last stands: multi-dimensional assessment of temporal changes of Mediterranean sandy habitats

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Abstract

Quantifying and monitoring alterations of ecological communities through time is a shared research priority of global conservation agendas and a also a core aim in the emerging branch of temporal ecology, especially in this time of global biodiversity crisis. With this paper, we aim at providing a comprehensive, habitat-based, multi-dimensional assessment of temporal changes characterizing Mediterranean coastal dunes in the last 10-15 years. Specifically, we assessed both taxonomic and functional changes using dissimilarity metrics informative of several biodiversity components, and we tested most of the observed changes for significance using null models. Furthermore, we also explored trends at the level of single species by analyzing species-abundance distributions at both time points and by statistically testing their changes in occurrence frequency and cover. Considerable changes could be observed in the taxonomic and the functional spheres, varying among habitats but spanning across levels of biological organization: from the community level to that of single species. This, together with the disappearance of 78 out of the 334 historical plots and with observed changes often exceeding “simulated changes”, revealed an intense vulnerability affecting most coastal dune habitats, particularly evident in upper beach and shifting dunes. Along with enhancing the knowledge of recent dynamics affecting these endangered communities, this study allowed identifying EU Habitats (*sensu* 92/43/EEC) that appear to be particularly at risk, thus supplying an important resource to direct future conservation efforts and management strategies.

1. Introduction

The increased rate at which humanity is transforming the biosphere is alarming: anthropogenic modifications span across spatial scales, affecting productivity and biodiversity of our natural systems in an unprecedented way (Vitousek et al., 1997; Ellis & Ramankutty, 2008). In the context of such a global biodiversity crisis (XXX), assessing the extent of temporal changes in ecological communities is both a core research challenge in the emerging field of temporal ecology (Wolkovich et al., 2014) and a shared priority of worldwide conservation agendas that responds to several urgent needs: understanding ecosystem dynamics and pinpointing their drivers, forecasting future changes and ecological tipping points, but also providing sound knowledge about the status of natural habitats to conservation managers and verifying the effectiveness of current conservation practices.

The need to devise improved methods and reliable indicators for assessing community changes has been variously highlighted (Magurran & Dornelas 2010). To this aim, resurveying studies (i.e. studies in which historical vegetation plots are revisited and re-sampled) offer a valuable framework/solution. Indeed, due to the large availability of historical data spanning across geographical areas and community types, resurveying studies can provide reliable estimates of change on wide spatial extents, overcoming the inner constraints of diachronic analyses based on large vegetation databases and, at the same time, constituting a cost-effective, fairly robust alternative to traditional methods such as, e.g., permanent plots (Chytrý et al., 2014; Hédľ et al., 2017; Kapfer et al., 2017). However, much of the effectiveness of resurveying studies depends on the quality of historical data. In this regard, the use of quasi-permanent (Kapfer et al., 2017) random plots allows to maximize the reliability of the results, while at the same time avoiding inconsistencies and bias deriving from the use of phytosociological data (Chytrý, 2001; Botta-Dukát et al., 2007; Lájler 2007).

As biodiversity is a complex, multi-faceted construct composed of many components (e.g. richness, relative abundance, composition, occurrence of key species) differently affecting ecosystem properties (Hooper et al., 2005), no single indicator can exhaustively summarize its change (Purvis & Hector, 2000). Therefore, we believe that to attain a thorough understanding of the structure and dynamics of

plant communities, the following aspects should be taken into account. First, efforts should be addressed at accounting for as many of the above-mentioned biodiversity components as possible. In this regard, several dissimilarity indices are available, whose use has been proved to be more informative on the nature of change than that of apparently standalone metrics such as, e.g., species richness (Buckland et al., 2005; Hillebrand et al., 2018). Second, studies where two or more dimensions of biodiversity are simultaneously investigated should be prioritized. Indeed, multi-dimensional studies have been shown to provide greater insights about the influence of biodiversity on ecosystem properties than those considering only one aspect, as different dimensions may feature contrasting trends (Devictor et al., 2010; Magurran & Dornelas, 2010; Naeem et al., 2016). In addition to taxonomic diversity, functional diversity is nowadays regarded as essential to understand community assembly processes as well as ecosystem functioning (Díaz et al., 2007; De Bello et al., 2010), and assessing its changes through time proved to be highly useful in revealing the contrasting role of different driving forces during successional processes or post-disturbance recovery (Purschke et al., 2013). Third, studies assessing temporal changes would greatly benefit from analyzing trends at multiple levels of biological organization (Magurran & Dornelas, 2010): as an example, single species can add valuable insights to the analysis of community-level metrics. Indeed, as individual species exert varying impacts on different ecosystem functions and processes within a community, their loss or gain might have different consequences depending on their identity and functional role (Rosenfeld, 2002; Lefcheck et al. 2015). Consequently, many studies started using selected species, known as “key”, “diagnostic” or “focal” species, for analyzing the quality of plant communities and detecting early warning of habitat disruption (Santoro et al., 2012; Del Vecchio et al., 2016; Angiolini et al., 2018).

Although covering a relatively small portion of the earth’s surface, coastal dunes are largely recognized for their outstanding conservation value. In these dynamic systems, a precise sequence of ecologically distinct plant communities, running perpendicular to the sea and commonly known as “coastal zonation” (Doing, 1985; Acosta et al., 2007), provides suitable habitats to a highly specialized, often rare and endangered flora (Acosta et al., 2009) and to a rich, equally adapted fauna (Doody, 2012), while also supporting fundamental pollinator networks (Fantinato et al., 2018). Beyond their naturalistic value, coastal dunes also provide essential ecosystem services such as, e.g., protection against storms and floods, climate regulation, groundwater storage, nutrient recycling (Everard et al., 2010; Arkema et al., 2013). Nevertheless, coastal dunes are currently listed among the most endangered ecosystems worldwide (Schlacher et al., 2007; Defeo et al., 2009). In the Mediterranean, uncontrolled urbanization and population growth characterizing the recovery from World War II led to a progressive deterioration of littoral landscapes, ultimately resulting in diffused fragmentation, biodiversity and habitat loss (Curr et al., 2000; Malavasi et al., 2013). As a result, several coastal dune habitats have been recently classified by the Red List of Habitats (Janssen et al., 2016) as either endangered or vulnerable. In this context, assessing their changes through time and monitoring their conservation status becomes a matter of utmost importance which cannot be further procrastinated if we aspire at reversing the current trend and avoid a complete disappearance of these habitats.

In light of these considerations, aim of the present study is to provide a comprehensive, habitat-based (*sensu* Annex I 92/43/EEC) quantification of temporal changes characterizing Mediterranean coastal dunes in the last 10-15 years, and test whether and how much observed changes exceed changes that could be expected under “random” circumstances. To pursue comprehensiveness, we: a) use metrics incorporating several of the previously recalled components of biodiversity; b) adopt a multi-dimensional approach by investigating both taxonomic and functional changes, and c) explore changes at both the community- and the species-level.

2. Materials and methods

2.1 Study area

The study focuses on coastal dune systems located along the Tyrrhenian and Adriatic coasts of Central Italy, covering a total of about 75 kilometers and belonging to two administrative regions (Lazio and Molise). In this area, characterized by a Mediterranean bioclimate (Carranza et al., 2008), Holocene coastal dunes occupy a narrow stripe along the seashore and are generally < 10 m in height.

