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Monitoring plant diversity in Mediterranean coastal landscapes: integration of field collected and remotely sensed data

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Short Abstract

Coastal dunes are facing an unprecedented loss of biodiversity mainly driven by human-related activities. By favoring habitat degradation and fragmentation and by facilitating the introduction of invasive species, anthropogenic pressures such as urbanization and tourism seriously threaten the biodiversity and functioning of dune ecosystems. In order to understand how anthropogenic and natural disturbances are altering these environments, and to identify effective strategies for managing coastal landscapes, new tools and approaches are urgently needed. In this regard, remote sensing allows the relationship between biodiversity and the environment to be investigated across a wide geographic extent, therefore representing a powerful tool for the analysis and monitoring of dune vegetation.

With the aim of analyzing plant diversity in Mediterranean coastal landscapes, in this thesis I focused on the integration of remotely sensed imagery and field-collected dune vegetation data. In particular, I characterized the morphological profile of coastal European Community-habitats (hereafter, EC-habitats; *sensu* EU Habitats Directive) and analyzed the influence of dune morphology in shaping the distribution of EC-habitats along the coastal zonation. Furthermore, I investigated the effect of shoreline dynamism on dune vegetation by analyzing changes in species richness, vegetation cover and diversity of plant communities undergoing different intensity of coastal erosion and accretion. Then I modelled the occurrence of the highly invasive *Carpobrotus* sp. along the Lazio dune system accounting for the simultaneous role of multiple drivers of invasion attributable to propagule pressure, abiotic and biotic factors. Predictions on *Carpobrotus* sp. occurrence were finally used to assess the invasibility of a group of coastal sites included in the Natura 2000 network of the Lazio region.

In each step of this project, remotely sensed data allowed robust analysis of how anthropogenic and natural processes shape plant diversity patterns in Mediterranean coastal landscapes. Results highlight that combining fine scale remote sensing imagery and field-collected vegetation data can effectively support the management and conservation of threatened ecosystems such as coastal dunes.

Keywords: dune vegetation; Geographic Information Systems (GIS); Light Detection And Ranging (LiDAR); orthophotos; invasive Species Distribution Model (iSDM); Natura 2000 network; coastal erosion and accretion.

Extended Abstract

Monitoring plant diversity in Mediterranean coastal landscapes: integration of field collected and remotely sensed data

Introduction

This PhD thesis dealt with the analysis of plant diversity pattern in Mediterranean coastal dunes as a function of geomorphological and biological processes extrapolated from high-resolution remotely sensed imagery including LiDAR (Light Detection and Ranging) and orthophotos. The main results of the following activities are reported:

- (A1) analysis of the relationship between European Community-habitats (hereafter, EC-habitats; *sensu* EU Habitats Directive) occurrence and dune morphology. (Chapter 1; Bazzichetto, M., Malavasi, M., Acosta, A. T. R., & Carranza, M. L. (2016). How does dune morphology shape coastal EC habitats occurrence? A remote sensing approach using airborne LiDAR on the Mediterranean coast. *Ecological indicators*, 71, 618-626)
- (A2) analysis of the influence of coastal erosion and accretion on dune vegetation. (Chapter 2; Bazzichetto, M., Sperandii, M. G., Acosta, A. T. R & Carranza, M.L. Disentangling the effect of coastal erosion and accretion on plant communities of Mediterranean dune ecosystems. *In prep.*)
- (A3) implementation of an invasive Species Distribution Model (iSDM) that accounts for the simultaneous influence of propagule pressure, abiotic and biotic (PAB) factors on the invasion of *Carpobrotus* sp. (Chapter 3; Bazzichetto, M., Malavasi, M., Barták, V., Acosta, A. T. R., Moudrý, V., & Carranza, M. L. (2018). Modeling plant invasion on Mediterranean coastal landscapes: An integrative approach using remotely sensed data. *Landscape and Urban Planning*, 171, 98-106)
- (A4) proposal of an iSDM-based methodology for assessing the vulnerability to plant invasion of protected coastal sites. (Chapter 4; Bazzichetto, M., Malavasi, M., Bartak, V., Acosta, A. T. R., Rocchini, D., & Carranza, M. L. (2018). Plant invasion risk: A quest for invasive species distribution modelling in managing protected areas. *Ecological Indicators*, 95, 311-319)

Materials and Methods

Analysis of the relationship between EC-habitats and dune morphology (A1)

The study was carried out on a Tyrrhenian dune system of central Italy. A set of 394 (2x2 meters) vegetation plots whose location was determined at random in a GIS environment were surveyed in spring (April-May) over the period 2006-2011 and assigned to six EC-habitats (*sensu* EU Habitats Directive). The mean values of a set of morphological and topographical variables (elevation, sea distance, slope, curvature, northness, eastness) were derived from a LiDAR Digital Terrain Model (2 m resolution) at a 4 m buffer radius around each vegetation plot in an ArcGIS environment. EC-habitat elevation, sea distance, slope and curvature were

compared using the non-parametric Kruskal-Wallis rank test, while the Dunn's test was performed to examine the difference between coupled habitat types. Differences among EC-habitat northness and eastness were tested using the parametric one-way ANOVA. Separate binomial Generalized Linear Models were fit for each habitat type to assess the relationship between EC-habitats occurrence and dune morphology. The presence/absence of each EC-habitat (in all 394 plots) was set as response variable and the morphological variables as predictors. Candidate models were compared using Akaike Information Criterion (AIC), with the model having lowest AIC being best. Finally, Bayesian Information Criterion (BIC) scores were computed to evaluate the strength of the relationship between EC-habitats and morphological variables.

Effects of coastal erosion and accretion on dune vegetation (A2)

Effects of coastal erosion and accretion on dune vegetation were investigated along the Lazio dune system using remotely sensed data. Polygons derived from aerial orthophotos and quantifying the amount of space gained or lost from 1994 to 2012 due to shoreline dynamism were retrieved from the “Geoportale Nazionale” (<http://www.pcn.minambiente.it/mattm/>). A polygon Shape Index (SI_{change}) was computed as the ratio between the area of each polygon and its perimeter. The SI_{change} was used as a surrogate of the intensity of coastal erosion and accretion processes. In particular, low values of SI_{change} (close to 0), corresponding to convoluted coastal polygons deployed parallel to the coastline, indicated low accretion or erosion intensity. In contrast, high SI_{change} values ($\rightarrow \infty$), corresponding to compact polygons, represented strong erosion and accretion phenomena. Vegetation data were extracted from the national database “RanVegDunes”, which collects random, georeferenced and standardized plots originally sampled between 2002 and 2015 (Sperandii et al., 2017). For each plot, a list of vascular plant species is given together with their relative cover. Analyses focused on the following habitat categories (classified according to the Eunis classification system, Davies et al., 2004): B1.1, sand beach drift lines; B1.3, shifting coastal dunes; B1.4, coastal stable dune grassland; B1.6, coastal dune scrub. Different regression techniques were implemented for conducting analyses at the community-level. In particular, Linear Models (LMs) and Poisson Generalized Linear Models (GLMs) were used to model the change in, respectively, habitat cover and species richness of each Eunis category as a function of SI_{change} . Furthermore, Regression Trees (RTs) based on conditional inference were used to identify a threshold in the SI_{change} . This threshold allowed plots characterized by significantly different species richness and cover to be grouped according to their erosion/accretion intensity. At the same time, the species-specific response to erosion/accretion of a set of focal species (belonging to the aforementioned Eunis categories) was investigated. To this end, a proportional test was used to assess the change in the occurrence frequency of the selected diagnostic species recorded in vegetation plots associated with increasing intensity of erosion/accretion.

Implementation of the PAB-based *Carpobrotus* sp. distribution model (A3)

The study was carried out along the Lazio dune system (central Italy). Both the response variable (presence/absence of *Carpobrotus* sp.) and the predictors used as input for implementing the distribution model were derived from remotely sensed imagery. Monodominant patches of *Carpobrotus* sp. and nine land cover types (‘ART’ Artificial areas;

‘AGR’ Agricultural areas; ‘AFF’ Afforestation; ‘WDV’ Woody dune vegetation; ‘SWV’ Semi-natural woody vegetation; ‘SHV’ Semi-natural herbaceous vegetation; ‘BPV’ Beach pioneer vegetation; ‘HDV’ Herbaceous dune vegetation; ‘WET’ Wetlands) were mapped through panchromatic digital aerial orthophotos with 1 m resolution. Three set of variables selected as surrogates for propagule pressure (P), abiotic (A) and biotic (B) factors that are likely to affect *Carpobrotus* sp. occurrence were mapped in an ArcGIS environment (Table 1). For each PAB proxy variable, a raster grid map with 5 m resolution was obtained for the whole study area. *Carpobrotus* sp. presences were sampled at the centroid of each invaded patch (n=2,189), while 4,000 absence points were randomly generated in the whole study area. PAB variables values were extracted from the raster cells intersecting the coordinates of the presence/absence points. The occurrence of the invasive species was modeled by means of a binomial Generalized Additive Model. The presence/absence of *Carpobrotus* sp. was set as response variable and the PAB predictors as independent variables. Model performance was evaluated by averaging the area under the ROC (relative operating characteristic) curve (AUC) values obtained in each run of a 5-fold cross validation and by visually inspecting the Hosmer-Lemeshow plot. An invasion risk map for the study area was built projecting the predicted probabilities of *Carpobrotus* sp. occurrences on a raster layer with 5 m resolution.

Table 1 PAB proxy variables along with methods (and software) used to compute them.

Factor	Predictors	Method (software)
Propagule pressure (P)	%ART, %AGR	Moving window (FRAGSTAT)
	Distance from major roads	Euclidean distance from highway and primary roads (ArcGIS)
Abiotic (A)	Elevation, slope, curvature	Derived from LiDAR DTM (ArcGIS)
	Sea distance	Euclidean distance from shoreline (ArcGIS)
Biotic (B)	%AFF, %WDV, %SWV, %SHV, %BPV, %HDV, %WET	Moving window (FRAGSTAT)

ISDM-based methodology for invasive species management in Natura 2000 sites (A4)

The invasion risk assessment was carried out in seven Sites of Community Importance (SCIs) belonging to the Natura 2000 coastal network of the Lazio region: Litorale a Nord-Ovest delle Foci del Fiora (site 1), Litorale tra Tarquinia e Montalto di Castro (site 2), Macchia grande di Focene e Macchia dello Stagneto (site 3), Lido dei gigli (site 4), Litorale di Torre Astura (site 5), Dune del Circeo (site 6), Duna di Capratica (site 7). The boundary of each SCI was overlaid to the invasion risk map produced in (A3) for the whole Lazio dune system. Then, site-specific invasion risk maps were extrapolated to derive histograms of the frequency of *Carpobrotus* sp. probabilities of occurrence estimated by the model. The continuous range of occurrence

probabilities was discretized in ten classes (from 0 to 1, by 0.1) and the three most frequent ones were used to assess the vulnerability to *Carpobrotus* sp. invasion of each SCI.

Results and Discussion

Analysis of the relation between EC-habitats and dune morphology (A1)

EC-habitats occurrence is not homogeneous along the coastal zonation but varies across the dune morphology (Table 2). Elevation and sea distance were the strongest morphological predictors of EC-habitats occurrence along the sea-inland vegetation zonation. The best fitting GLMs highlighted that sea distance was significantly related to 5 out of the 6 habitat types, and elevation was associated to 4 EC-habitats. The former morphological variables efficiently described the ecological condition along the sea-inland stress gradient. The results underscore how airborne LiDAR can be a powerful tool for the management of threatened and fragile ecosystems such as coastal dunes.

Table 2 Mean $\pm$ C.I. (confidence interval) calculated for elevation, sea distance, slope and curvature. Different superscripted letters indicate significant differences between coupled EC-habitats (Dunn's test, $p < 0.05$). Northness and eastness did not exhibit significant differences among habitat types (one-way ANOVA, $p > 0.05$).

EC-habitat code	Elevation	Sea distance	Slope	Curvature
1210	1.70 $\pm$ 0.14 ^a	30.49 $\pm$ 3.24 ^a	5.12 $\pm$ 0.92 ^a	-0.003 $\pm$ 0.008 ^a
2110	2.62 $\pm$ 0.25 ^b	44.63 $\pm$ 4.25 ^b	7.01 $\pm$ 0.97 ^b	-0.009 $\pm$ 0.009 ^a
2120	3.60 $\pm$ 0.43 ^c	49.23 $\pm$ 7.19 ^b	8.34 $\pm$ 1.65 ^{b-c}	0.006 $\pm$ 0.014 ^{a-b}
2210+2230	3.94 $\pm$ 0.37 ^c	86.54 $\pm$ 14.73 ^c	7.88 $\pm$ 1.06 ^{b-c}	-0.009 $\pm$ 0.011 ^a
2250	5.58 $\pm$ 0.86 ^d	125.93 $\pm$ 16.59 ^d	9.21 $\pm$ 1.85 ^{b-c}	0.020 $\pm$ 0.018 ^b
2260	5.01 $\pm$ 0.60 ^d	141.24 $\pm$ 17.44 ^d	8.63 $\pm$ 0.96 ^c	0.003 $\pm$ 0.004 ^{a-b}

Effects of coastal erosion and accretion on coastal vegetation (A2)

Coastal dynamics have consistent effects on dune vegetation, with specific impacts across the coastal zonation. Erosion has negative effects on plant communities closer to the shoreline (B1.1 and B1.3). RTs showed significantly lower values of species richness and habitat cover in plots of sand beach drift lines communities (B1.1) exposed to high erosion intensity ($SI_{change} \geq 3.7$). A similar pattern was observed for shifting coastal dunes (B1.3), being characterized by a lower species richness in high erosion condition ($SI_{change} \geq 4.1$). As for focal species, we observed a decrease in the occurrence frequency of *Chamaesyce peplis* in sand beach and drift lines communities experiencing strong erosion. On the other hand, a significantly higher occurrence frequency of *Elymus farcuts* was observed in areas associated with high erosion.

Coastal accretion appears to positively influence dune vegetation typical of the inner sectors of the coastal zonation. Indeed, both LMs and RTs highlighted a positive effect of accretion on species richness in the coastal scrub communities of the fixed dunes (B1.6). Among the analyzed focal species, *Lonicera implexa* was found to occur more frequently in coastal sectors characterized by low accretion condition.

The results highlight how coastal erosion and accretion both affect dune vegetation in terms of plant communities' species richness and cover. The negative effect of erosion on foredune

vegetation is of particular concern. Indeed, erosion can seriously affect the complex interaction between sediment and vegetation altering the process of embryonic and mobile dunes formation which guarantees many of the ecosystem services provided by coastal dunes.

Implementation of the PAB-based *Carpobrotus* sp. distribution model. (A3)

The deviance explained by the model was 57.4%, highlighting that the integration of propagule pressure, abiotic and biotic factors into a single model can capture the processes driving *Carpobrotus* sp. occurrence. The mean of the AUC scores computed through a 5-fold cross validation was 0.94, indicating that the model could accurately predict both the presence and absence of the invasive species along the study area.

The combined influence of propagule pressure, abiotic and biotic factors is not homogeneous across the coastal landscape, with invasion success being affected by the context-specific contribution of each PAB driver. *Carpobrotus* sp. establishment seems to be favored in discontinuous urban areas and in proximity of major roads. Moreover, *Carpobrotus* sp. occurrence is predicted to be high in coastal areas located at intermediate elevation and distances from the sea. This sector offers milder environmental condition than the upper beach and, at the same time, is characterized by a mosaic of herbaceous dune vegetation intermingled at patches of bare ground that favors *Carpobrotus* sp. invasion. The use of remotely sensed data allowed to model the relationship between the invasive species and the recipient environment on a large geographic extent and to highlight the coastal sectors that are most likely to be invaded in the future.

ISDM-based methodology for invasive species management in Natura 2000 sites (A4)

Invasion by *Carpobrotus* sp. does not proceed homogeneously along the Lazio coast, making some protected areas more vulnerable to invasion than others. According to the three most frequent classes of *Carpobrotus* sp. occurrence probabilities, SCIs can be grouped into sites characterized by low invasibility (LI) or medium-high invasibility (MHI) (Table 3). In sites at low invasibility (sites 1, 2, 3 and 5) the most frequent probability classes of *Carpobrotus* sp. occurrence were 0 and 0.1, while in sites at medium-high invasibility (sites 4, 6 and 7) the predicted probabilities showed a bimodal distribution with the most frequent classes assuming both low and high probability values. This highlights the need of identifying site-specific management strategies that take into account both the actual and predicted occurrence of *Carpobrotus* sp. Indeed, early detection and eradication should be carried out in sites sparsely colonized by *Carpobrotus* sp. and associated to a predicted low invasion risk (sites 1, 2, 3 and 5). On the other hand, strategies aimed at controlling the expansion of the invasive plant should be addressed in heavily invaded protected areas (sites 4 and 6). Finally, resources should be prioritized in sites that have so far experienced few invasion events, while being associated to a high invasibility (site 7).

Table 3 *Three most frequent probability (P) classes of *Carpobrotus* sp. occurrence and relative invasibility of each SCI. LI: Low Invasibility; MHI: Medium-High Invasibility.*

Site	1 st	2 nd	3 rd	Invasibility
Litorale a N-W delle Foci del Fiora (site 1)	<i>P</i> =0	<i>P</i> =0.1	<i>P</i> =0.2	LI
Litorale tra Tarquinia e Montalto di Castro (site 2)	<i>P</i> =0	<i>P</i> =0.1	<i>P</i> =0.2	
Macchia grande di Focene e Macchia dello Stagneto (site 3)	<i>P</i> =0	<i>P</i> =0.1	<i>P</i> =0.3	
Litorale di Torre Astura (site 5)	<i>P</i> =0	<i>P</i> =0.1	<i>P</i> =0.2	
Lido dei Gigli (site 4)	<i>P</i> =0	<i>P</i> =0.1	<i>P</i> =0.8	MHI
Dune del Circeo (site 6)	<i>P</i> =0	<i>P</i> =0.8	<i>P</i> =0.9	
Duna di Capratica (site 7)	<i>P</i> =0.8	<i>P</i> =0.7	<i>P</i> =0.9	

Conclusions and future perspectives

This PhD thesis dealt with the analysis of the influence of geomorphological (A1 and A2) and biological (A3 and A4) processes on dune vegetation diversity patterns through the integration of field-collected vegetation data and remotely sensed imagery. In particular, the use of remotely sensed data allowed investigating the relationship between coastal plant communities and the former processes on a wide geographic extent. Analyses led to the identification and proposal of monitoring and conservation strategies aimed at maintaining the biodiversity and functioning of Mediterranean coastal dune ecosystem.

Introduction

Connecting land and sea, coastal dunes are peculiar ecosystems characterized by harsh abiotic conditions (e.g. wind, salinity, instability of the substrate, lack of nutrients) limiting successful establishment to a highly specialized flora and fauna (Martínez et al., 2004; Acosta et al., 2009). The intensity of these conditions naturally decreases while moving landwards, giving rise to a steep sea-inland environmental gradient that determines the occurrence, over a short distance, of a highly diverse assemblage of unique habitats. Besides being of outstanding naturalistic and conservation value, these habitats provide numerous ecological services such as groundwater storage (Rhymes et al., 2015), storm protection (McLachlan & Brown, 2006) and climate mitigation (Carranza et al., 2018), while also representing a preferred location for human recreation (Schlacher et al., 2008).

Nevertheless, coastal dunes are currently listed among the most threatened ecosystems worldwide (Janssen et al., 2016; Powell et al., 2018). A long history of urbanization, agricultural and reforestation expansion, together with shoreline modifications, have led to dramatic transformations of the coastal landscape (Defeo et al., 2009; Malavasi et al., 2013, 2016a). At the same time, biological invasions, which are strongly favored in densely populated areas and globally associated to a general reduction of biodiversity across ecosystems (Russell & Blackburn, 2017), have not spared coastal dunes, which are among the most invaded habitats in Europe (Chytrý et al., 2008).

As a result, *psammophilous* communities have been substantially altered in their diversity and composition, with negative implications on their capacity to feed the ecomorphodynamic process of dune formation and building that guarantees the supply of many of the above listed ecosystem services (Feagin et al., 2005; Duran & Moore, 2013). The alarming degradation of dune ecosystems, together with the remarkable speed of biodiversity loss and the increasing rate of invasion by non-native species, urgently calls for the identification and implementation of new scientific approaches for effectively supporting coastal managers (Defeo et al., 2009; Poeta et al., 2014).

In this regard, remote sensing technologies have proved to be effective for investigating ecological processes and the resulting diversity patterns across different ecosystems, spatial and temporal scales (Pettorelli et al., 2014, 2015; Rose et al., 2015). Remotely sensed data have been successfully used to disentangle the role of anthropogenic and natural factors affecting coastal ecosystems (Kerr & Ostrovsky, 2003). For instance, LiDAR (Light Detection And Ranging) and satellite-derived imagery have been used to describe the relationship between dune morphology and plant diversity, enhancing our knowledge on the ecomorphodynamic process of dune formation and building (Ward et al., 2013; Yousefi Lalimi et al., 2017). At the same time, remotely sensed data characterized by high spectral and spatial resolution have been used to both detect and model biological invasions (Rocchini et al., 2015; Malavasi et al., 2018).

In this light, this PhD thesis focused on combining field-collected vegetation data and remotely sensed imagery to model the relationship between plant diversity, natural and anthropogenic processes in coastal dunes habitats. In particular, the aims of this thesis were to:

1. characterize the morphological profile of coastal European Community-habitats (*sensu* EU Habitats Directive) and analyze their distribution along the dune morphology of a Tyrrhenian dune system.
2. assess the effect of coastal erosion and accretion on Mediterranean dune vegetation, quantifying changes in terms of species richness, vegetation cover and diversity of plant communities, focusing on a wide portion of the sea-inland gradient.
3. model the occurrence of the highly invasive *Carpobrotus* sp. along the Lazio dune system accounting for the simultaneous effect of multiple drivers of invasion.
4. propose a model-based methodology for assessing the risk of invasion posed by *Carpobrotus* sp. in Natura 2000 coastal sites of the Lazio region.

State-of-the-art

In Mediterranean coastal dunes, harsh abiotic conditions shape vegetation structure and cover, thereby producing a fine-grained assemblage of plant communities occurring in a relatively short space. In most cases, such a spatial arrangement of habitats is further fragmented by anthropogenic pressures, resulting in a complex and dynamic mosaic of phytocoenoses. For this reason, field-collected high-resolution data should be the preferred choice for analyzing dune vegetation dynamics at the appropriate spatial and temporal scales. However, as exhaustive field sampling is often infeasible for collecting the amount and quality of data needed, alternative approaches can be implemented for analyzing vast areas. In this context, remote sensing instruments allow conducting cost-effective and recurrent observations over wide geographic extents while retrieving a huge amount of spatial data that can, in turn, be used to generate meaningful variables for, e.g., modelling species-environment relationship or monitoring ecosystem quality. The use of remote sensing datasets has substantially changed the scale at which ecologists look at environmental processes and the way they interpret resulting patterns. At the same time, remote sensing has provided conservation science with an improved capacity of identifying effective management strategies. In practice, remote sensing has boosted our capacity of monitoring, detecting, mapping, and predicting environmental changes at a wide geographic extent.

In coastal ecology, the use of remote sensing spans from monitoring dune volume changes over time (Woolard & Colby, 2002; White & Wang, 2003) to modelling vegetation patterns as a function of dune morphology (Kim & Yu, 2009; Ward et al., 2013; Yousefi Lalimi, 2017). At the same time, remote sensing approaches were used to investigate how basic environmental processes (e.g. habitat loss and fragmentation, biological invasions and sand redistribution phenomena) affect the biodiversity of coastal ecosystems. As an example, Malavasi et al. (2014, 2016) used high-resolution aerial orthophotos to explore how changes in the spatial landscape pattern influence the introduction of invasive species and the diversity of plant communities in Mediterranean coastal dunes. Underwood et al. (2007), on the other hand, mapped invasive plant species colonizing Californian dune ecosystems through satellite imagery, while Carranza et al. (2010) described the landscape configuration of Tyrrhenian coastal sectors invaded by *Carpobrotus* sp.

Beyond being a robust tool for mapping the biophysical properties that shape the distribution and abundance of species across landscapes (Turner et al., 2003), remote sensing has provided key environmental parameters for evaluating ecological theories on the ground. For instance, Malavasi et al. (2018) tested the validity of the “habitat amount hypothesis” formulated by Fahrig (2013) in coastal ecosystems, deriving landscape metrics from fine-scale land-cover maps through a linear buffering approach.

Overall, a general consensus has been reached on the efficacy of remote sensing for supporting ecological studies. The increasing availability of high spatial and spectral resolution remote sensing data has helped to dispel concerns about a problematic mismatch between the scales provided by remote sensing and those interesting ecologists (see Turner et al., 2003 and Kerr & Ostrovsky, 2003). This thesis stresses the potential of remote sensing for analyzing vegetation dynamics in highly dynamic, structurally complex and finely grained ecotonal

ecosystems, such as coastal dunes. Moreover, it evidences how the integration of field-collected data and remote sensing techniques can provide standard methodologies for assessing ecosystem integrity.

Chapter 1

*How does dune morphology shape coastal EC habitats occurrence?
A remote sensing approach using airborne LiDAR on the
Mediterranean coast*

How does dune morphology shape coastal EC habitats occurrence? A remote sensing approach using airborne LiDAR on the Mediterranean coast

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Abstract

We examined the relationship between coastal habitats (*sensu* European Union Habitats Directive) and local dune morphology along a Mediterranean coastal dune system by integrating field collected vegetation data and remotely sensed imagery. Specifically, we described the morphological profile of each EC habitat based on the morphological variables that are most likely to affect their occurrence, including elevation, slope, curvature, northness, eastness and sea distance. In addition, we assessed the role and strength of each morphological variable in determining the occurrence of EC habitats.

We used 394 random vegetation plots representative of six EC habitats (Habitat 1210: “Annual vegetation of drift lines”; Habitat 2110: “Embryonic shifting dunes”; Habitat 2120: “Shifting dunes along the shoreline with *Ammophila arenaria*”; Habitat 2210 and 2230: “*Crucianellion maritimae* fixed beach dunes” and “*Malcolmietalia* dune grasslands”; Habitat 2250: “Coastal dunes with *Juniperus* spp.”; Habitat 2260: “*Cisto-Lavanduletalia* dune sclerophyllous scrubs”) found along the Tyrrhenian coast of central Italy. We derived each morphological variable from a DTM (Digital Terrain Model) obtained from 2-m resolution LiDAR (Light Detection And Range) images. The mean value of each variable was calculated at different spatial scales using buffer areas of increasing radius (2 m, 4 m, 8 m) around each vegetation plot. Mean morphological values for each EC habitat were compared using Kruskal-Wallis rank test. The role and strength of the relationship between habitat type and the morphological variables were assessed using Generalized Linear Models.

EC habitats occur differentially across dune morphology, and the role and strength of each morphological variable define habitat specificity. Dune elevation and sea distance were determined to be the key factors in shaping EC habitat occurrence along this section of the Mediterranean coast. Identification of the close relationship between habitat type and morphological variables deriving from airborne LiDAR imagery points to the high potential of such remote sensing tool for analyzing and monitoring the integrity of coastal dune

ecosystems. As airborne LiDAR enables the rapid collection of extremely accurate topographic data over large areas, it also offers useful information for the management of these threatened and fragile ecosystems.

Keywords: elevation, sea distance, plant community, field vegetation data, conservation strategy.

1. Introduction

Coastal dunes comprise nearly three-quarters of the world's shorelines (Bascom, 1980). They provide unique habitat assemblages due to a steep environmental sea-inland gradient, which supports a highly specialized and characteristic flora and fauna (Acosta et al., 2009; Martínez et al., 2004). In addition, coastal dunes offer numerous ecological services, such as filtration of large volumes of seawater, nutrient recycling, flood control and storm protection (Liquete et al., 2013; McLachlan and Brown, 2006). In recent years, however coastal dune ecosystems have been increasingly transformed by urban, industrial, agricultural and reforestation expansion, as well as shoreline and harbor development (Malavasi et al., 2016a, 2013; Schlacher et al., 2007; Sitzia et al., 2014). They represent prime locations for human recreation and support many coastal economies around the world (Schlacher et al., 2008). Consequently, coastal sandy ecosystems are currently one of the most threatened ecosystems in Europe, especially concerning biodiversity loss (EEA, 2008). The degradation of the littoral landscape is particularly striking on the Mediterranean coastline (Miccadei et al., 2011); most of the plant communities growing on coastal dunes lining the Mediterranean have been listed as EC Habitats in Annex I of the Habitats Directive (European Commission, 2007).