2.2 Vegetation sampling and resampling

Historical data used for the resurveying study were extracted from RanVegDunes, a database of georeferenced, random 4 m² relevés (i.e. plots) sampled in coastal dune systems of Central Italy

between 2002 and 2015 (Sperandii et al., 2017). For each plot, data consisted of a list of recorded species, together with cover values estimated on a percentage scale and following the shoot presence criterion (Cancellieri et al., 2017). Historical plots were included in the resurveying study according to their original sampling year and community type. To maximize the chance of detecting changes, we selected from the database all plots that were originally sampled between 2002 and 2007, excluding those classified as Mediterranean shrubs and forests. Following these criteria, we included in the resurveying study 334 plots belonging to the following communities, identified in terms of EU Habitats (ex Annex I 92/43/EEC): 1210 Annual vegetation of drift lines, 2110 Embryonic shifting dunes, 2120 Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes), 2210 Crucianellion maritimae fixed beach dunes, 2230 Malcolmietalia dune grasslands. (see Table 1 for a detailed description of the analyzed communities). However, as some plots could not be clearly classified into a specific EU Habitat due to their being highly disturbed or highly invaded by alien species, which in turn caused the lack of diagnostic species, we labeled them as not classifiable (NC plots, $n = 45$). Resampling activities took place during two sampling seasons (2017 and 2018), allowing us to track changes on a period of 10 to 15 years. Indeed, due to highly dynamic nature, even short time-spans can be enough to track vegetation changes in coastal dune ecosystems (Sperandii et al., 2019). In order to reduce potential variability deriving from seasonality, we performed the resurvey during April and May, therefore respecting the timing of the original survey. Plot positions were relocated using a GPS unit on which historical geographic coordinates were stored. Once the plot was relocated, species were recorded and cover was estimated following the same methods used by original surveyors.

2.3 Plant traits

Trait data were extracted from “TraitDunes”, a database registered on the global platform TRY (<https://www.try-db.org/TryWeb/Home.php>) and including plant traits data measured on coastal dune species in the same areas covered by this study. For this study, we extracted from TraitDunes data on plant height and Specific Leaf Area (SLA), while obtaining data on plant life span from national literature (Pignatti, 1982). Plant height is generally associated with competitiveness and with tolerance or avoidance of environmental stress, while Specific Leaf Area is a structural trait informative of relative growth rate, photosynthetic rate, and nutrient concentration (Cornelissen et al., 2003). Plant life span, on the other hand, is an indicator of population persistence (Pérez-Harguindeguy et al., 2013). As complete trait data are mostly not available for analyses, several trait-based studies adopt, as a rule of thumb, that of sampling (or collecting) trait information only for those species summing up to at least 80% of the total abundance in a community, which has been proven an adequate method to analyze CWM (Pakeman, 2014; Májeková et al., 2016). For this reason, we identified all the plots that didn't comply with this 80% relative abundance threshold using R package traitor (function *sampleSpecies*, Götzenberger, 2015; Májeková et al., 2016) and removed them from further functional analysis, together with their old or new corresponding plots. Similarly, disappeared plots, together with their corresponding plots at T0, were also excluded from further functional analysis.

Table 1. Denomination and description of EU Habitat types included in the resurveying this study

EU Habitat ex Annex I 92/43/EEC (number of historical plots resurveyed)	Dune morphology	Habitat description
1210 Annual vegetation of drift line (upper beach, $n = 90$)	Upper beach	Pioneer annual formations characterizing the strandline zone of the beach, exposed to wind disturbance and flooding
2110 Embryonic shifting dunes ($n = 79$)	Embryo dunes	Pioneer, perennial and halophilous community of the low embryo-dunes dominated by <i>Elymus farctus</i> . Characterized by low vegetation cover and poor sandy substrate.
2120 Shifting dunes along the shoreline with <i>Ammophila arenaria</i> ($n = 45$)	Mobile dunes	Seaward and semi-permanent cordons of dune systems dominated by the rhizomatous tussock grass <i>Ammophila arenaria subsp. australis</i>

2210 <i>Crucianellion maritimae</i> fixed beach dunes (<i>n</i> = 24)	Transition dunes	Perennial community of the inland side of fixed dunes dominated by <i>Crucianella maritima</i> and other chamaephytes
2230 <i>Malcolmietalia</i> dune grasslands (<i>n</i> = 51)	Transition dunes	Annual, species-rich community colonized by small terophytes in dry, interdunal depressions of the coast

2.3 Data analysis

This work represents the final product of a resurveying study carried out between 2017 and 2018. A previous study focusing on temporal changes in coastal dunes (Sperandii et al., 2019) only used a part of this dataset (i.e. 188 pairs of plots resurveyed in 2017), which is instead entirely analysed in this paper (*n*=668, corresponding to 334 pairs of old and new plots).

2.3.1 Temporal changes in taxonomic diversity

To summarize information on changes in community composition and dominance structure we used two dissimilarity metrics reflecting local immigration and extinction processes, recently formalized under the general term of “species exchange ratio” (Hillebrand et al., 2018). The first one, to be used on presence-absence data, is computed as:

$$SER_r = (S_{imm} + S_{ext})/S_{tot}$$

with S_{imm} being the sum of immigrations (species exclusive of T1), S_{ext} being the sum of extinctions (species exclusive of T0), and S_{tot} representing the total number of species present across the two samples. Re-expressed into the better known matching components of beta-diversity a , b , and c (*sensu* Koleff et al., 2003), such formula becomes $(b + c)/(a + b + c)$, therefore corresponding to the complement of the widely-used Jaccard’s similarity index (Jaccard, 1912). SER_r is bounded between 0 and 1, where 0 means that all species persisted and 1 means that all original species were replaced. The second metric, named SER_a , is an extension of SER_r that focuses on temporal differences between species proportional abundances. It is computed as:

$$SER_a = \sum (p_i - p'_i)^2 / (\sum p_i^2 + \sum p_i'^2 - \sum p_i p'_i)$$

with p_i and p'_i being the proportional abundances of the i^{th} species at time 0 and 1, respectively. Values of this metric also range between 0 to 1, where 0 means that the species identity and structure of the community did not change and 1 that all species were replaced. To investigate the directionality of change, two additional indices ($SER_{r,loss}$ and $SER_{r,gain}$) were computed by decomposing SER_r as shown in Legendre & Salvat (2015). These indices inform about how much of the total dissimilarity can be attributed to species loss or gain.

These four metrics (SER_r , its associated components of loss and gain, and SER_a) were calculated for each couple of plots (old vs new plot). To test for significant differences in the intensity of change among communities (identified through EU Habitat categories), a Kruskal-Wallis test was performed on values of these metrics using package “coin” (function: “Kruskal_test”, Hothorn et al., 2006;2008) and a Dunn’s non-parametric all-pairs comparison test was then performed using package “PMCMRplus” (function: “kwAllPairsDunnTest”; Pohlert, 2018).

Additionally, to assess whether and how much observed compositional changes differed from changes that could be expected under simulated, “quasi-random” circumstances, we developed a null model incorporating both a fixed and a stochastic component. The fixed component can be identified in the fact that, for each species, we derived extinction and colonization probabilities from observed data, while the stochastic component can be explained with our generating n simulated matrices filled with presences or absences randomly drawn based on the colonization and extinction probabilities that were earlier derived. The null model, which was named “Random-Extinction-Colonization” (REC) model, was built according to the following steps. First, for each species in its own habitat, a probability of extinction and a probability of colonization were estimated from the community matrices as follows (# stands for “number of cases”):

$p_i^{ext} = (\# \text{ the species } i \text{ was present in a plot at } T_0 \text{ but was not present in the same plot at } T_1) / (\text{number of plots occupied by species } i \text{ at } T_0)$

$p_i^{col} = (\# \text{ the species } i \text{ was present in a plot in } T_1 \text{ but was not present in the same plot in } T_0) / (\text{number of plots not occupied by species } i \text{ at } T_0)$.

Thus, p_i^{ext} and p_i^{col} were estimated as the relative frequencies of, respectively, local extinctions and colonizations of the i^{th} species recorded in the data.

Second, 1000 simulated T_1 matrices were generated using the following procedure:

1. For each plot where the species i was present in the observed T_0 matrix, generate its corresponding presence/absence in the simulated T_1 matrix by drawing a random value from Bernoulli distribution with probability $1 - p_i^{ext}$, i.e. simulate its possible extinction.
2. For each plot where the species i was **not** present in the observed T_0 matrix, generate its corresponding presence/absence in the simulated T_1 matrix by drawing a random value from Bernoulli distribution with probability p_i^{col} , i.e. simulate its possible colonization.
3. Repeat steps 1 and 2 for each species.

Third, for each of the 1000 simulated T_1 matrices, dissimilarity values (in this case, SERr and its two components of loss and gain) were calculated between each plot in the observed T_0 matrix and its corresponding plot in the simulated T_1 matrix. This resulted in a vector of 1000 simulated dissimilarity values for each plot. The observed dissimilarity value for each plot was then compared with 0.025 and 0.975 quantiles of the simulated dissimilarity values for that plot.

2.3.2 Temporal changes in functional diversity

Changes in the functional footprint of Mediterranean coastal dunes were assessed using two approaches: functional dissimilarity and community weighted mean (CWM) values.

Functional dissimilarity (or functional β -diversity) can be interpreted as the dissimilarity in the functional space occupied by two communities and is computed as $F_{dis} = \text{Volume not shared} / \text{Total volume}$, resulting therefore equivalent to the well-known Jaccard's dissimilarity index based on the number of species (Villéger et al., 2011;2013). For each couple of plots, functional dissimilarity was computed using three functional traits: plant height, Specific Leaf Area (SLA) and plant life span. Specifically, a synthetic multidimensional space was built following the methodology described in Villéger et al. (2011) by first using Gower's distance (Gower, 1966) to compute functional distances among species, and then performing a principal co-ordinates analysis (PCoA) on the distance matrix and extracting the first two axes. Finally, functional dissimilarity between each pair of coupled plots was computed using R package betapart (function *functional.beta.pair*, Baselga et al., 2018) Given that to quantify the convex hull volume needed for characterizing a community in the functional space (and, consequently, computing functional dissimilarity between communities), the number of species must be higher than then number of dimensions, plots that did not comply to this rule (i.e. plots with species richness < 3) were removed, together with their historical counterparts. Functional dissimilarity was therefore computed on a set of 180 couple of plots. Then, to test whether these 180 observed values of functional dissimilarity exceeded values that could be expected given simulated, "quasi-random" conditions, we applied the same "Random-Extinction-Colonization" (REC) model that we used for taxonomic dissimilarity. However, as functional dissimilarity can't be computed for plots whose species richness is lower than the number of dimensions, the REC model was modified as follows: in those simulated plots whose generated species richness, after running the REC model, was lower than 3, we asked the model to randomly assign n presences to reach the required threshold. It should be noted that this modification is prevalently affecting the most species-poor community (Habitat 1210).

Community weighted mean (CWM) values of plant height, SLA and life span were computed, for each plot at T_0 and at T_1 , using R package FD (function *functcomp*, Laliberté et al., 2014). More specifically, because of preliminary data cleaning described in section 2.3, CWM were computed on three subsets of the original dataset ($n=221$ pairs for plant height, $n=156$ pairs for SLA and $n=255$ pairs for life span). For plant height and SLA, CWM were calculated on log-transformed trait values (Májeková et al., 2016). To test whether changes in CWM values between T_0 and T_1 differed among single communities (identified through EU Habitats) linear regression models were used. For plant height and SLA, the temporal difference (delta) in CWM (CWM value at $T_1 - \text{CWM value at } T_0$) was modeled as a

function of the EU habitat, as classified at T_0 . As to lifespan, the abundance of each individual class ("perennial" and "not perennial") was computed. Given that, in each plot, such abundances are complementary and sum up to 1, we fitted a linear model specifying the temporal difference (Δ) in the abundance of perennial species as response variable, and EU habitat at T_0 as predictor.

2.3.3 Trends in occurrence frequency and cover of focal species

To characterize community changes at the level of single species, we followed two approaches. First, for each of the analyzed communities, species-abundance distributions were analyzed at T_0 and at T_1 by producing rank-abundance plots (also known as Whittaker plots). This was done using R package "BiodiversityR" (function: "rankabundance"; Kindt & Coe, 2005). Rank-abundance plots are recognized among the most informative methods for visualizing species-abundance distributions, and are particularly effective when illustrating changes in time (Magurran, 2013). In addition, trends in occurrence frequency and cover were analyzed for 38 focal species, which were chosen by selecting, among the "diagnostic" and "characteristic" species listed by the Italian Interpretation Manual of the 92/43/EEC Habitats Directive (Biondi et al. 2009), those that were sufficiently represented in our database. To obtain a synthetic measure of change we computed, for each species in its own reference community, mean occurrence frequency and cover at T_0 and at T_1 , together with their differences (value at T_1 – value at T_0). Mean occurrence frequency was computed dividing the number of species occurrences recorded during a specific survey by the total number of plots sampled during that survey, and the same was done to obtain mean cover. For each species, changes in occurrence frequency and cover between T_0 and T_1 were then tested using, respectively, McNemar's non-parametric test for dependent data (Agresti, 2003) and exact Wilcoxon-Pratt signed rank tests for paired samples. These tests were performed in R using packages "exact2x2" (function: `menemar.exact`; Fay, 2010) and "coin" (function: `wilcoxsign.test`; Hothorn et al., 2006;2008).

3. Results

3.1 Temporal changes in taxonomic diversity

At the time of the resurvey, 78 out of 334 plots were disappeared: mostly, they were found to be completely unvegetated or submerged by the sea. About 70% of these disappeared plots originally belonged to upper beach and embryo dunes, but there were plots disappearing also in more inland habitats (see Appendix I).

In all investigated communities, values of SER_c and SER_a were medium to high: average SER_c values ranged from 0.68 in fixed dunes (Habitat 2210) to 0.88 in upper beach (Habitat 1210), while average SER_a values ranged from 0.75 in fixed dunes (Habitat 2210) to 0.94 in upper beach (Habitat 1210), indicating large and simultaneous shifts in both species identity and in the dominance structure (Fig. 1).

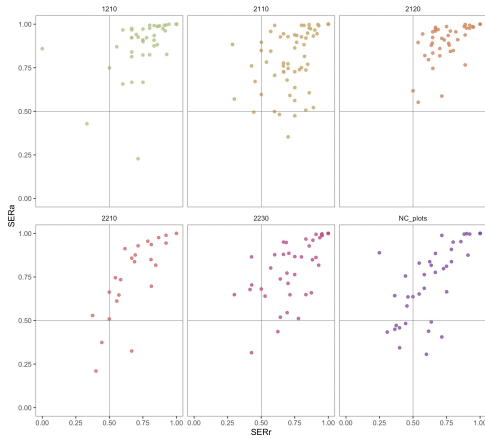


Fig.1 SER_r and SER_a plotted on the two axes. In each habitat, the majority of the points lies in the upper-right quadrant, indicating large and simultaneous shifts in both species identity and in the dominance structure.

Significant differences were found when testing values of SER_r (Kruskal-Wallis $p < 0.001$) and SER_a against habitat. Values of both metrics in upper beach (Habitat 1210) were found to be significantly different from those of all other habitats (see Appendix II for detailed results of post-hoc tests).