The remarkable speed of coastal dune degradation and biodiversity loss increases the urgency of identifying and implementing standard screening procedures that stress the benefits and drawbacks of different management scenarios (Defeo et al., 2009; Poeta et al., 2014). Scientifically sound instruments capable of describing and monitoring coastal dune ecosystems are crucial for determining conservation priorities aimed at maintaining coastal dune integrity and ecosystem services over time (Acosta et al., 2003b; Drius et al., 2013). Remotely sensed imagery is an effective tool for mapping and modeling natural and artificial environments and enhancing our understanding of ecosystem functioning (Lefsky et al., 2002). Moreover, remote sensing offers a cost-effective means for conducting recurrent observations over vast areas (Turner et al., 2003). The use of modern sensors to identify important areas of biodiversity, determine species distributions and model community responses to environmental and anthropogenic changes is of growing interest among ecologists and landscape planners (Mairota et al., 2015; Turner et al., 2003). Remote sensing is particularly effective for mapping the key environmental parameters and biophysical properties that shape the distribution and abundance of species across landscapes (Alexander et al., 2016; Turner et al., 2003).

Airborne LiDAR (Light Detection And Range) is particularly effective for collecting accurate elevation data over large areas, thus extending spatial analysis into the third dimension (z) and reducing the amount of time and expense required to collect field data (Jensens, 2007). The creation of topographical maps is currently the largest and fastest growing area of LiDAR application, along with its widespread use in commercial land surveys (Flood and Gutelius, 1997). More recently, airborne laser altimetry has been used to map coastal geomorphology, improving knowledge of many geomorphic processes; it has been used, for instance, for monitoring coastal erosion and accretion rates, sediment transport and budgets, and for flood hazard assessments (Brock et al., 2009, 2004; Sallenger et al., 2007, 2003, 1999), as well as for analyzing ecological processes in coastal and estuarine habitats (Chust et al., 2008; Sallenger et al., 2007). Moreover, research carried out by Ward et al. (2013) has demonstrated

the usefulness of LiDAR derived elevation data in analyzing the distribution of vegetation in areas characterized by micro-topographical relief, such as coastal dunes.

However, the utilization of LiDAR images for describing and monitoring the impacts of abiotic and biotic factors on extensive coastal dune systems requires further study. Indeed, in well-preserved dune ecosystems, the typical dune vegetation zonation is closely related to the morphological and sedimentological features of the dune system (Aboudha et al., 2003; Acosta et al., 2007), changing along an environmental gradient from the shoreline to the inland regions (Acosta et al., 2003a; Isermann, 2005; Lane et al., 2008; Šýkora et al., 2004). The relationships between plant communities and local dune morphology have been previously described by field research at local scales (Acosta et al., 2007; Kempeneers et al., 2009; Kim and Yu 2009; Ruocco et al., 2014; Ward et al., 2010; Woolard and Colby, 2002), but few studies have focused on large coastal areas or on the integration of recent and accurate topographic maps with field data.

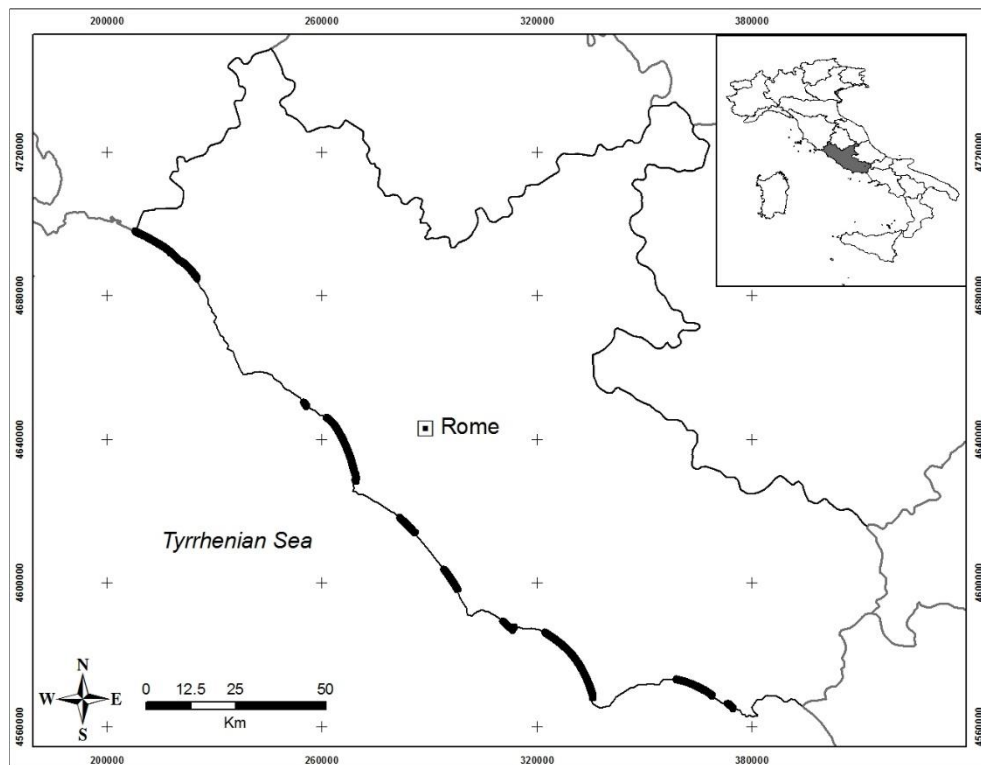
The present study was undertaken to examine the relationship between coastal dune vegetation and local dune morphology in a broad strip of the Mediterranean coast by integrating field collected vegetation data and remotely sensed images. We analyze the occurrence of habitat types *sensu* 92/43/EEC Habitats Directive (EEC, 1992; European Commission, 2013) of conservation concern in relation with morphological variables (LiDAR derived) that more likely affect the presence of each habitat type, including the elevation, slope, curvature, northness, eastness and sea distance. In particular, we aim to i) describe the morphological profile of each EC habitat, and ii) assess the role and strength of each morphological variable in determining the occurrence of the EC habitats.

2. Materials and methods

2.1 Study area

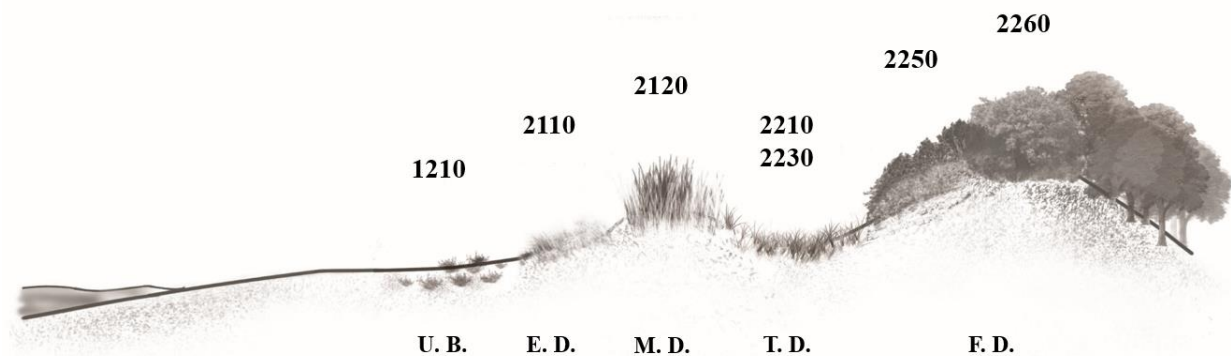
The study was carried out on the Tyrrhenian coast of central Italy and focused on recent coastal dunes (Holocene) hosting a highly specialized native flora (Izzi et al., 2007) and plant communities that have been associated to different habitat types *sensu* 92/43/EEC Habitats Directive (EEC, 1992; Prisco et al., 2012). The area includes 9 study sites located along the coast of the Lazio region (Fig. 1), where recent dunes harbor remnant natural seashore vegetation (Malavasi et al., 2016b). Recent dunes occupy a narrow strip along the seashore (< 500 m). The dunes are low (< 10 m in height) and are relatively simple in structure. Beaches vary in width, from a few meters to approximately 40 m and are backed by a section of low embryo dunes, typically a single mobile dune ridge, dune slacks and, finally, a stabilized dune zone (Acosta et al., 2003a). Vegetation on the dune profile follows a compressed zonation along the sea-inland environmental gradient, from the pioneer communities of the upper beach to the woody communities (Mediterranean *macchia* and evergreen forests) of the inland fixed dunes (Acosta et al., 2007) (Fig. 2).

Fig. 1- Study area.



Sampling sites where recent dunes harbor remnant natural vegetation are shown in black. Coordinates are given in datum: WGS 84, UTM 33N.

Fig. 2- EC habitats (*sensu* 92/43/EEC Habitat Directive) distribution along the study area coastal dune profile.



1210: Vegetation of the drift lines; 2110: Embryonic shifting dunes; 2120: Shifting dunes along the shoreline with *Ammophila arenaria*; 2210: *Crucianellion maritimae* fixed beach dunes; 2230: *Malcomietalia* dune grasslands; 2250: Coastal dunes with *Juniperus* spp.; 2260: *Cisto-Lavanduletalia* dune sclerophyllous scrubs. U.B.: Upper Beach; E.D.: Embryo Dune; M.D.: Mobile Dune; T.D.: Transition Dune; F.D.: Fixed Dune; (picture, Federico Romiti). For details concerning plant communities' diagnostic species and number of plots see table 1.

2.2 Vegetation

Vegetation plots were randomly collected on coastal dunes in spring (April–May) over the period 2006–2011; the plots covered most of the coastal EC habitat types that are present in central Italy (Acosta et al. 2007; Carranza et al., 2008; Prisco et al., 2012). The mean distance between neighboring plots was 66 m (lower quartile 40 m; upper quartile 107 m). The plots were 2 m × 2 m wide, dimensions determined to be adequate for describing coastal dune habitats (e.g., Acosta et al., 2007; Carboni et al., 2011). The complete list of vascular plant species and the relative percentage cover was reported. According with the interpretation manual of the EC habitats (Biondi et al., 2009), the 394 plots covered 6 EC habitat types (Tab. 1): ‘1210’: Annual vegetation of the drift lines (n= 53); ‘2110’: Embryonic shifting dunes (n= 54); ‘2120’: Shifting dunes along the shoreline with *Ammophila arenaria* (n= 39); ‘2210’ and ‘2230’: *Crucianellion maritimae* fixed dunes and *Malcomietalia* dune grasslands (n= 96); ‘2250’: Coastal dunes with *Juniperus* spp. (n= 42); and ‘2260’: *Cisto-Lavanduletalia* dune sclerophyllous scrubs (n= 90) (for details regarding vegetation data and classification to EC habitat categories, see Carboni et al., 2011). As habitats ‘2210’ and ‘2230’ typically occur in a complex mosaic in the transition between mobile dunes and fixed dunes (Acosta et al., 2003a), we decided to combine them into a single category.

Tab. 1- Habitat types (*sensu* 92/43/EEC Habitat Directive) present in the study area along the sea-inland vegetation zonation with their corresponding phytosociological associations, zone along the dune profile, diagnostic species and number of vegetation plots (N).

	Vegetation of the drift lines	Vegetation of the embryo dunes	Vegetation of the mobile dunes	Vegetation of the transition dunes		<i>Juniperus</i> scrub	Mediterranean macchia
EC code	1210	2110	2120	2210	2230	2250	2260
	Annual vegetation of the drift lines	Embryonic shifting dunes	Shifting dunes along the shoreline with <i>Ammophila arenaria</i>	<i>Crucianellion maritimae</i> fixed beach dunes	<i>Malcomietalia</i> dune grasslands	Coastal dunes with <i>Juniperus</i> spp.	<i>Cisto-Lavanduletalia</i> dune, sclerophyllous scrubs
Phytosociological association	<i>Salsolo kali-Cakiletum maritimae</i> Costa & Manzanet 1981	<i>Elymetum farcti</i> Br.-Bl. 1933 <i>Echinophoro spinosae-Elymetum farcti</i> Géhu 1987	<i>Ammophiletum arenarie</i> Br.-Bl. (1921) 1933 <i>Echinophoro spinosae-Ammophiletum arenarie</i> (Br.-Bl. 1933) Géhu, Rivas-Martinez, R.Tx 1972	<i>Crucianelletum maritimae</i> Br.-Bl. 1933 <i>Pycnocomo rutifolii-Crucianelletum maritimae</i> Géhu, Biondi, Géhu-Franck, Toffetani 1987	<i>Sileno coloratae-Vulpietum membranaceae</i> (Pignatti 1953) Géhu & Soppola 1984 <i>Sileno coloratae-Ononidetum variegatae</i> Géhu et al. 1986 <i>Vulpio fasciculatae-Silenetum coloratae</i> Pignatti 1953 corr. Diez-Garretas & Asensi 2003	<i>Asparago acutifolii-Juniperetum macrocarpa</i> Géhu & Biondi 1994 <i>Juniperetum macrocarpae-phoeniceae</i> Pedrotti & Cortini Pedrotti 1976	<i>Phillyreo latifoliae-Ericetum scopariae</i> Blasi, Stanisci, Filesì, Milanese, Perinelli, Riggio 2002
Zone along the dune profile	Upper beach	Embryo dune	Mobile dune	Transition dune		Fixed dune	Fixed dune
Main diagnostic or characteristic species	<i>Cakile maritima</i>	<i>Elymus farctus</i>	<i>Ammophila arenaria</i>	<i>Crucianella maritima</i> , <i>Malcolmia ramosissima</i>		<i>Juniperus oxycedrus</i>	<i>Pistacia lentiscus</i>
N=	53	74	39	96		42	90

2.3 Morphological variables

Airborne LiDAR imagery were acquired in 2008 during the PST-A mission (Piano Straordinario di Telerilevamento Ambientale; Ministero dell'Ambiente e della Tutela del Territorio e del Mare). From the LiDAR imagery, we derived a DTM (Digital Terrain Model) of 2-m resolution to achieve a reliable and detailed representation of the dune morphology (Woolard and Colby, 2002) in an ArcGIS environment (ArcGIS 10.1; ESRI, 2011). The DTM was then used to derive a set of morphological variables that, according to previous studies, are significantly related to the dune vegetation (Acosta et al., 2007; Kim and Yu, 2009; Ruocco et al., 2014; Wilson and Gallant, 2000), consisting of elevation, slope, curvature, northness, eastness and sea distance (Tab. 2).

To detect the appropriate scale at which morphological parameters operate on coastal dune plant communities, we analyzed morphological variables around each vegetation plot at three increasing buffer areas (radius: 2 m, 4 m, 8 m), then calculated the mean value for each morphological variable for each buffer area. Sea distance was computed by tracking the shortest line from the plot to the shoreline in an ArcGIS environment (Tab. 2). Shoreline was derived from the land cover map of the study area elaborated in Malavasi et al. (2016a).

Tab. 2- Dune morphological variables derived from the LiDAR Digital Terrain Model (DTM).

	Description	Unit of measurement
Elevation	The above sea-level value.	Meter (m)
Slope	Maximum change in elevation over the distance between the cell and its eight neighbors.	Degree (deg)
Curvature	Second derivative of the surface. Positive curvature values indicate that the surface is upwardly convex. Negative curvature values indicate that the surface is upwardly concave. Curvature values equal to 0 indicate that the surface is flat.	Adimensional (ad)
Northness	$N = \cos(\text{aspect})$, where “ <u>aspect</u> ” identifies the downslope direction of the maximum rate of change in value from each cell to its neighbors.	Adimensional (ad)
Eastness	$E = \sin(\text{aspect})$, where “ <u>aspect</u> ” identifies the downslope direction of the maximum rate of change in value from each cell to its neighbors.	Adimensional (ad)
Sea distance	Shortest point to line distance.	Meter (m)

2.4 Statistical analysis

We used two different statistical procedures to describe the morphological profiles of the EC habitats at different scales and to assess the role and the strength of the relationship between habitat type and morphological variables.

First, an Anderson Darling normality test was performed for each of the six morphological variables (elevation, slope, curvature, northness, eastness and sea distance) to determine whether a parametric or non-parametric approach would be implemented for habitat comparison. We compared habitat elevation, sea distance, slope and curvature using the non-parametric Kruskal-Wallis rank test. To examine the differences between coupled habitats, we used Dunn’s paired comparison test (R package FSA; Ogle, D.H 2015); finally, northness and eastness were tested using parametric one-way ANOVA. Morphological parameter variability within the various habitat types was graphically compared using box-plots.

Next, we assessed the relationship between the occurrence of the habitat types and the morphological variables using Generalized Linear Models (GLMs). The presence/absence of each habitat type was set as the response variable (in all 394 plots) with the dune morphology parameters set as the explanatory variables. GLM models were constructed for each of the six habitat types, with model quality compared using Akaike Information Criteria (AIC) (Akaike, 1974), with the model having the lowest AIC being best. To assess the strength of the relationship between each morphological parameter and habitat type, we calculated Bayesian Information Criterion (BIC) values (Raftery, 1995) using the equation:

$$\text{BIC} = z^2 - \log(N)$$

where z is the z -value (z^2 is the Wald statistic) and ‘ N ’ is the sample size (number of plots). The null hypothesis is $H_0: \beta = 0$ (no relationship between the morphological variable and the habitat type). BIC values below zero indicate that there is no evidence to reject the null hypothesis, whereas BIC values between 0 and 2 indicate a weak relationship; values between 2 and 6 indicate a medium relationship; values between 6 and 10 indicate a strong relationship; and finally, a very strong relationship is indicated by values above 10 (Zuur et al., 2007).

All analyses were performed with R software (R Core Team, 2015).

3. Results

3.1 EC habitats and dune morphology

The occurrence of EC habitats is not homogeneous in coastal dune systems but varies across the sea-inland gradient (Tab. 3, 4 and Fig. 3). Given that the general trends of the morphological variables were not significantly different at the 2- and 8-m buffers (Appendix 1) compared to those at 4 m (elevation, sea distance, slope, curvature; Kruskal-Wallis rank test, $p > 0.05$; northness and eastness; one-way ANOVA, $p > 0.05$), we focused on the results of the analyses concerning the 4 m buffer radius.

Elevation was significantly different among all habitat types (Kruskal-Wallis test, $p < 0.05$), and comparisons between coupled habitats showed significantly different elevation values for all of them (Dunn’s test, $p < 0.05$), with the exception of the mobile dune habitat (‘2120’) versus the transition dune habitat (‘2210+2230’) and for the fixed dune habitats (‘2250’ versus ‘2260’). Habitat located on the highest sector of dunes was identified to be the fixed dune habitat (‘2250’), whereas the upper beach habitat (‘1210’) occurred in the lowest dune sector.

Distance from the coastline also differed significantly among the habitat types (Kruskal-Wallis test, $p < 0.05$). However, paired comparisons demonstrated that the embryo dune habitat (‘2110’) was located at the same distance of the mobile dune habitat (‘2120’), similarly to the fixed dune habitats (‘2250’ and ‘2260’). The furthest habitat from the coastline was the fixed dune habitat (‘2260’), whereas the closest one was the upper beach habitat (‘1210’).

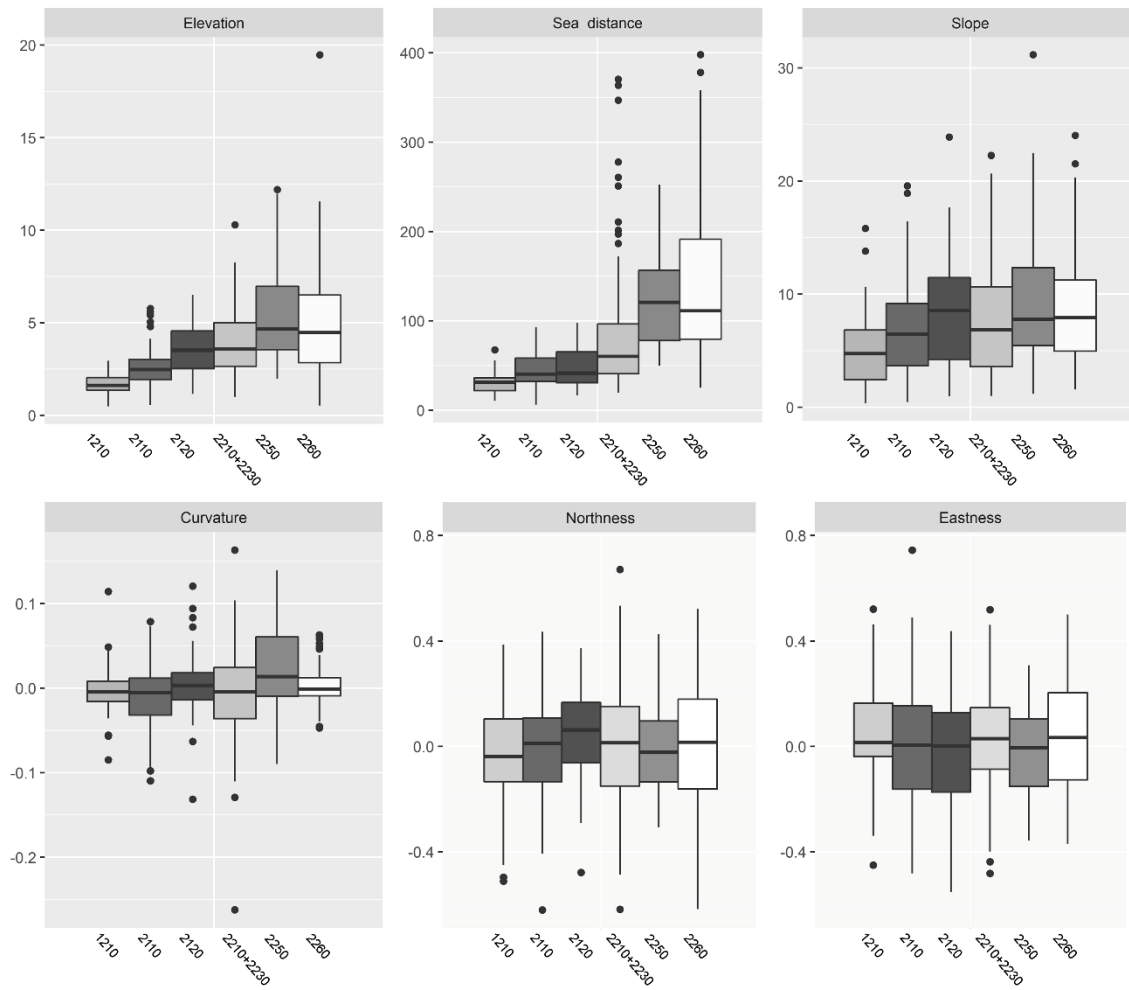
The slope differed significantly among habitats (Kruskal-Wallis test, $p < 0.05$). The paired Dunn’s test revealed that the upper beach habitat (‘1210’) assumed different slope values when compared to the other habitat types, and the embryo dune habitat (‘2110’) differed from the fixed dune habitat (‘2260’). The fixed dune habitat (‘2250’) occurred on the steepest sectors of the dune systems, whereas the upper beach habitat (‘1210’) was typically found in the flattest zones. Finally, the mobile dune (‘2120’) and the fixed dune (‘2250’, ‘2260’) habitats exhibited the most prominent values for this variable.

Curvature differed significantly among the EC habitats (Kruskal-Wallis test, $p < 0.05$). The paired Dunn’s comparisons demonstrated that the upper beach (‘1210’), the embryo dune (‘2110’) and the transition dune (‘2210 + 2230’) habitats differed from the fixed dune habitat (‘2250’). However, all habitats had curvature values close to zero; in particular, the upper beach

habitat ('1210') assumed the mean curvature value closest to zero, whereas the fixed dune habitat ('2250') had the highest mean value.

No significant differences were detected among habitats for northness and the eastness (one-way ANOVA, $p > 0.05$). Thus, we did not perform any comparisons among coupled habitats.

Fig. 3- Statistical distribution (median, and lower and upper first quartile) of the LiDAR derived morphological variables across the EC habitats.



Dark grey background: significant differences among EC habitat types (Kruskal-Wallis rank test, $p < 0.05$). Light grey background: no significant differences among EC habitat types (one-way ANOVA, $p > 0.05$). See Tab. 1 for description of EC codes.

Tab. 3- Mean $\pm$ C.I. (confidence interval) calculated for the morphological variables (elevation, sea distance, slope, curvature, northness and eastness) for each habitat type (1210, 2110, 2120, 2210+2230, 2250, 2260).

Habitat code	Morphological variables					
	Elevation	Sea distance	Slope	Curvature	Northness	Eastness
1210	1.70 $\pm$ 0.14 ^a	30.49 $\pm$ 3.24 ^a	5.12 $\pm$ 0.92 ^a	-0.003 $\pm$ 0.008 ^a	0.024 $\pm$ 0.055	0.049 $\pm$ 0.049
2110	2.62 $\pm$ 0.25 ^b	44.63 $\pm$ 4.25 ^b	7.01 $\pm$ 0.97 ^b	-0.009 $\pm$ 0.009 ^a	-0.013 $\pm$ 0.045	0.008 $\pm$ 0.052
2120	3.60 $\pm$ 0.43 ^c	49.23 $\pm$ 7.19 ^b	8.34 $\pm$ 1.65 ^{b-c}	0.006 $\pm$ 0.014 ^{a-b}	0.050 $\pm$ 0.059	-0.009 $\pm$ 0.067
2210+2230	3.94 $\pm$ 0.37 ^c	86.54 $\pm$ 14.73 ^c	7.88 $\pm$ 1.06 ^{b-c}	-0.009 $\pm$ 0.011 ^a	0.018 $\pm$ 0.047	0.022 $\pm$ 0.041
2250	5.58 $\pm$ 0.86 ^d	125.93 $\pm$ 16.59 ^d	9.21 $\pm$ 1.85 ^{b-c}	0.020 $\pm$ 0.018 ^b	-0.009 $\pm$ 0.057	-0.016 $\pm$ 0.054
2260	5.01 $\pm$ 0.60 ^d	141.24 $\pm$ 17.44 ^d	8.63 $\pm$ 0.96 ^c	0.003 $\pm$ 0.004 ^{a-b}	0.012 $\pm$ 0.046	0.003 $\pm$ 0.004

Different superscripted letters indicate significant differences between EC habitats (Dunn's multiple comparison test, $p < 0.05$). No significant differences were detected among the habitat types for eastness and northness (one-way ANOVA, $p > 0.05$).

3.2 Response of EC habitats to the morphological variables

The best fitting GLMs indicated a significant relationship between sea distance and five (upper beach – ‘1210’; fore dune – ‘2110’; mobile dune – ‘2120’; fixed dune – ‘2250’ and ‘2260’) out of the six EC habitats. Elevation was significantly related to four habitat types (upper beach – ‘1210’; embryo dune – ‘2110’; fixed dune – ‘2250’ and ‘2260’) (Tab. 4).

The presence of the upper beach habitat (‘1210’) was strongly associated with elevation and the distance from the sea and weakly related to eastness. The embryo dune habitat (‘2110’) was significantly associated with elevation and sea distance, exhibiting a weak relationship with the former variable but a much stronger one with the latter. For the mobile dune habitat (‘2120’), the best fitting model selected sea distance as the most influential variable, with a relationship of medium strength. For the transition dune habitat (‘2210+2230’), the only environmental variable selected by the model was curvature but even that association was weak. The occurrence of the fixed dune habitat (‘2250’) was significantly related to elevation and sea distance, exhibiting a strong relationship with both these variables, and resulted weakly associated with curvature. Elevation, sea distance and slope were the selected variables for the fixed dune habitat (‘2260’). The highest reported BIC value was for sea distance, followed by elevation and slope.

Tab. 4- GLMs (Generalized Linear Models) for each habitat type (EC habitat; response variable: presence/absence, explanatory variables: morphology variables).

GLM	Habitat																	
	1210 (AIC=164,01)			2110 (AIC=329,93)			2120 (AIC=241,62)			2210 + 2230 (AIC=437,21)			2250 (AIC=239,42)			2260 (AIC=341,94)		
	<i>p</i>	<i>z</i>	BIC	<i>p</i>	<i>z</i>	BIC	<i>p</i>	<i>z</i>	BIC	<i>p</i>	<i>z</i>	BIC	<i>p</i>	<i>z</i>	BIC	<i>p</i>	<i>z</i>	BIC
Elevation	***	-4.693	19.43	*	-2.126	1.93							**	2.990	6.35	**	2.879	5.7
Sea distance	***	-4.089	14.13	***	-3.523	9.81	**	-2.870	5.65				**	3.064	6.8	***	7.016	46.62
Slope		-1.392	-0.65													*	2.059	1.65
Curvature								1.192	-1.17	*	-2.217	2.32	*	2.030	1.53			
Northness								1.505	-0.33									
Eastness	*	2.048	1.59													.	1.762	0.51

Minimal Adequate Model based on AIC (Akaike Information Criteria) ('***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$; '.' $p < 0.1$) are listed. The relative strengths of habitat 'preference' based on the BIC values are shown in different shades of grey.

4. Discussion

Analyses of the relationships between EC habitat types (EEC, 1992) and dune morphology over a wide Mediterranean coastal area using combined field-collected vegetation data and remotely sensed LiDAR imagery revealed that plant communities occur differently across the dune zonation and that the role and strength of each morphological variable differed among the EC habitats.