Decomposing SER_r into its components of loss and gain revealed a substantially homogeneous pattern throughout the communities: loss was dominant in the majority of habitats (Fig. 2B).

Taxonomic dissimilarity, summarized by SER_r , was significantly larger than simulated dissimilarity in 1.11% (Habitat 2110) to 13.33% (NC plots) of the plots (Fig. 2C). On average, observed loss exceeded simulated loss more often than gain. Specifically, observed taxonomic loss was significantly higher than what could be expected under quasi-random circumstances in 4.17% (Habitat 2210) to 34.44% (Habitat 1210) of the plots. Finally, values of observed taxonomic gain significantly exceeded simulated ones in 4.17% (Habitat 2210) to 14.44% (Habitat 1210) of the plots. Detailed proportions about the proportion of plots with observed changes significantly larger than simulated changes are reported, for each habitat and each index, in Appendix III.

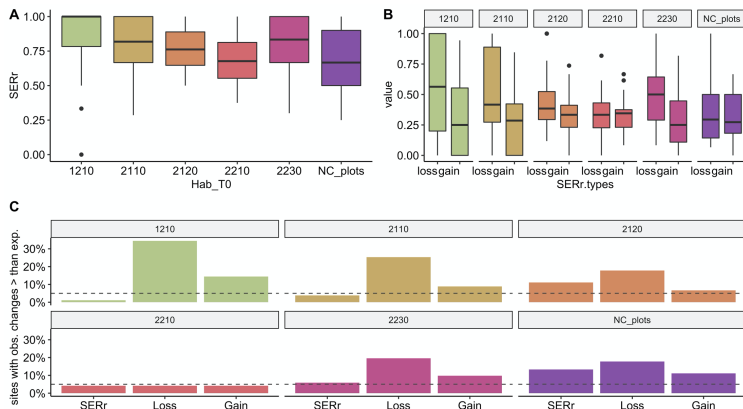


Fig. 2. A) boxplots displaying values of the Species Exchange Ratio metric based on presence-absence (SER_p) distributed among different European Habitats. B) values of $SER_{r,loss}$ and $SER_{r,gain}$ distributed among EU Habitats. C) Proportion of plots with non-random observed changes. For each dissimilarity metric (SER_r and its components of loss and gain), vertical bars represent the proportion of plots whose observed change was significantly larger than change simulated by the REC model. The dashed line represents an alpha level of 0.05, corresponding to the probability of the simulations obtained by the REC null model being exposed to Type 1-error.

3.2 Temporal changes in functional diversity

Functional dissimilarity was also medium to high (average values of F_{dis} ranged from 0.63 in NC plots to 0.79 in Habitat 1210, see Fig. 3A). Significant differences (Kruskal-Wallis $p < 0.001$) were found in values of F_{dis} among communities, and in particular between coastal dune grasslands (Habitat 2230) and: upper beach (Habitat 1210, $p = 0.010$), embryo dunes (Habitat 2110, $p < 0.001$) and shifting dunes (Habitat 2120, $p = 0.017$). When decomposing F_{dis} into its loss and gain component, gain was found to be, in general, the prevailing component (Fig. 3B). Observed functional dissimilarity, summarized by F_{dis} , was found to be significantly larger than simulated dissimilarity in 0% (Habitat 1210) to 8.33% (NC_plots) of the plots. Values of observed functional loss significantly exceeded those simulated by the model in 0% (Habitat 1210, 2210) to 12.12% (Habitat 2120) of the sites.

When compared to functional loss, the proportion of plots with observed gain values significantly higher than simulated ones was generally lower, ranging from 0% (Habitat 2210, 2230) to 5.56% (Habitat 1210). Detailed proportions about the proportion of plots with observed changes significantly larger than simulated changes are reported, for each habitat and each index, in Appendix III.

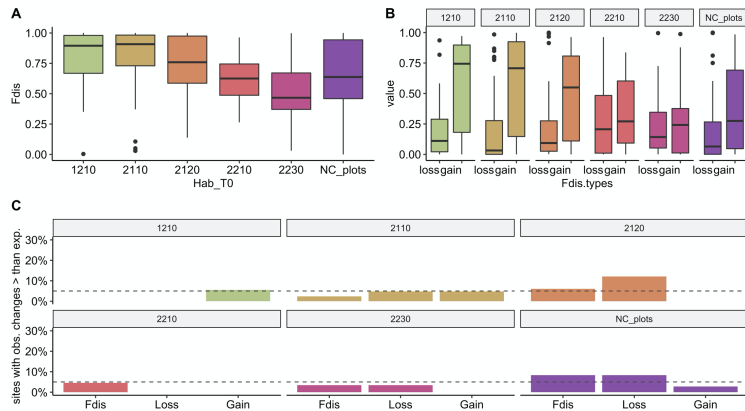


Fig. 3. A) boxplots displaying values of functional dissimilarity (F_{dis}) distributed among different European Habitats. B) values of $F_{dis,loss}$ and $F_{dis,gain}$ distributed among EU Habitats. C) Proportion of plots with non-random observed changes. For each dissimilarity metric (SER_r and its components of loss and gain), vertical bars represent the proportion of plots whose observed change was significantly larger than change simulated by the REC model. Where no bar appears, the proportion of plots experiencing non-random changes, as returned by the REC model, is zero. The dashed line represents an alpha level of 0.05, corresponding to the probability of the simulations obtained by the REC null model being exposed to Type 1-error.

During the analyzed time period, considerable changes could be also observed in values of the analyzed plant traits. Results of linear models revealed that changes in plant height and specific leaf area (SLA) were only significant in shifting dunes (Habitat 2120, Fig. 4), which experienced a decrease in plant height ($t = -7.253$, $p < 0.001$) and an increase in SLA ($t = -8.240$, $p < 0.001$).

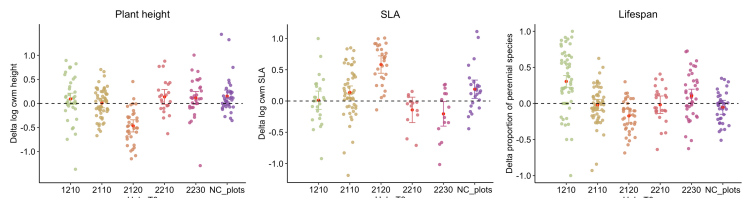


Fig. 4. Temporal changes in community weighted mean (CWM) values computed on log-transformed plant height (left panel) and SLA (middle panel) and in the relative abundance of perennial species, distributed among EU Habitats. The dashed line represents no change. Points standing above and below the line represent, respectively, plots that increased or decreased in their CWM value. For each habitat, confidence intervals are represented by an error bar, and the mean estimate is visualized as a red point on the error bar.

As to life span, the relative abundance of perennial species (fig. 4) significantly increased in upper beach (Habitat 1210; $t = 7.438$, $p < 0.001$) while substantially decreasing in shifting dunes (Habitat 2120; $t = -3.550$, $p < 0.001$).

3.3 Trends in occurrence frequency and cover of focal species

In all analyzed communities, the analysis of rank abundance plots and species-abundance distributions revealed considerable changes between the two time points (see Fig. 5 and Appendix IV for species-abundance distributions at T₀ and T₁).

Changes in relative abundances were evident in all habitats, although especially in upper beach and shifting dunes. Here, the most abundant species at T₀ (respectively, *Cakile maritima* and *Ammophila arenaria* subsp. *australis*) were replaced, at T₁, by *Elymus farctus*, diagnostic species of embryo dunes. In addition, a marked decreasing trend over time could be observed in the relative abundance value of the species ranked first, suggesting changes in the dominance structure and evenness of the communities.