4.1 EC habitats and dune morphology

Most of the plant communities were found at different and increasing elevation ranges moving inland, a result similar to that reported by Ward et al. (2013) for Baltic dunes. The upper beach habitat with annual vegetation of the drift lines ('1210') was generally located in the lower sectors of the dune system, followed by the embryo dune habitat ('2110'); proceeding inland, the mobile dune habitat with *Ammophila arenaria* ('2120') shared similar mean elevation values with the transition dune habitat ('2210+2230'). Finally, the fixed dunes with woody vegetation, *Juniperus* spp. communities and *Cisto-Lavanduletalia* sclerophyllous scrubs ('2250' and '2260', respectively) occurred in the higher dune sectors.

The dune habitats were located at varying distances from the shoreline. The upper beach habitat ('1210') was generally the closest to the sea, followed by the fore dune habitat ('2110') and the mobile dune habitat ('2120'), which tended to occur at the same distance from the sea, and the transition dune habitat ('2210+2230'). The fixed dune habitats with woody vegetation ('2250' and '2260') typically inhabited the inner sectors of the dune system. Indeed, coastal dune vegetation is progressively exposed to lower environmental stress with increasing distance from the sea (Forey et al., 2009; Wilson & Sykes, 1999). As noted in previous studies of the Mediterranean coastline (Angiolini et al., 2013; Ruocco et al., 2014), as well as on Baltic (Burnside et al., 2008) and Pacific (Kim and Yu, 2009) coasts, the sea distance variable is one of the main drivers of differentiation of plant community occurrence along coastal zones.

With respect to slope, in accordance with the observations reported by Acosta et al. (2007), we confirmed that plant communities are located at specific ranges of slope values. The upper beach habitat ('1210') typically occurred in the flattest parts of the dune systems, whereas *Juniperus* spp. scrub habitats ('2250') were generally found in the steepest sections. Moreover, although we did not detect significant differences, relying on the mean values, the mobile dune habitat ('2120') occurred on steeper slopes than did embryo dune ('2110') and transition dune ('2210+2230') habitats. This is most likely due to the presence of the large tussock grass *Ammophila arenaria*, the canopies of which reduce airflow velocities and, consequently, push dune expansion seaward through the accumulation of sand (Hesp, 2002).

As regards the curvature, dune systems consist in blow-wind deposits of sand shaped by the vegetation and organized in convex dune ridges and relatively flat terraces (Maun, 2009). Our result confirms such observation that clearly depicts the overall curvature surface profile found along the Mediterranean coastal zonation. The upper beach habitat ('1210') occurred on slightly upwardly concave to flat surfaces. Proceeding inland, the embryo dune habitat ('2110') settled on the concave sector between the upper beach and the seaward slope of the mobile

dune. As regard to the mobile dune habitat ('2120'), the *Ammophila arenaria*'s clumps, trapping and accumulating the sand particles eroded by the windward side of the mobile dune (Tsoar, 2002), extend in height the dune crest on upwardly convex surfaces. *Crucianellion maritimae* and particularly *Malcolmietalia* grasslands communities ('2210+2230'), being not tolerant to water stress (Ciccarelli, 2015), occurred on concave interdunal depressions located between the mobile and the fixed dune habitats, where the water table is often closer to the surface compared to other dune sectors. Going landward, the fixed dune habitat ('2250') settled on the most prominent convex ridges along the zonation. The innermost sector of the stable dunes was characterized by a more gentle convex profile where *Phillyreo latifoliae-Ericetum scopariae* occurred. Overall, we underline the differences between annuals species of the upper beach and perennials species of the embryo and mobile dunes in shaping the dune morphology. Annuals have small size, limited lateral spread and little or no litter accumulation (Boorman, 1982). Perennials, growing horizontally and vertically in response to burial (Maun, 2009), promote the sand deposition (Levin et al., 2008) modeling the dune structure more efficiently than annuals.

No significant differences were detected among the EC habitats concerning aspect, most likely due to the way the study area develops along the Tyrrhenian coast, in which narrow seaward dune strips are deployed from the upper beach to the fixed dune along with the same orientation.

Overall, elevation and sea distance were identified as the most discriminating variables in determining the occurrence of the EC habitats along a typical coastal dune profile. However, we emphasize the partial overlap of values for all of the morphological variables, especially for mobile dune ('2120'), embryo dune ('2110') and transition dune ('2210+2230') habitats, suggesting that dune habitats are not clearly delineated but in most cases characteristic plant communities are gradually transitional (Acosta et al. 2003a,b; Biondi, 2007).

4.2 Responses of EC habitats to the morphological variables

The presence of the upper beach habitat ('1210') was strongly related to sea proximity and low elevation. This community (*Salsolo kali-Cakiletum maritimae*) occurs along the first accumulation of drift material growing on areas with harsh abiotic conditions and disturbance. Indeed, these environments are characterized by low nutrient levels, high salinity and exposure to salt spray, continuous wind abrasion and sand burial (Acosta et al., 2009; Forey et al, 2009; Garcia-Mora et al., 1999).

Similarly, the embryo dune habitat with *Elymus farctus* ('2110') was closely related to sea distance and elevation. *Elymetum farctii* and *Echinophoro spinosae-Elymetum farctii* often occur in close association with upper beach vegetation ('1210') and, quite commonly, the two form an ill-defined linear mosaic of vegetation strung out along and just above strandlines subject to varying periods of erosion and accretion (Rodwell, 1995). Alternatively, where accretion has gone unchecked, better-defined and wider zones of *Elymus farctus* vegetation may be established above the strandline (Rodwell, 1995). This habitat, colonized by perennial dune species that are able to withstand burial, constitutes the initial seaward stages of dune construction (Acosta and Ercole, 2015) and therefore may occupy a broader range of elevations

than upper beach habitat ('1210'), including ripples or other raised sand surfaces. Hence, this plant community often settles in morphologically different areas from both the drift line of the upper beach and the taller mobile dunes containing *Ammophila arenaria*.

Indeed, the mobile dunes habitat ('2120') was associated solely with sea distance, and did not exhibit any association with elevation. Previous studies have shown that the tussock grass characteristic of this habitat form is incapable of growing too close to the sea and can only tolerate a substratum containing less than 1% sea salt, although it can be found both on low and tall dunes (Huiskes, 1979). This grass species contributes to sand accumulation and tall dune formation and can endure burial of up to 1-m annually through rapid production of elongated stem internodes and roots that extend to depths of 2 m to the site of initial sand accumulation (Hesp, 2002). It is the most effective dune species in forming the seaward cordons along the Mediterranean basin (Acosta and Ercole, 2015).

Concurrently, embryo and mobile dune habitats ('2110' and '2120') consolidate the substrate and also contribute to dune formation by acting as initial wind blocks that create conditions favorable to the formation of the transition and fixed dune communities prevalent in the inner dune sectors.

Proceeding inland, the transition dune habitats containing *Crucianella maritima* communities and *Malcolmietalia* dune grasslands ('2210+2230') did not exhibit any relationship with elevation nor sea distance, most likely because the embryo and mobile dunes protect them from salt spray and natural disturbances, allowing the transition dune habitat to spread over a wide range of the dune morphology. However, we highlight some specific values of curvature, speculating that both *Crucianellion maritimae* fixed beach dunes and *Malcolmietalia* dune grasslands prefer deep sand and interdunal depressions.

Fixed dune habitats ('2250' and '2260'), located farthest from the shoreline, were both strongly associated with elevation and sea distance. Being less tolerant of natural stressors and disturbances, these communities are generally found on the more stable and sheltered inner sectors of the dune system. Fixed dune species grow on stable substrates, with low salt spray and relatively rich soils (Acosta et al. 2009; Wiedemann and Pickart, 2008).

Overall, we observed a prominent role of elevation and sea distance in determining the occurrence of most of the EC habitat types. Along the Mediterranean coast, as was likewise observed by Ward et al. (2013) for the Baltic coast and by Barrett et al. (2006) for the salty Lake Lefroy (Western Australia), elevation is associated with the differences in soil moisture and water availability (Kim and Yu, 2009). Moreover, sea distance is probably related to the spatial pattern of cations, soil pH and salt spray along the sea-inland gradient (Hundt, 1985; Kim and Yu, 2009; van der Valk, 1974; Wilson and Sykes, 1999). Sea distance has been considered to be a good proxy of the sea-inland gradient in coastal dune ecosystems (Angiolini et al., 2013; Barrett, 2006; Burnside et al., 2008; Fenu et al. 2013; Mijovic et al., 2012; Ruocco et al., 2014; Ward et al., 2010).

5. Conclusion

In this paper, we examined the relationships between EC habitats and dune morphology in Mediterranean coastal systems. Dune elevation and sea distance were determined to be the key factors in affecting habitat occurrence in these coastal zones. The plant communities located in the extremities of the coastal zonation are related to specific ranges of elevation and sea distance, reflecting their different adaptations to the conditions prevalent along the steep sea-inland environmental gradient. The annual vegetation growing in the drift lines was found to occur in sectors closest to the sea, thus exhibiting high tolerance to stress and disturbance conditions. The embryo dune and mobile dune habitats, composed of perennial species that withstand sand burial, consolidate the substrate and create the initial sand accumulations contributing to shelter the innermost habitats. The centrally located transition dune habitat displayed a weak association with elevation and sea distance. Finally, the fixed dune habitats exhibited a marked adaptation to the less harsh conditions of the inner sector zones.

Our findings highlight the advantages of combining LiDAR images and field collected vegetation data for the analysis of areas with low vegetation cover, such as coastal dunes. This integrated approach effectively describes the relationship between EC habitat occurrence and dune morphology offering a trustworthy framework for the interpretation of the role of environmental factors in shaping vegetation patterns. Moreover, the broad study area and the high number of vegetation replicates used in this study enabled the calculation of reliable confidence intervals and hence, reliable statistical comparisons between habitats.

Our approach provided valuable information for use in coastal management and for the development of more effective conservation initiatives. Moreover, the presented methodology represents a cost-effective practice that matches the European strategies aimed at the conservation of the biodiversity (Weiers et al., 2004). From an applied perspective, it could be proposed to perform semi-automatic mapping of the EC habitats in order to test their classification accuracy. Furthermore, the comparison among LiDAR derived DTM (Digital Terrain Model) can be used to detect changes in the dune morphology over time (White and Wang, 2003), constituting a sound tool to monitor geomorphic processes on large temporal scales in coastal ecosystems. Bearing this in mind, we hope that similar studies will be implemented over increasingly larger scales in order to identify and monitor early-warning signals of potential threats to these fragile ecosystems.

Appendix 1

Tab. buffer 2- Mean $\pm$ I.C. (confidence interval) calculated for the morphological variables (elevation, sea distance, slope curvature, northness and eastness) for each habitat-type (1210, 2110, 2120, 2210+2230, 2250, 2260).

Morphological variables					
Habitat code	Elevation	Slope	Curvature	Northness	Eastness
1210	1.69 $\pm$ 0.15 ^a	5.27 $\pm$ 1.08 ^a	-0.004 $\pm$ 0.008 ^a	-0.009 $\pm$ 0.114	-0.015 $\pm$ 0.108
2110	2.59 $\pm$ 0.24 ^b	6.97 $\pm$ 1.09 ^b	-0.011 $\pm$ 0.009 ^a	-0.003 $\pm$ 0.091	-0.047 $\pm$ 0.097
2120	3.59 $\pm$ 0.43 ^c	8.34 $\pm$ 1.90 ^b	0.006 $\pm$ 0.014 ^{a-b}	0.040 $\pm$ 0.130	0.024 $\pm$ 0.131
2210+2230	3.90 $\pm$ 0.37 ^c	7.83 $\pm$ 1.18 ^b	-0.007 $\pm$ 0.010 ^a	-0.007 $\pm$ 0.083	-0.003 $\pm$ 0.080
2250	5.61 $\pm$ 0.87 ^d	9.36 $\pm$ 2.26 ^b	0.019 $\pm$ 0.019 ^b	-0.109 $\pm$ 0.131	0.016 $\pm$ 0.126
2260	5.02 $\pm$ 0.60 ^d	8.47 $\pm$ 1.24 ^b	-0.008 $\pm$ 0.021 ^a	0.022 $\pm$ 0.087	0.029 $\pm$ 0.081

Different superscripted letters indicate significant differences between EC habitats (Dunn's multiple comparison test, $p < 0.05$). No significant differences were detected among the habitat types for eastness and northness (one-way ANOVA, $p > 0.05$).

Tab. buffer 8- Mean $\pm$ I.C. (confidence interval) computed for the morphological variables (elevation, sea distance, slope curvature, northness and eastness) for each habitat-type (1210, 2110, 2120, 2210+2230, 2250, 2260).

Habitat code	Morphological variables				
	Elevation	Slope	Curvature	Northness	Eastness
1210	1.70 $\pm$ 0.14 ^a	4.61 $\pm$ 0.69 ^a	0.000 $\pm$ 0.001 ^{a-b-c}	0.013 $\pm$ 0.026	0.009 $\pm$ 0.025
2110	2.61 $\pm$ 0.24 ^b	6.84 $\pm$ 0.82 ^b	-0.001 $\pm$ 0.003 ^a	-0.008 $\pm$ 0.023	-0.014 $\pm$ 0.028
2120	3.57 $\pm$ 0.42 ^c	8.44 $\pm$ 1.35 ^{b-c}	0.002 $\pm$ 0.005 ^{b-c}	0.009 $\pm$ 0.030	0.001 $\pm$ 0.031
2210+2230	3.96 $\pm$ 0.36 ^c	7.81 $\pm$ 0.83 ^{b-c}	-0.001 $\pm$ 0.003 ^{a-b}	0.011 $\pm$ 0.020	0.015 $\pm$ 0.022
2250	5.48 $\pm$ 0.82 ^d	9.18 $\pm$ 1.53 ^c	0.005 $\pm$ 0.005 ^c	-0.006 $\pm$ 0.032	-0.015 $\pm$ 0.037
2260	5.02 $\pm$ 0.60 ^d	8.63 $\pm$ 0.96 ^c	0.003 $\pm$ 0.004 ^{a-c}	0.007 $\pm$ 0.022	0.017 $\pm$ 0.019

Different superscripted letters indicate significant differences between EC habitats (Dunn's multiple comparison test, $p < 0.05$). No significant differences were detected among the habitat types for eastness and northness (one-way ANOVA, $p > 0.05$).