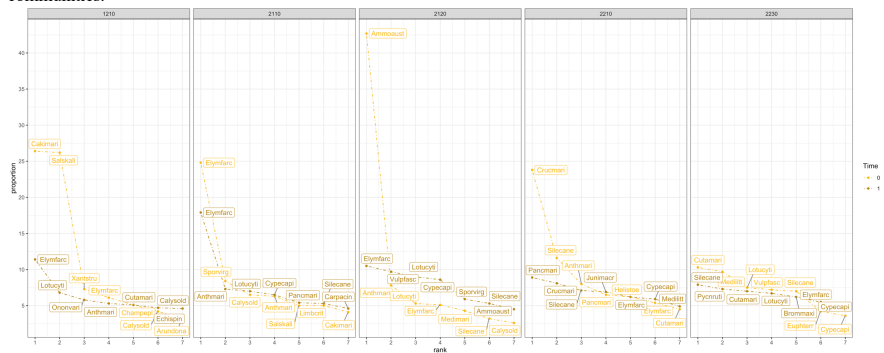


Fig. 5. Rank-abundance plots at T₀ and at T₁ for the analyzed EU Habitats. For simplicity, only the seven most abundant species for each habitat at each time point are listed. To keep the plots as tidy as possible, species names were abbreviated using eight-letter abbreviations. An alphabetically ordered list of abbreviations used and complete names follows (for the sake of simplicity, nominal subspecies are not reported). AMMOAUST: *Ammophila arenaria* subsp. *australis*, ANTHMARI: *Anthemis maritima*, ARUNDONA: *Arundo donax*, BROMMAXI: *Bromus diandrus* subsp. *maximus*, CAKIMARI: *Cakile maritima*, CALYSOLD: *Calystegia soldanella*, CARPACIN: *Carpobrotus acinaciformis*, CHAMPEPL: *Chamaesyce pepelis*, CRUCMARI: *Crucianella maritima*, CUTAMARI: *Cutandia maritima*, CYPECAPI: *Cyperus capitatus*, ECHISPIN: *Echinophora spinosa*, ELYMFARC: *Elymus farctus*, EUPHTERR: *Euphorbia terracina*, HELYSTOE: *Helichrysum stoechas*, JUNIMACR: *Juniperus oxycedrus* subsp. *macrocarpa*, LIMBCRIT: *Limbarda crithmoides*, LOTUCYTI: *Lotus cytiosides*, MEDILITT: *Medicago littoralis*, MEDIMARI: *Medicago marina*, ONONVARI: *Ononis variegata*, PANCMARI: *Pancretrium maritimum*, PYCNRUTI: *Pycnocedon rutilifolium*, SALSALKALI: *Salsola kali*, SILECANE: *Silene canescens*, SPORVIRG: *Sporobolus virginicus*, VULPFASC: *Fulpia fasciculata*, XANTSTRU: *Xanthium strumarium*.

McNemar's and Wilcoxon signed rank tests revealed that changes in occurrence frequency and cover of focal species were often significant, and widespread among the analyzed habitats. Changes in occurrence frequency were significant for 16 out of the 38 tested diagnostic species, which all experienced a decrease over time (Fig. 6). *Ammophila arenaria* subsp. *australis* and *Cakile maritima* underwent the most negative trend, their occurrence frequencies dropping, respectively, by 79.5% and 53.5%. As to changes in standardized cover, half of the species tested (19 out of 38) experienced significant changes. Negative trends were more common than positive trends, which were only observed in a few species diagnostic of embryo and shifting dunes.

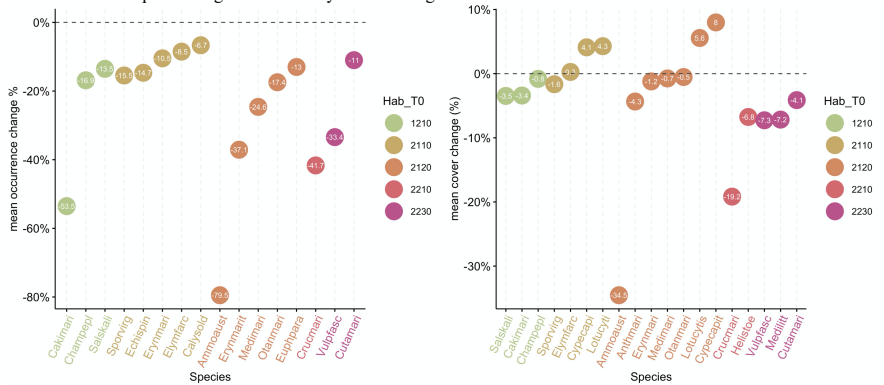


Fig. 6. Changes in mean occurrence frequency and cover of the diagnostic species of each habitat. Only species that underwent significant changes are reported.

4. Discussion

Our results reveal that the last 10-15 years considerably reshaped coastal dune habitats of Central Italy. Observed taxonomic changes, effectively summarized by relatively the high values of dissimilarity indices and mostly driven by species loss, suggest strong shifts in the species composition and in the dominance structure of most EU habitats. Transformations in the functional profile, on the other hand, were particularly visible in upper beach and mobile dunes, as highlighted by the CWM analysis. Though varying among habitats, changes were evident at both the community level and at the species level. This, together with the disappearance of almost 25% of the historical plots and with observed changes often exceeding “simulated changes” (though with substantial differences among EU habitats and analyzed indices), should draw attention to the fate of one of the most vulnerable ecosystems on earth (Schlachter et al., 2007; Janssen et al., 2016).

Altogether, results point to the first portion of the coastal zonation (upper beach and foredunes) having experienced the most intense changes throughout the analyzed time-span, thus confirming first evidences by Sperandii et al. (2019). Although this is generally acknowledged as the most dynamic sector in one of the most dynamic ecosystems (Acosta et al., 2003; 2009), a more in-depth analysis of these transformations mostly hints at diffused and possibly ongoing degradation processes.

Upper beach was among the most affected communities in terms of both disappeared plots and compositional shifts. Here, taxonomic changes were particularly intense and appeared to be dominated by the loss component. Indeed, in the last 10-15 years annual species diagnostic of this habitat (cf. *Cakile maritima*, *Salsola kali*, *Chamaesyce pepelis*) substantially decreased in their occurrence frequency, and typical companion species (cf. *Xanthium strumarium*) similarly dropped in their proportional abundance. Analyzing rank-abundance plots and species abundance distributions reveals that, in survived plots, these species were replaced by perennial species characteristic of embryo dunes (cf. *Elymus farctus* and *Lotus cytisoides*). If we consider that about 63% of historical upper beach plots disappeared, we may interpret these as successional phenomena (Doing, 1985) taking place in “survived” plots that were probably less exposed to high disturbance, and therefore a) persisted throughout the years and b) could host a “normal” successional dynamic. This consideration, which,

however, only concerns a limited proportion of historical upper beach plots, is further confirmed by the functional analysis ran on survived plots, which outlines a high functional dissimilarity, driven by the gain component and probably reflecting the significant increase in perennial species over time (cf. community weighted mean analysis).