Chapter 2

Disentangling the effect of coastal erosion and accretion on plant communities of Mediterranean dune ecosystems

Disentangling the effect of coastal erosion and accretion on plant communities of Mediterranean dune ecosystems

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Abstract

In coastal dunes, a close ecomorphodynamic interaction/relationship connects vegetation and sand, giving rise to the characteristic dunal landscape while guaranteeing the provision and maintenance of fundamental ecosystem services. However, sand redistribution processes (i.e. erosion and accretion) can alter such ecomorphodynamism, leading to serious consequences in terms of biodiversity and functioning of coastal dune ecosystems. In this study we explore the effect of erosion and accretion processes along a wide portion of the sea-inland gradient on Mediterranean dune plant communities. In particular, by developing a measure for quantifying the intensity of erosion and accretion, we assess whether and how different intensities of sand redistribution processes affect richness, cover and diversity of coastal dune plant communities using different regression techniques. Results show how the influence of sand redistribution processes varies considerably along the sea-inland gradient, with expected consequences on the integrity of dune systems. In particular, the effect of erosion seems to be particularly marked on foredune communities, which play a key role in the ecomorphodynamic process of dune formation, while decreasing as we move landward. On the other hand, accretion featured an opposite trend, apparently influencing only Mediterranean shrubs. Results highlight the importance of constantly monitoring changes in sand redistribution dynamics in order to enhance the conservation of coastal dune habitats, while also guaranteeing the associated ecosystem services.

Keywords: erosion, accretion, dune vegetation, EUNIS.

1.Introduction

In the last decades, the close relationship between biodiversity and ecosystem functioning has been widely acknowledged (Cardinale et al., 2012; Maestre et al., 2012; Tilman et al., 2014). Not only changes in species richness, but also alterations in the composition of communities proved to affect ecosystem functioning by modifying the ecological interactions underpinning ecosystem processes and services (Díaz et al., 2013; Oliver et al., 2015). For these reasons, understanding how environmental changes, through their impact on specific communities, influence ecosystem functioning is currently a challenging task for ecologists.

In coastal dunes, harsh environmental conditions limit the establishment to a highly specialized and diverse flora that, beyond being of considerable naturalistic value, contributes to the maintenance of essential ecosystem services, including coastal defense (McLachlan & Defeo, 2017), groundwater storage (Rhymes et al., 2015), and climate mitigation (Drius et al., 2016; Carranza et al., 2018). Most of the aforementioned ecosystem services are guaranteed by the ecomorphodynamic interaction between dune vegetation and sand (Stallins & Parker, 2003; Durán & Moore, 2013). Indeed, being adapted to sand burial, *psammophilous* plants are able to retain sediment by controlling its movement, therefore determining dune morphology and stabilization over time (Maun, 2008).

Despite their notable conservation value and the numerous benefits they provide, coastal dunes are currently among the most severely threatened ecosystems on Earth (Defeo et al., 2009; Janssen et al., 2016; Powell et al., 2018). In this regard, coastal erosion, hardened by human-related activities (e.g. construction of harbors, groins and dams; Eurosion, 2004), is one of the main threats affecting the integrity of dune ecosystems (Brown & McLachlan, 2002; Feagin et al., 2015). Indeed, there is evidence of a global trend of sandy beaches retreating due to coastal erosion (Bird, 2011), with strong consequences on the biodiversity and functioning of these environments (Schlacher et al., 2007). As an example, in coastal areas undergoing erosion, the existence of artificial barriers (e.g. roads and buildings facing dunes) particularly limits plant growth and dispersion (Doody, 2004; Feagin et al., 2005), therefore severely altering the ecomorphodynamic process of dune formation/building (Schlacher et al., 2007).

On the other hand, the influence of coastal accretion on dune vegetation has been rarely addressed in a targeted manner (but see Bitton & Hesp, 2013 and Miller, 2015). Overall, coastal progradation is likely to increase sand deposition, which can also limit vegetation establishment on dunes, depending on both the level of burial and the species-specific adaptation to burial (Maun, 2008). However, its effect has been mainly studied on single coastal plant species (Maun, 2009; Wilson & Sykes, 1999), while it is still not clear how dune plant communities respond to accretion as a whole.

Up to our knowledge, few studies explored the effects of erosion and accretion on dune plant communities (but see Bitton & Hesp, 2013 and Miller, 2015), and even less accounted for their simultaneous influence along the entire sea-inland gradient.

As understanding how sand redistribution processes affect dune vegetation is crucial for preserving the functioning of coastal environments and their associated ecosystem services (Schlacher et al.,

2007), the present study attempts to quantify the effect of erosion and accretion on Mediterranean dune vegetation. In particular, focusing on a wide portion of the sea-inland gradient, we analyzed (i) the influence of increasing erosion/accretion on plant communities' species richness, diversity and evenness; (ii) changes in the cover of dune vegetation. Moreover, we explored the specific response of a set of diagnostic (i.e. focal) species to erosion and accretion processes.

To achieve these aims, we developed a measure for quantifying shoreline dynamics (occurrence and intensity) at the landscape scale, which allowed us to conduct a robust analysis of the effects of sand redistribution processes on dune vegetation on a wide spatial extent.

2. Materials and methods

2.1. Study area

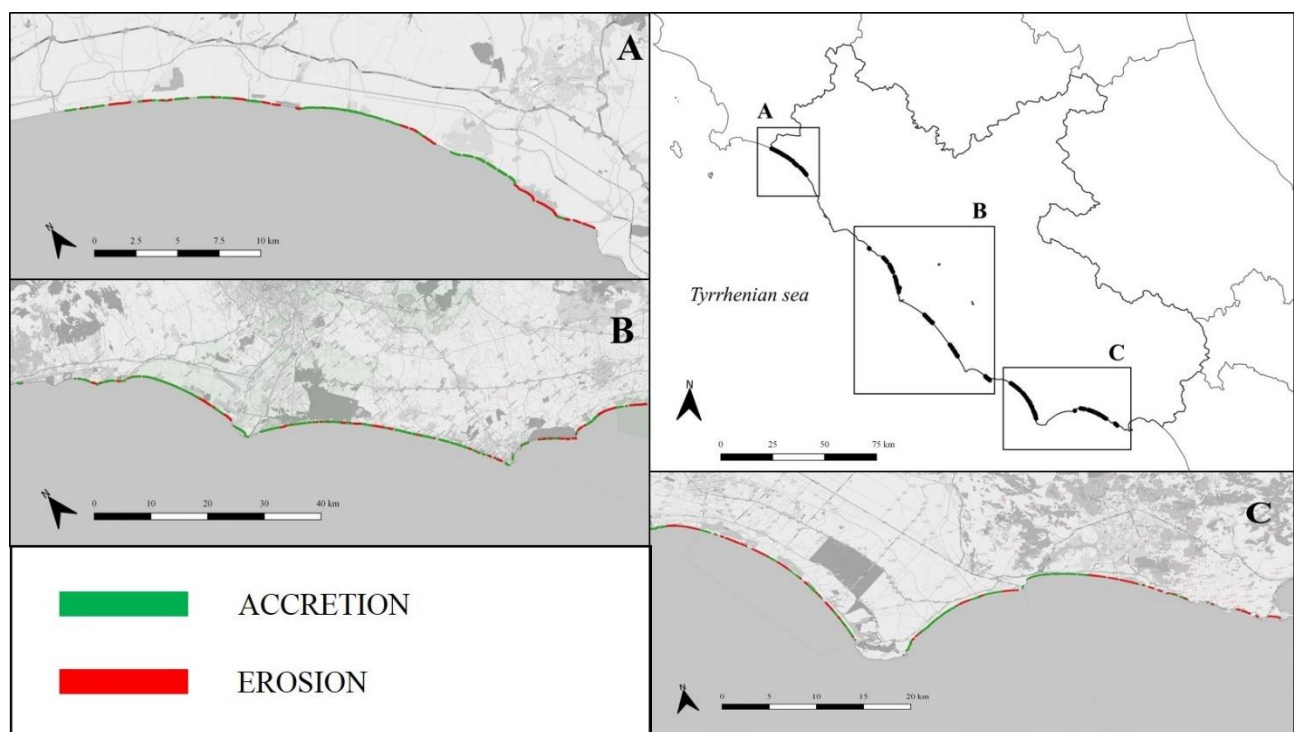


Figure 1. Study area.

The study was carried out on the Tyrrhenian coast of Central Italy (Fig. 1). In this area, characterized by a Mediterranean climate (Pesaresi et al., 2017), holocenic dune systems occupy a narrow strip along the seashore (<500 m), are low (<10 m in height) and relatively simple in structure. Sandy beaches vary in width from a few meters to approximately 40 m. In well-preserved coastal dunes of the study area, vegetation is usually structured in a sequence of plant communities (i.e. coastal zonation) featuring pioneer communities of the upper beach followed by a section of low embryo dunes, typically a single ridge of shifting dunes, coastal dune grasslands and, finally, Mediterranean coastal shrubs (Acosta et al., 2003a; Carranza et al., 2008).

It should be noticed that the dune system of the study area is characterized by an interchange of areas undergoing both erosion and accretion processes (MATTM-Regioni, 2017).

2.2. Vegetation and floristic data

Vegetation and floristic data was extracted from the “RanVegDunes” database (Sperandii et al., 2017), a national database including random georeferenced 4-m² relevés recorded between 2005 and 2015 and distributed along the Lazio coast (Fig. 1). For each vegetation plot, a list of recorded vascular plant species is available, together with relative abundance values measured on a percentage scale. Additionally, each plot is assigned to a level-3 EUNIS category according to the EUNIS habitat classification system (Davies et al., 2004). For this study, we selected 534 plots belonging to four EUNIS categories: sand beach drift lines (B1.1), shifting coastal dunes (B1.3), coastal stable dune grassland (B1.4) and coastal dune scrub (B1.6). The selected EUNIS categories represent most of the coastal zonation, from annual pioneer communities of the upper beach to coastal dune scrub (see Tab. 1).

Table 1. Description of the communities and diagnostic species selected for this study. For each community, the number of observations used for the analyses is reported.

Level type (number of observations)	3-EUNIS	Description and correspondence with EU habitats (ex Annex I 92/43/EEC)	Diagnostic species
B1.1 Sand beach drift lines (N = 73)		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 peplis</i> (L.) Prokh., <i>Polygonum maritimum</i> L., <i>Salsola kali</i> L.
B1.3 Shifting coastal dunes (N = 203)		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.,

Otanthus maritimus (L.) Hoffmanns. & Link
subsp. *Maritimus*,

Pancratium maritimum L.,

Sporobolus virginicus Kunth

B1.4 Coastal stable dune grassland (N = 116)	Stable dune grasslands including chamaephytic communities of the inland dunes dominated by <i>Crucianella maritima</i> (EU hab 2210 - <i>Crucianellion maritimae</i> fixed beach dunes) and annual, species-rich communities colonizing dry interdunal depressions (EU hab 2230 - <i>Malcolmietalia</i> dune grasslands)	<i>Bromus diandrus</i> Roth subsp. <i>maximus</i> (Desf.) Soó, <i>Crucianella maritima</i> L., <i>Cutandia maritima</i> (L.) Barbey, <i>Lagurus ovatus</i> L., <i>Medicago littoralis</i> Loisel., <i>Ononis variegata</i> L., <i>Phleum arenarium</i> L. subsp. <i>caesium</i> H. Scholz, <i>Pseudorhiza pumila</i> (L.) Grande, <i>Pycnocomon rutifolium</i> (Vahl) Hoffmanns & Link, <i>Silene canescens</i> Ten., <i>Sixalix atropurpurea</i> (L.) Greuter & Burdet, <i>Vulpia fasciculata</i> (Forssk.) Fritsch
B1.6 Coastal dune scrub (N = 142)	Shrub communities including formations dominated by <i>Juniperus</i> spp. and formations dominated by sclerophyllous shrubs	<i>Juniperus oxycedrus</i> L. subsp. <i>macrocarpa</i> (Sibth. & Sm.) Neilr., <i>Lonicera implexa</i> Aiton subsp. <i>Implexa</i> , <i>Phillyrea angustifolia</i> L., <i>Pistacia lentiscus</i> L.

We extracted species richness and vegetation cover values for each plot. In particular, species richness was calculated as the total number of species recorded in each plot (hereafter, species richness), while vegetation cover was computed by summing up the percentage cover of each species recorded in a given plot (hereafter, vegetation cover). It should be noticed that, since this value can exceed 100% ground cover, for each EUNIS category we standardized cover values between 0 and 1. To this aim, we divided the values of the vegetation cover recorded in each plot by the maximum value measured in its EUNIS category.

To explore the response of diagnostic species to coastal erosion/accretion, following the Italian Interpretation Manual of the Habitats Directive (Biondi et al., 2009) we selected those that were most abundant in our database (see Tab. 1) for each analyzed community (identified through its EUNIS category). Diagnostic species have been increasingly used to detect habitat modifications due to their vulnerability to environmental changes (Santoro et al., 2012a; Del Vecchio et al., 2016; Angiolini et al., 2017).

2.3. Coastal erosion and accretion data

Data describing coastal erosion and accretion conditions were gathered from the Italian “Geoportale Nazionale” (<http://www.pcn.minambiente.it/mattm/en/wfs-service/>) and imported in an ArcGIS environment (ArcGIS 10.1; ESRI, 2011). Specifically, data consisted in a vector layer of polygons representing the overall change in coastal spatial extent occurred from 1994 to 2012 due to the retreating and progradation of the shoreline. Coastal polygons were derived by tracking temporal changes of the shoreline position through the photointerpretation of high-resolution aerial orthophotos (for details see <http://www.pcn.minambiente.it/mattm/progetto-coste/>). The following information were associated to each coastal polygon in the attribute table: dynamic condition (erosion or accretion), area (expressed in m²) and length (expressed in m).

In order to quantify the intensity of erosion and accretion processes occurred during the analyzed period in the study area, a Shape Index (hereafter, SI_{change}) accounting for both compactness and size of the polygons was computed as:

$$SI_{change} = A_{polygon}/P_{polygon}$$

where $A_{polygon}$ is the area of the coastal polygon (associated to erosion or accretion), while $P_{polygon}$ is its perimeter. Basically, low values of the SI_{change} (area/perimeter ~ 0) represent small, thin and convoluted polygons indicating stable-to-low intensity of erosion/accretion processes, while high values of SI_{change} (area/perimeter $\rightarrow \infty$) stand for wide and compact polygons, featuring high intensity of erosion/accretion phenomena (Fig. 2).