In shifting dunes, changes appear even more dramatic. Here, the dominance structure after the resurvey appears to be completely transformed and hints at a general degradation of the habitat: the diagnostic *Ammophila arenaria* subsp. *australis*, which is the most abundant species in historical shifting dunes, substantially decreases in both its occurrence frequency and cover, and is replaced by *Elymus farctus*, likely suggesting negative trends in the sand budget (Doing, 1985; Sykes & Wilson, 1990). Several other perennial diagnostic species (*Medicago marina*, *Eryngium maritimum*, *Anthemis maritima*) either decrease in their occurrence frequency or in their abundance, whereas on the other hand an alarming increase in terophytes appears to take place (cf *Vulpia fasciculata*, which becomes the second most abundant species at T₁). These results appear highly consistent with the functional analysis ran on survived plots, which reports a non-random, high functional dissimilarity where loss prevails, a significant decrease in both mean plant height of the plots and proportion of perennial species, and a parallel, substantial increase in SLA values. In this regard, the decrease in plant height is clearly connected to the loss of *Ammophila arenaria* subsp. *australis* and to the parallel increase of smaller-sized species (e.g. *Elymus farctus*, *Lotus cytisoides*, *Sporobolus virginicus*, *Cyperus capitatus*). The increase in SLA values, on the other hand, appears to be more closely related to the increase of fast-growing, annual species (cf. *Vulpia fasciculata* and *Silene canescens*). Indeed, SLA is regarded as a good proxy of a plant's potential growth rate, and high SLA values generally characterize species with low investments in leaf "defences" and lifespan (Cornelissen et al., 2003).

Although other habitats appear to have only been affected to a lesser extent, some negative signals can be anyway retrieved from the analysis of focal species, and could be interpreted as early warning of habitat disruption (Del Vecchio et al., 2016). In embryo dunes, a relatively marked decrease in the occurrence of *Elymus farctus* took place together with that of *Sporobolus virginicus*, another rhizomatous diagnostic species of this habitat that has been shown to respond to increased disturbance with reductions in regeneration success and spread capacity (Balestri & Lardicci, 2013). Similarly, fixed dunes experienced an alarming decrease in *Crucianella maritima*, a rare suffruticose chamaephyte featuring a highly fragmented distribution and currently considered as particularly endangered (Carboni et al., 2010). On the other hand, despite previous insights about temporal trends experienced by this habitat (Sperandii et al., 2018) coastal dune grasslands appeared as the most stable community, being mostly characterized by a replacement in annual species.

Overall, two trends emerge when looking at results from the null models: on the one hand, observed taxonomic changes were higher-than-expected (although to a variable extent) in all habitats except for fixed dunes (Hab 2210), and these changes were most often driven by the component of species loss. On the other hand, shifting dunes were the only EU Habitat displaying a simultaneous, strong signal of non-random changes affecting both the taxonomic and the functional sphere, further warning about the extent of degradation processes affecting this community already highlighted by other analyses. In this regard, however, it should be noted that, due to inner constraints of the algorithm used (see par. 2.3.2), simulations of functional dissimilarity (and of its two components of loss and gain) might have somehow underestimated the significance of observed changes, especially in upper beach. Additionally, the significance of these findings should be weighted on the type of community involved. Upper beach is the closest community to the seashore, the most exposed to both natural (i.e. winter storms, tidal oscillations, cf Davy & Figueroa, 1993) and anthropogenic stressors (i.e. trampling, beach recreational activities), and its strong adaptations to disturbance, such as its almost exclusive composition in annual species, make it highly shifting and ephemeral (Doing, 1985; Davy & Figueroa, 1993; Maun, 2009), thus calling for cautiousness when interpreting temporal changes (Sperandii et al., 2019). Shifting dunes, on the contrary, are mostly formed by perennial species, making the detection of important changes in this community hardly attributable to "inner, inter-annual variability". Moreover, hosting a number of rhizomatous sand-binding species (cf. *Ammophila arenaria* subsp. *australis*), this habitat plays a pivotal role in dune formation and stabilization, being therefore of utmost importance in the provision of key ecosystem services (Van der Biest et al., 2017) such as protection against coastal hazards (Arkema et al. 2013; Aucelli et al., 2018), so we should be aware that the degradation and the eventual loss of this habitat would have a cascade effect on the entire ecosystems and on the wide range of services provided.

5. Conclusions

With this paper, we provide a habitat-based quantification of taxonomic and functional patterns characterizing coastal dune ecosystems of Central Italy, highlighting those habitats that experienced the most dramatic transformations and therefore offering sound and useful insights for directing conservation and management efforts. As human activity historically modified natural vegetation in Central Italy as well as across the whole Mediterranean (Malavasi et al., 2018; Defeo et al., 2009; Doxa et al., 2017) coastal dune systems of our study area can be considered representative of typical Mediterranean coastal dune systems, and our trends could be therefore potentially representative of Mediterranean coastal dune systems. We believe that working on different facets of change (i.e. taxonomic and functional) and at multiple levels of biological organization (i.e. community and species) allowed us to gain a fair picture of what happened in these last 10-15 years and to identify EU habitats (*sensu* 92/43/EEC) that appear to be more “at risk”. Based on our findings, upper beach, but especially shifting dunes underwent the most negative trend, and should be therefore the target of urgent and specific conservation and restoration measures. However, early warnings of degradation could be also observed in other communities, and should be consequently foster their monitoring. As is often the case in research, we believe there is still much room for improving this picture: in this sense, we believe that a first, crucial challenge, would be to identify potential causes and drivers of such changes. Indeed, the development of effective management practices should include not only a thorough knowledge of the habitat, but also identification of the processes taking place and of their causes.

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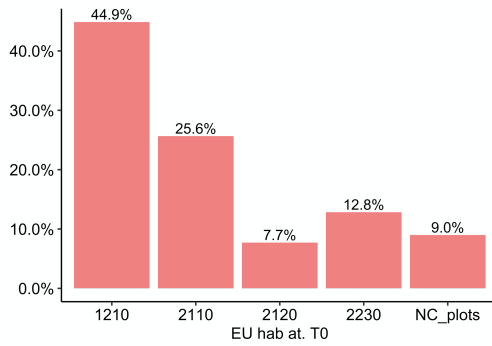
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Appendix I. Distribution of disappeared plots among EU habitats.



Appendix II. Results of Dunn’s all-pairs tests on pairwise comparisons of SER_r and SER_a. In the table, Holm-corrected p-values are reported.

<i>Index</i>	<i>EU Hab T0</i>	<i>1210</i>	<i>2110</i>	<i>2120</i>	<i>2210</i>	<i>2230</i>
SER _r	<i>2110</i>	0.00569	-	-	-	-
SER _r	<i>2120</i>	0.00081	1	-	-	-
SER _r	<i>2210</i>	0.00000893	0.09428	0.61478	-	-
SER _r	<i>2230</i>	0.02970	1	1	0.11267	-
SER _r	<i>NC plots</i>	0.00000091	0.12771	1	1	0.16492
SER _a	<i>2110</i>	0.00013	-	-	-	-
SER _a	<i>2120</i>	0.01085	1	-	-	-
SER _a	<i>2210</i>	0.00000067	0.12715	0.09833	-	-
SER _a	<i>2230</i>	0.00062	1	1	0.22303	-
SER _a	<i>NC plots</i>	0.00000028	0.38959	0.30563	1	0.60532

Appendix III. Proportion of plots with taxonomic and functional dissimilarity above 95% confidence limits of the REC null model.

<i>Index or component tested</i>	<i>EU Hab</i>	<i>Proportion of plots (%) with taxonomic change higher than expected</i>	<i>Proportion of plots (%) with functional change higher than expected</i>
Dissimilarity	1210	1.1	0
Dissimilarity	2110	3.8	2.4
Dissimilarity	2120	11.1	6.1
Dissimilarity	2210	4.2	4.5
Dissimilarity	2230	5.9	3.4
Dissimilarity	NC plots	13.3	8.3
Loss	1210	34.4	0
Loss	2110	25.3	4.8
Loss	2120	17.8	12.1
Loss	2210	4.2	0
Loss	2230	19.6	3.4
Loss	NC plots	17.8	8.3
Gain	1210	14.4	5.6
Gain	2110	8.9	4.8
Gain	2120	6.7	0
Gain	2210	4.2	0
Gain	2230	9.8	0

Appendix IV. Species abundance distributions for each analyzed habitat at T₀ and at T₁. For simplicity, only the seven most abundant species for each habitat at each time point are listed. Proportional abundance values were computed as the ratio between the total cover of the species in the habitat and the total cover of all species in that habitat.

EU Habitat	Species T ₀	rank	Proportional abundance T0 (%)	Species T ₁	Proportional abundance T1 (%)
1210 Annual vegetation of drift line (Upper beach)	<i>Cakile maritima</i>	1	26,4	<i>Elymus farctus</i>	11,4
	<i>Salsola kali</i>	2	26,2	<i>Lotus cytoides</i>	6,8
	<i>Xanthium strumarium</i>	3	7,3	<i>Ononis variegata</i>	5,8
	<i>Elymus farctus</i>	4	6,1	<i>Anthemis maritima</i>	5,3
	<i>Chamaesyce peplis</i>	5	5,1	<i>Cutandia maritima</i>	5,1
	<i>Calystegia soldanella</i>	6	4,2	<i>Calystegia soldanella</i>	4,7
	<i>Arundo donax</i>	7	3,2	<i>Echinophora spinosa</i>	4,6
2110 Embryonic shifting dunes (Embryo dunes)	<i>Elymus farctus</i>	1	24,8	<i>Elymus farctus</i>	17,9
	<i>Sporobolus virginicus</i>	2	8,4	<i>Anthemis maritima</i>	7,3
	<i>Calystegia soldanella</i>	3	6,5	<i>Lotus cytoides</i>	7
	<i>Anthemis maritima</i>	4	6,3	<i>Cyperus capitatus</i>	6,5
	<i>Salsola kali</i>	5	5	<i>Pancratium maritimum</i>	5,4
	<i>Limbarda crithmoides</i>	6	5	<i>Silene canescens</i>	5,3
	<i>Cakile maritima</i>	7	4,1	<i>Carpobrotus acinaciformis</i>	4,6
2120 Shifting dunes along the shoreline with <i>Ammophila</i> <i>arenaria</i>	<i>Ammophila arenaria</i>	1	42,7	<i>Elymus farctus</i>	10,5
	<i>Anthemis maritima</i>	2	7,8	<i>Vulpia fasciculata</i>	9,7
	<i>Lotus cytoides</i>	3	5,3	<i>Lotus cytoides</i>	9
	<i>Elymus farctus</i>	4	5,1	<i>Cyperus capitatus</i>	8,6
	<i>Medicago marina</i>	5	4,3	<i>Sporobolus virginicus</i>	5,9
	<i>Silene canescens</i>	6	3,2	<i>Silene canescens</i>	5,3
	<i>Calystegia soldanella</i>	7	2,6	<i>Ammophila arenaria</i>	4,5
2210 <i>Crucianellion</i> <i>maritimae</i> fixed beach dunes	<i>Crucianella maritima</i>	1	23,8	<i>Pancratium maritimum</i>	8,9
	<i>Silene canescens</i>	2	11,6	<i>Crucianella maritima</i>	8,1
	<i>Anthemis maritima</i>	3	8	<i>Silene canescens</i>	7,1
	<i>Pancratium maritimum</i>	4	6,5	<i>Juniperus oxycedrus macrocarpa</i>	6,9
	<i>Helichrysum stoechas</i>	5	6,2	<i>Elymus farctus</i>	6,2
	<i>Elymus farctus</i>	6	5,4	<i>Cyperus capitatus</i>	5,9
	<i>Cutandia maritima</i>	7	4,5	<i>Medicago littoralis</i>	4,9
2230 <i>Malcolmietalia</i> dune grasslands	<i>Cutandia maritima</i>	1	10,3	<i>Silene canescens</i>	7,9
	<i>Medicago littoralis</i>	2	9,7	<i>Pycnocomon rutifolium</i>	7,3
	<i>Lotus cytoides</i>	3	7,5	<i>Cutandia maritima</i>	7
	<i>Vulpia fasciculata</i>	4	7,2	<i>Lotus cytoides</i>	6,7
	<i>Silene canescens</i>	5	7	<i>Bromus diandrus maximus</i>	6,2
	<i>Euphorbia terracina</i>	6	4,2	<i>Elymus farctus</i>	5,5
	<i>Cyperus capitatus</i>	7	3,6	<i>Cyperus capitatus</i>	4,6

Discussion

During the last three years, I have been dealing with the assessment of temporal changes in coastal dune communities of Central Italy by using different approaches, analyzing different aspects of biodiversity (taxonomic and functional), and working at multiple levels of biological organization (community and species). While in the first year I extracted trends out of a large database of randomly sampled plots, the following years were dedicated to planning and implementing a large resurveying study aimed at revisiting, after 10 to 15 years, 334 historical coastal dune plots belonging to the first portion of coastal zonation (from drift line communities up to coastal dune grasslands) and covering about 75 km of coasts located in two administrative regions.

Chapter 1 includes a diachronic analysis of Italian coastal dune habitats performed by extracting temporal trends out of “RanVegDunes”, a large database including 979 randomly sampled, standardized, georeferenced floristic plots. Analyses were run on a subset of 858 plots referring to herbaceous and shrub formations (from sand beach drift lines up to Mediterranean coastal scrub), with each plot being sampled once between 2002 and 2015 in different spatial locations along sandy coastlines of 5 Italian administrative regions (Lazio, Campania, Abruzzo, Molise and Puglia).

Throughout the analyzed time-span, I found evidences of a significant decrease in species richness and cover of coastal dune grasslands (EU Habitat 2230), further supported by a decrease in the cover of two of their characteristic species (*Cutandia maritima* and *Medicago littoralis*). Individual trends experienced by single species revealed interesting insights also in other communities, alerting about signs of habitat deterioration that could not be detected at the habitat level. This was the case for *Crucianella maritima* and *Juniperus oxycedrus* ssp. *macrocarpa*, which all experienced a marked decrease over the years: the first is a rare and endangered chamaephyte featuring a highly fragmented distribution, while the second is a Mediterranean shrub characterizing the EU priority habitat 2250* - Coastal dunes with *Juniperus* spp.

Another striking trend emerged analyzing temporal patterns of invasion. In shifting coastal dunes, a concerning increase in the cover of *Carpobrotus* sp. was detected, which appeared particularly alarming considering that, in the same community, a significant decline in the cover of *Ammophila arenaria* subsp. *australis*, key sand-binding species of mobile dunes, was observed. This chapter confirmed diachronic analyses based on random plots as useful and versatile tools in the study of temporal trends in coastal dune habitats,

providing preliminary knowledge on their short-to-medium temporal dynamics, while also possibly contributing to the development of conservation activities and of species-specific measures.

In **Chapter 2**, based on data collected during the first year of the resurveying study I perform an analysis of temporal changes at the community- and at the species level while disentangling the relative role of “species turnover” and “nestedness effect” in driving such changes. As this project was the first implementation of a resurveying study based on quasi-permanent random plots in coastal dunes, it also served for testing the effectiveness of the method in these ecosystems, especially considering that historical plots were resurveyed after 10 to 15 years, which is generally considered a short/medium time-span.