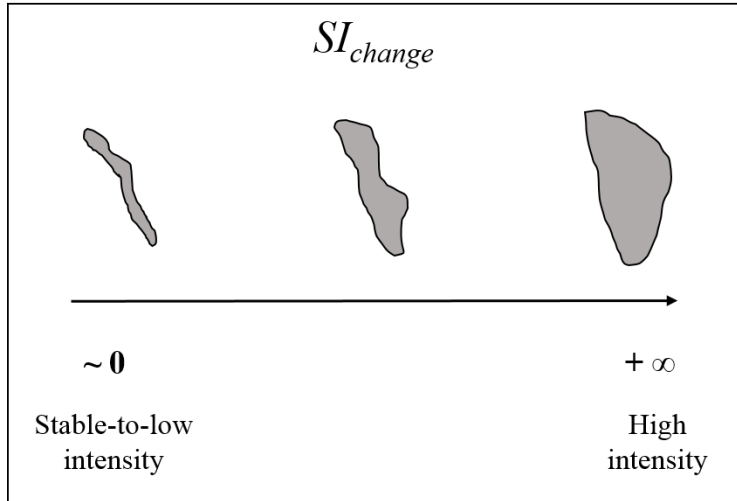


Fig. 2- Figure representing the geometry of coastal polygons (erosion or accretion) changing at increasing value of the SI_{change} . The more SI_{change} values are far from 0 the more the polygon is wide and compact, and more intense are erosion/accretion processes characterizing the corresponding coastal sector.

In order to analyze the effects of erosion and accretion intensity on coastal dune vegetation, each sampled plot was spatially joined to a unique polygon by its proximity. Given that low-lying sandy beaches of the Lazio system undergone, to some degree, either erosion or accretion processes during the analyzed period, it was possible to associate all the vegetation plots to one of the former processes.

2.4. Statistical analyses

Statistical analyses were conducted separately in erosion and accretion sectors to independently highlight the effect of each process on the vegetation characterizing the selected EUNIS categories (Tab. 1).

2.4.1. Coastal erosion/accretion vs dune plant communities

The influence of sand redistribution processes on plant species richness and vegetation cover was assessed by modelling erosion and accretion as a function of SI_{change} through different regression techniques.

For each EUNIS category, Generalized Linear Models (GLMs) were implemented for exploring the change in species richness due to the aforementioned coastal processes, setting the species richness as response variable and SI_{change} as predictor. Models were fitted assuming a Poisson distributed error term and using a log transformation of the mean. Since standard error can be biased in Poisson models due to over- or underdispersed data, we estimated the dispersion parameter for each Poisson fitted model. In case of significant over-/underdispersion being detected (function dispersiontest, “AER” R package; Kleiber & Zeileis, 2008), a QuasiPoisson model was fitted.

For each EUNIS category, Linear Models (LMs) were used to assess the influence of coastal erosion and accretion on vegetation cover, setting vegetation cover as response variable and SI_{change}

as predictor. Standardized vegetation cover values were transformed on a logit scale to meet the assumptions required by LMs.

In both GLMs and LMs, we accounted for nonlinear relationships between response variables and SI_{change} by including the latter as quadratic term in the models and testing whether its inclusion significantly increased the model fit.

Subsequently, with the aim of examining the effect of increasing intensity of erosion/accretion on coastal vegetation, regression trees based on conditional inference (function `ctree`, “party” R package; Hothorn et al., 2006) were implemented in those EUNIS categories highlighted by the models as significantly affected by coastal erosion/accretion. Specifically, we used regression trees to identify a threshold that, breaking the continuous range of SI_{change} (for both species richness and vegetation cover), would divide sampled plots in statistically different groups (high erosion/accretion vs. low-to-stable erosion/accretion conditions). In this regard, regression trees have been successfully employed for identifying environmental thresholds describing plant diversity patterns (Palpurina et al., 2015; Svitok et al., 2016).

Only in those communities (i.e. EUNIS categories) suggested by the regression models as being significantly affected by coastal erosion/accretion processes, using the information obtained from the regression trees, we analyzed how diversity and evenness differed between areas featuring low-to-stable and high erosion/accretion conditions. To this aim, we used rarefaction/extrapolation curves (hereafter, R/E curves) based on Hill numbers (Chao et al., 2014). Hill numbers integrate information on both species richness and species relative abundances in a class of diversity indices that differ only by an exponent q . In particular, Hill numbers correspond to species richness, Shannon and Simpson diversity of the assemblage when q is equal to 0, 1 and 2, respectively. Rarefaction/extrapolation curves allow statistical comparisons of assemblages’ diversity by interpolating/extrapolating Hill numbers from a reference sample size to smaller/larger number of sampling units and by providing confidence intervals of the diversity estimators through bootstrap (Chao et al., 2014; Hsieh et al., 2016). Rarefaction/extrapolation curves (based on sampling-unit incidence frequencies data) were implemented using the function `iNEXT` included in the “iNEXT” R package (Hsieh et al., 2018). In particular, R/E curves were implemented for q equal to 1 and 2.

2.4.2. Coastal erosion/accretion vs diagnostic species

Changes in the occurrence frequency of diagnostic species were tested between groups identified by the regression trees only in those EUNIS categories that were found to be affected in terms of species richness by coastal erosion/accretion. For each focal species, the change in occurrence frequency was tested performing a 2-sample test for equality of proportions (function `prop.test`, “stats”, Yates correction disabled; R Core Team, 2017). In particular, we tested the null hypothesis of equality of proportions of species occurrences recorded in vegetation plots associated to low-to-stable and high erosion/accretion condition.

3. Results

Overall, erosion and accretion did not affect homogeneously species richness and vegetation cover of the tested EUNIS categories. Specifically, coastal erosion appeared to negatively influence both

species richness and vegetation cover of the sand beach drift line communities (B1.1), while affecting only species richness in shifting coastal dunes (B1.3) and in stable dune grasslands (B1.4). On the other hand, accretion processes seemed to positively influence species richness of coastal dune scrub (B1.6). Overall, communities' diversity and evenness resulted to be favored in low-to-stable erosion sectors and in areas undergoing high accretion condition.

3.1. Effects of coastal erosion

Species richness was negatively affected by increasing erosion intensity in EUNIS communities occurring closest to the sea (sand beach drift line, B1.1; shifting coastal dunes, B1.3). At the same time, we observed a negative effect on the species richness of coastal dune grasslands (B1.4) for very high SI_{change} values. No effect was detected in habitats occurring landward, such as coastal dune scrub (B1.6). (See Tab. 2 for model outcomes and Appendix A for figures representing the effect of coastal erosion in EUNIS categories B1.1, B1.3 and B1.4).

Table 2. Model outcomes reporting the effect of coastal erosion on species richness of EUNIS categories. P/QP: Poisson/QuasiPoisson model. The values of the z-test and t-test are reported in case of Poisson and QuasiPoisson models, respectively. The uppercase ² identifies the quadratic term for SI_{change} , included through the R function "poly()" that fits orthogonal polynomials for reducing collinearity issues.

EUNIS	P/QP	Formula	Estimate	Std. Error	t/z-value	Pr(> t/z)
B1.1 Sand beaches drift lines	QP	Sp. Rich. ~ SI_{change}	-0.0591	0.02528	-2.338	0.0245
B1.3 Shifting coastal dunes	P	Sp. Rich. ~ SI_{change}	-0.0325	0.0146	-2.218	0.0265
B1.4 Coastal stable dune grassland	P	Sp. Rich. ~ SI_{change} + $(SI_{change})^2$	-0.4693 -0.9272	0.3364 0.3489	-1.395 -2.658	0.1630 0.0079
B1.6 Coastal dune scrub	QP	Sp. Rich. ~ SI_{change}	0.0133	0.0244	0.544	0.589

For species richness of drift line communities (B1.1), regression tree split the observations in two statistically different groups at the threshold of $SI_{change} = 3.777$ (Appendix B, Fig. B1), with plots occurring in high erosion conditions significantly poorer in species than plots occurring in coastal sectors associated to low-to-stable erosion. The same pattern could be observed for shifting coastal dunes, whose species richness turned out to be lower in plots occurring above the SI_{change} threshold of 4.157, thus subjected to high erosion conditions (Appendix B, Fig. B2). Although a negative effect on species richness of coastal stable dune grassland (B1.4) was observed in case of strong erosion, regression tree did not split vegetation plots in groups.

Vegetation cover appeared to decrease significantly with increasing values of SI_{change} in drift line communities (Tab. 3; Appendix A, Fig. A4). Here, regression tree split vegetation plots in two groups at the SI_{change} threshold of 3.714 (Appendix B, Fig. B3). Consistently with species richness, vegetation cover appeared to be significantly lower in plots occurring in coastal sectors undergoing strong erosion.

Table 3. Model outcomes representing the effect of coastal erosion on vegetation cover of EUNIS categories. vegetation cover values were standardized and logit-transformed.

EUNIS	Formula	Estimate	Std. Error	t-value	Pr(> t)
B1.1 Sand beaches drift lines	H. Cov. $\sim$ SI_{change}	-0.2666	0.0788	-3.384	0.0016
B1.3 Shifting coastal dunes	H. Cov. $\sim$ SI_{change}	-0.0280	0.0359	-0.780	0.4374
B1.4 Coastal stable dune grassland	H. Cov. $\sim$ SI_{change}	-0.0787	0.0614	-1.282	0.205
B1.6 Coastal dune scrub	H. Cov. $\sim$ SI_{change}	0.0258	0.0364	0.709	0.481

R/E curves showed that drift line (B1.1) assemblages occurring in coastal sectors associated with low erosion were more diverse and more even than those located in areas subjected to high erosion (Fig. 3). The same pattern was observed for coastal shifting dunes (B1.3) (Fig. 3).

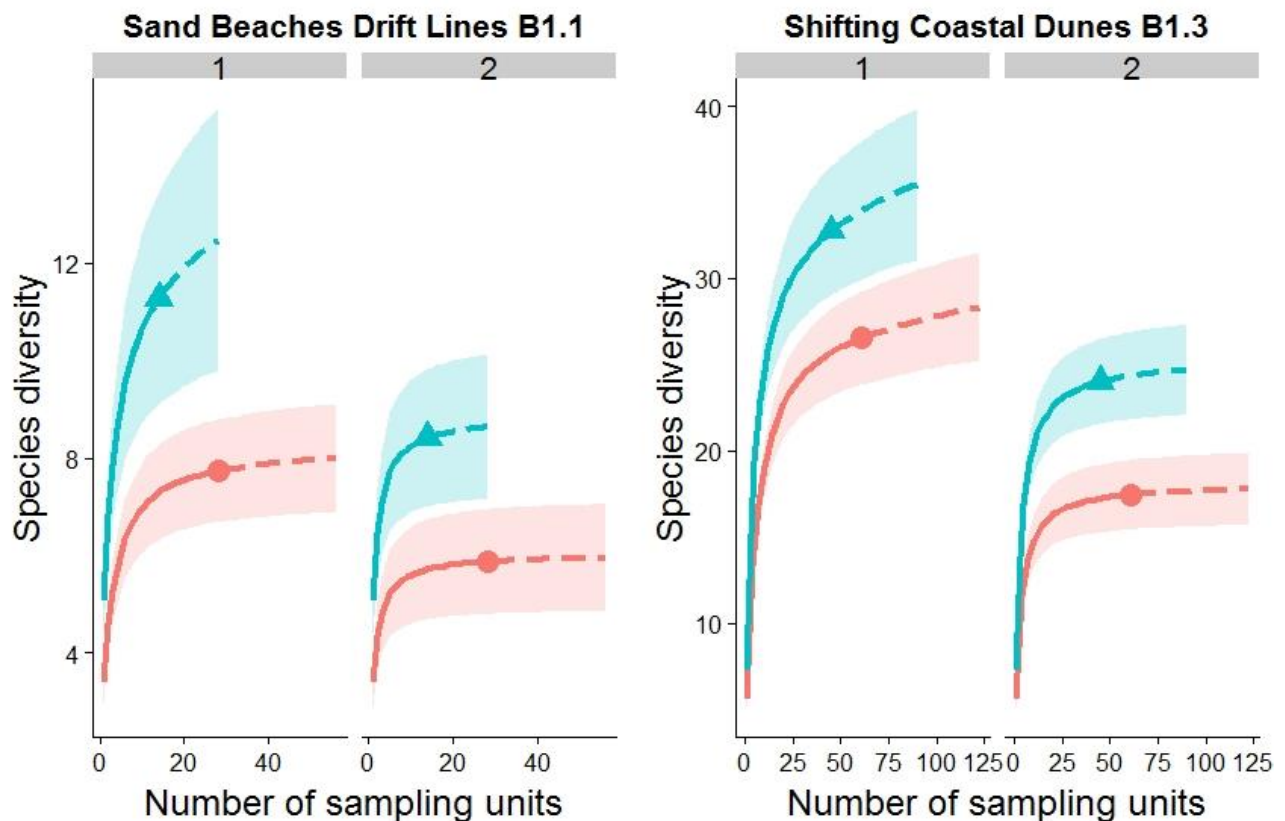


Figure 3. Rarefaction/Extrapolation (R/E) curves for $q = 1$ (Shannon diversity) and $q = 2$ (Simpson diversity) for vegetation plots belonging to B1.1 and B1.3 EUNIS categories and occurring in coastal sectors associated to low (blue curve) and high (red curve) erosion. In both figures, lines represent Shannon

diversity values interpolated (solid line) and extrapolated (dashed line) from the reference sample (observed).

Regarding focal species, only *Chamaesyce peplis*, typical of the upper beach (B1.1), was found to occur less frequently in high erosion conditions ($\chi^2 = 10.92$, p -value = 0.0009).

In foredune communities (B1.3), the occurrence frequency of *Pancratium maritimum* and of *Cyperus capitatus* was significantly higher in plots associated to low erosion conditions (*P. maritimum*: $\chi^2 = 10.69$, p -value = 0.0011; *C. capitatus*: $\chi^2 = 4.06$, p -value = 0.04). On the contrary, *Elymus farctus* occurred more frequently in proximity of coastal sectors experiencing strong erosion ($\chi^2 = 7.64$, p -value = 0.0057).

See Appendix C for the results of the proportional tests performed on the entire set of selected focal species.

3.2. Effects of coastal accretion

Species richness was found to increase significantly along with SI_{change} only in coastal dune scrub (B1.6). (See Table 4 for model outcomes and Appendix A for figures representing the effect of coastal accretion on EUNIS category B1.6).

Table 4. Model outcomes regarding the effect of coastal accretion on species richness of EUNIS categories. P/QP: Poisson/QuasiPoisson model. The values of the z-test and t-test are reported in case of Poisson and QuasiPoisson models, respectively. The uppercase ² identifies the inclusion of the quadratic term for SI_{change} .

EUNIS	P/QP	Formula	Estimate	Std. Error	t/z-value	Pr(> t/z)
B1.1 Sand beaches drift lines	P	Sp. Rich. ~ SI_{change}	0.0415	0.0360	1.154	0.248
B1.3 Shifting coastal dunes	P	Sp. Rich. ~ SI_{change}	-0.01260	0.0125	-1.007	0.314
B1.4 Coastal stable dune grassland	P	Sp. Rich. ~ SI_{change}	-0.0282	0.0180	-1.564	0.118
B1.6 Coastal dune scrub	QP	Sp. Rich. ~ SI_{change}^2	0.0333	0.0159	2.093	0.0394

As for vegetation cover, no significant effect was detected in any of the EUNIS categories (Tab. 5).