Though only based on 188 out of the 334 plots included in the resurveying study, results already hinted at considerable transformations characterizing coastal dune ecosystems during the analyzed time-span. More than 20% of the historical plots actually disappeared, resulting unvegetated or submerged by the sea. At the same time, a beta-diversity analysis revealed substantial compositional changes which turned out to be mainly driven by a “species turnover” effect and mostly involved the first portion of the coastal zonation (i.e. drift line communities, embryo and shifting dunes). Further analyses on focal species confirmed this negative trend, revealing the disappearance of key diagnostic species of both drift line communities (*Cakile maritima*, *Salsola kali*, *Chamaesyce pepelis*) and foredunes (*Eryngium maritimum*, *Calystegia soldanella*, *Echinophora spinosa*). The most alarming warning, however, came from foredunes, where *Ammophila arenaria* subsp. *australis* and *Elymus farctus*, key species known for their fundamental role in dune formation and stabilization, underwent a considerable decrease in their occurrence frequency.

Finally, in **Chapter 3** I provide a comprehensive, habitat-based, multi-dimensional assessment of temporal changes characterizing Mediterranean coastal dunes of Central Italy in the last 10-15 years. This is the conclusive work of the resurveying project, where I analyzed the complete set of historical and resurveyed data. Confirming preliminary results emerged from Chapter 2, this work provided further evidences of dramatic transformations, spanning across levels of biological organization and affecting both taxonomic and functional diversity of coastal dune communities in the last 10-15 years. This, together with the disappearance of 78 out of the 334 historical plots and with observed changes often exceeding changes simulated by null models, revealed an intense vulnerability characterizing most coastal dune habitats. Drift line communities (EU Habitat 1210) and

shifting dunes with *Ammophila arenaria* (EU Habitat 2120) were identified as being particularly “at risk”. In drift line communities, about 63% of the historical plots disappeared during the last 10-15 years. In those that survived, diagnostic species of the habitat (cf. *Cakile maritima*, *Salsola kali*, *Chamaesyce pepelis*) and typical companion species (cf. *Xanthium strumarium*) substantially decreased in their occurrence frequency and/or in their proportional abundance, and were replaced (as also confirmed by the functional analysis) by perennial species characteristic of embryo dunes (cf. *Elymus farctus* and *Lotus cytisoides*). This, in spite of a general negative trend experienced by this habitat, is the only evidence of “normal” successional dynamics taking place in plots that survived, probably because they were located in more sheltered sites and/or were less exposed to high disturbance. In shifting dunes, changes were even more dramatic: the diagnostic *Ammophila arenaria* subsp. *australis* decreased in its occurrence frequency by almost 80% and was replaced by *Elymus farctus* (diagnostic species of embryo dunes). Several other perennial species (*Medicago marina*, *Eryngium maritimum*, *Anthemis maritima*) either decreased in their occurrence frequency or in their abundance, whereas on the other hand an alarming increase in terophytes appears to take place (cf. *Vulpia fasciculata*, which becomes the second most abundant species at T₁). Such results were confirmed by the functional analysis ran on survived plots, which reported a non-random, high functional dissimilarity dominated by the loss component, a significant decrease in both mean plant height of the plots and proportion of perennial species, and a parallel, substantial increase in Specific Leaf Area (SLA) values. While coastal dune grasslands appeared as the most stable community, being mostly characterized by a replacement in annual species, further signs of habitat degradation emerged from the analysis of focal species in embryo dunes and in fixed dunes.

General conclusions

Aim of this project was to assess taxonomic and functional patterns of temporal changes in coastal dune systems, while at the same time highlighting drivers of change.

In this regard, I believe that the use of metrics informative of different components of biodiversity (e.g. composition, relative abundance, occurrence of key species), together with the inclusion of multiple dimensions (i.e. taxonomic and functional) and levels of biological organization (i.e. community and species), allowed me to provide a fairly comprehensive and reliable picture of changes characterizing coastal dune habitats of Central Italy in the last 10-15 years. Along with enhancing the knowledge of temporal dynamics in these vulnerable ecosystems, I also identified, throughout the chapters, the communities that appear to be more “at risk”, therefore supplying an important resource to direct future conservation efforts and management strategies.

It could be argued that the two approaches used for quantifying temporal trends (the diachronic analysis based on a large vegetation database and the resurveying study) did not provide completely homogeneous results. Indeed, the diachronic analysis revealed a negative trend experienced by coastal dune grasslands that was not confirmed by the resurveying study. In this regard, a few considerations should be made. First, the two approaches are not directly comparable: on the one hand, the diachronic analysis focused on coastal dune systems located on a much wider study area (five administrative regions against the two analyzed by the resurveying study), and on the other hand the variables summarizing temporal changes differed between the two approaches. Second, although the diachronic analysis highlighted, in coastal dune grasslands, a negative trend that was not detected by the resurveying study, it also hinted at early warnings of habitat degradation in shifting dunes and in other communities (e.g. fixed dunes dominated by *Crucianella maritima*), which were later confirmed by the resurveying study. That being said, one of the outcompeting advantages of resurveying studies based on quasi-permanent plots over methods that do not allow direct comparisons between old and new plots is the reliability of the estimations, as also pointed out by Chytrý et al., 2014; Kapfer et al., 2017.

Although a more in-depth analysis of the drivers of change is still missing, field observations and preliminary landscape analyses allowed to identify a few potential determinants, whose relative importance will be more accurately tested in the next months. The first one is coastal erosion, directly connected to the loss of most historical plots, especially on the Adriatic coast.

Whereas erosion is a natural process, it is accelerated erosion that appears to be the problem, and this is generally driven by anthropogenic impacts or activities such as, e.g. sea level rise as a result of global warming, decreased sediment supply, construction of harbours and coastal defence structures (Pranzini et al., 2015).

Urbanization could also have acted as a major driver of change. Especially on the Adriatic coast, the construction of harbours, resorts and tourism facilities appeared to have strongly reshaped the dunal landscape during the analyzed time-span.

A third candidate is tourism, a general word that I am using here to include activities spanning from human trampling to mechanical cleaning of the beach. Whereas tourism can also cause the disappearance of some plots (especially in pioneer communities of the drift line), its main consequences are visible in the composition and structure of vegetation communities. Finally, invasion by alien species (mostly *Carpobrotus* sp., *Agave americana*, *Yucca gloriosa*, *Oenothera* sp.) also appeared to have severely impacted coastal dune communities. At the observational scales of this study, its main effects could be observed in the alteration of species composition: however, more profound consequences, such as modifications in soil parameters, are also known (Santoro et al., 2011; Novoa et al., 2014).

In conclusion, assessing changes through time is a challenging ecological task whose difficulty increases the more we extend our spatial and temporal scale of interest. For this reason, the need for a unified framework in the field of temporal ecology has been recently highlighted (Wolkovich et al., 2014). This will hopefully lead, in the near future, to the development of a variety of new methods and tools to: a) implement standardized protocols for the collection of new data; b) support the integration of new and existing temporal datasets; c) improve data analysis and provide theoretical and practical frameworks to solve current issues.

Although the picture started taking its shape, there is still room for improvement, something we can only attain if we keep collecting and analyzing data, i.e. if we keep monitoring ecosystems, possibly engaging specialists from other disciplines in the process. Meanwhile, however, an effective implementation of conservation and restoration measures is urgently needed, especially in shifting dunes with *Ammophila arenaria*: this habitat plays a pivotal role in dune formation and stabilization, being therefore of utmost importance in the provision of key ecosystem services (Van der Biest et al., 2017) such as protection against coastal hazards (Arkema et al., 2013; Aucelli et al., 2018). In this regard, it is our duty as vegetation scientists to raise awareness, at least among public managers and

administrators, on the importance of protecting this plant community and its key species, whose loss would have a cascade effect on the entire ecosystems: a future without *Ammophila arenaria* could likely mean a future without coastal dunes as we know them.

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