Table 5. Model outcomes showing the effect of coastal accretion on vegetation cover of EUNIS categories. Vegetation cover values were standardized and logit-transformed.

EUNIS	Formula	Estimate	Std. Error	t-value	Pr(> t)
B1.1 Sand beaches drift lines	H. Cov. $\sim$ SI_{change}	-0.014	0.1011	-0.139	0.891
B1.3 Shifting coastal dunes	H. Cov. $\sim$ SI_{change}	-0.0021	0.0337	-0.063	0.9496
B1.4 Coastal stable dune grassland	H. Cov. $\sim$ SI_{change}	0.0301	0.0440	0.683	0.4977
B1.6 Coastal dune scrub	H. Cov. $\sim$ SI_{change}	-0.0517	0.0377	-1.373	0.1735

Regression tree performed on species richness divided the plots in two statistically different groups at SI_{change} equal to 4.941 (Appendix B, Fig. B4), with plots undergoing high accretion being statistically richer in species than those occurring in low-to-stable accretion zones.

Diversity and evenness of the coastal dune scrubs (B1.6) appeared to be higher in coastal sectors characterized by high accretion, as evidenced by the R/E curves (Fig. 4).

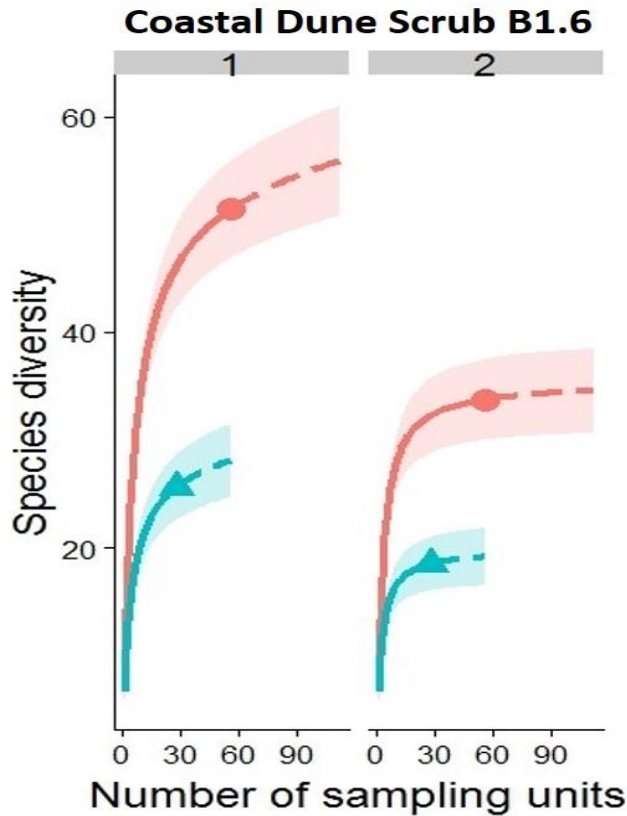


Figure 4. Rarefaction/Extrapolation (R/E) curves for $q = 1$ (Shannon diversity) and $q = 2$ (Simpson diversity) for vegetation plots belonging to the B1.6 EUNIS category occurring in coastal sectors associated to low (blue curve) and high (red curve) accretion. In both figures, lines represent Shannon diversity values interpolated (solid line) and extrapolated (dashed line) from the reference sample (observed).

As regard to the focal species, the occurrence frequency of *Lonicera implexa* was significantly higher in coastal sectors subjected to low accretion ($\chi^2 = 10.29$, p -value = 0.0013).

See Appendix C for the results of the proportional tests performed on the entire set of selected focal species.

4. Discussion

In this study, we described and quantified effects driven by erosion and accretion on Mediterranean dune plant communities. By combining different statistical tools, we observed that erosion appears to negatively affect plant communities of the sectors closest to the shoreline, while accretion, even though slightly, seems to positively influence plant communities of the fixed dunes. At the same time, no particularly selective effect of erosion and accretion was detected when exploring the response of a set of focal species to sand redistribution processes.

4.1. Effects of erosion

Results suggest that erosion breaks off coastal zonation, with the potential effect of hardening the so-called process of coastal “squeezing” in urbanized coastal areas (see Doody, 2004; Feagin et

al., 2005; Malavasi et al., 2013). As observed by Acosta et al. (2006) and Bertacchi et al. (2016) in Mediterranean sandy ecosystems and by Bitton & Hesp (2013) and Miller (2015) in Atlantic dunes, erosion appears to negatively affect plant communities colonizing the sectors closest to the shoreline. Indeed, we observed that, due to their proximity with the shoreline, drift line communities and shifting dunes occurring in areas undergoing strong erosion are subjected to a substantial change not only in terms of species richness and vegetation cover, but also of communities' diversity and evenness. Furthermore, results highlight that strong erosion can produce negative effects also on plant communities establishing landward, such as coastal dune grasslands (B1.4).

Along the coastal zonation, the most remarkable impact of erosion was observed in pioneer communities of the upper beach (B1.1). Here, both species richness and vegetation cover tend to decrease when the intensity of erosion increases. Moreover, R/E curves show that B1.1 communities tend to be less even when occurring in coastal sectors undergoing strong erosion. However, it should be noticed that, as pioneer communities of the upper beach are characterized by a restricted pool of species discriminated by a relatively low cover (Prisco et al., 2012; Sperandii et al., 2019), even a minimum loss in their species assemblage can cause a significant reduction in their diversity, evenness and cover. Nevertheless, the loss of species characterizing drift line communities is able to trigger the weakening of the ecomorphodynamic processes which are the basis of dune building and formation. Indeed, pioneer communities of the drift lines constitute the first barrier to sand movement, affecting the development of the embryo dunes (Prisco et al., 2012). In this regard, the diagnostic species *Chamaesyce peplis* was found to occur less in high erosion conditions than in stable-to-low erosion sectors.

Shifting coastal dunes (B1.3) were similarly affected, showing a substantial decrease not only in the species richness but also, as highlighted by the R/E curves, in the diversity and evenness of communities located in coastal sectors undergoing strong erosion. The detrimental effect of erosion processes on the diversity of such communities might have, in turn, worrying implications on their functionality. Indeed, shifting coastal dunes are characterized by species, such as *Elymus farctus* and *Ammophila arenaria*, that due to their being tolerant to burial and capable of accumulating sand (Maun, 2009) play a pivotal role in the formation and stabilization of embryonic and mobile dunes. Interestingly, we observed that *Elymus farctus* occurs more frequently in coastal sectors undergoing high erosion. This could be in line with Doing (1985), who reported that *Elymus farctus* tends to replace *Ammophila arenaria* in condition of low sand budget, although our analysis on diagnostic species did not highlight any substantial difference in the occurrence of *Ammophila arenaria*. At the same time, we found that erosion has a negative impact on *Pancratium maritimum*, which decreases in its occurrence frequency where the intensity of erosion is high. In this regard, Balestri and Cinelli (2004) observed that the germination of *P. maritimum* might be prevented in coastal sites characterized by low deposition of sand due to coastal erosion.

The slightly negative effect of strong coastal erosion on species richness of stable dune grasslands (B1.4) could be also related to the detrimental influence of erosion phenomena on upper beach (B1.1) and, in particular, on shifting dunes (B1.3). Indeed, well-developed foredunes plant communities act as a barrier to disturbance factors coming from the sea (e.g., salt spray, wave

action), therefore providing favorable conditions for landward communities to successfully establish and grow (Ehrenfeld, 1990; Durán & Moore, 2013). For these reasons, in case of foredunes damaging due to strong erosion, negative implications on the diversity of stable and fixed coastal dunes plant communities are highly likely.

4.2. Effects of accretion

Although a positive influence of increasing sand deposition on *psammophilous* species could be expected, as burial is known to favor their establishment and growth in shifting dunes communities (Maun, 2008, 2009), we did not observe any effect of accretion on this coastal sector.

A positive effect of accretion on the species richness, diversity and evenness of plant dune communities was observed only in coastal dune scrub (B1.6). In this case, our results show that species richness is higher in areas experiencing substantial shoreline progradation. Consistently, R/E curves suggest that such communities are more evenly distributed in sectors experiencing high, rather than stable-to-low, accretion. These results seem to be in line with the hypothesis that sand accumulation favors the formation of well-developed foredunes, which in turn promote higher plant diversity in landward sectors of coastal zonation. However, these findings should be interpreted carefully. Indeed, it should be considered that landward communities, especially Mediterranean coastal shrubs, are subjected to human-related disturbance factors not considered in this study that may promote the introduction of ruderal species (Acosta et al., 2006; Buffa et al., 2012). In this regard, we observe that *Lonicera implexa* was the only diagnostic species showing a difference in its occurrence frequency, occurring more frequently in sectors experiencing high accretion.

5. Conclusion

In this study, we provide evidence of coastal erosion/accretion influencing dune vegetation diversity, while showing that the influence of sand redistribution processes notably varies along the sea-inland gradient, with expected implications not only on dune ecosystem functioning, but also on the capacity to provide the associated ecosystem services. In particular, the negative effect of erosion on foredune communities is particularly alarming, as these are the cornerstone of ecomorphodynamic processes of dune formation.

Results highlight the need of constantly monitoring changes in communities' features due to shoreline dynamics in order to early detect alteration of the ecomorphodynamic process. To this aim, *SIchange* proved to be an effective measure for quantifying the magnitude of sand redistribution processes, allowing investigation of their effect on a wide geographic extent.

In this context, preserving ecosystem functioning, through the maintenance of a proper ecomorphodynamism, guarantees the supply of key coastal ecosystem services. Bearing this in mind, with this study we stress the need of preserving dune plant communities for their role in feeding the ecomorphodynamic process, beyond protecting plant diversity for its intrinsic naturalistic value.

Appendix A

Effects of coastal erosion

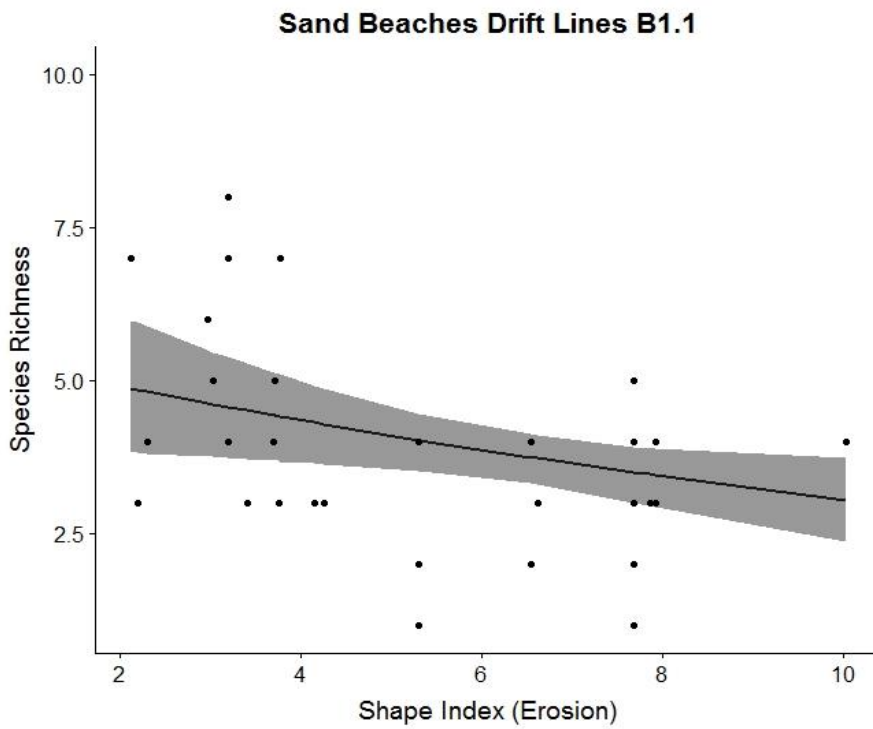


Figure A1. Effect of coastal erosion on species richness of sand beaches drift lines (B1.1). Grey bands represent the 95% confidence intervals computed as 0.025 and 0.975 quantiles from 500 bootstrap samples.

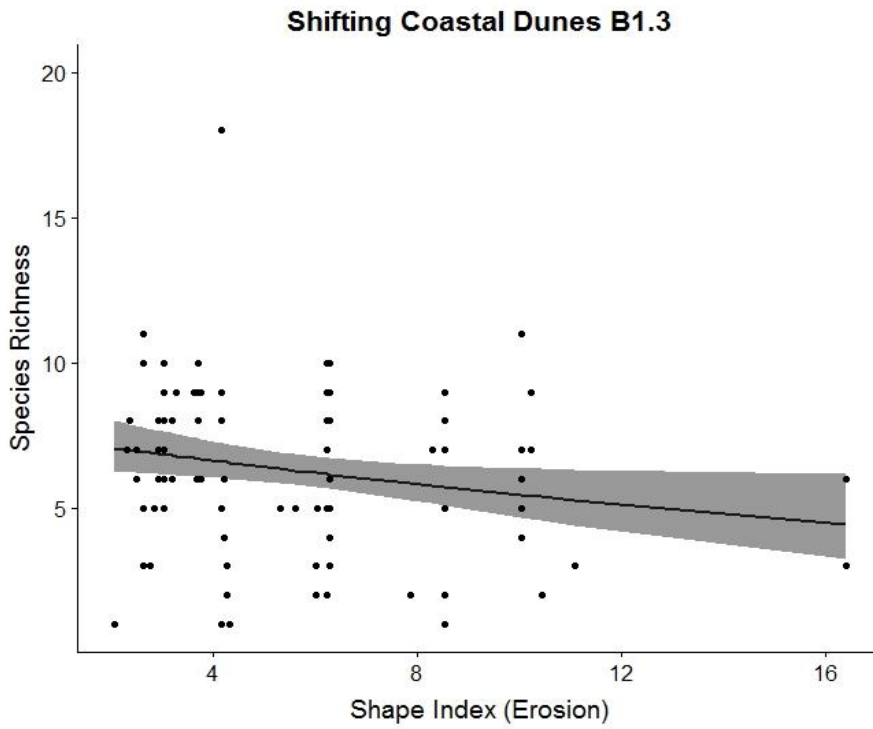


Figure A2. Effect of coastal erosion on species richness of shifting coastal dunes (B1.3). Grey bands represent the 95% confidence intervals computed as 0.025 and 0.975 quantiles from 500 bootstrap samples.

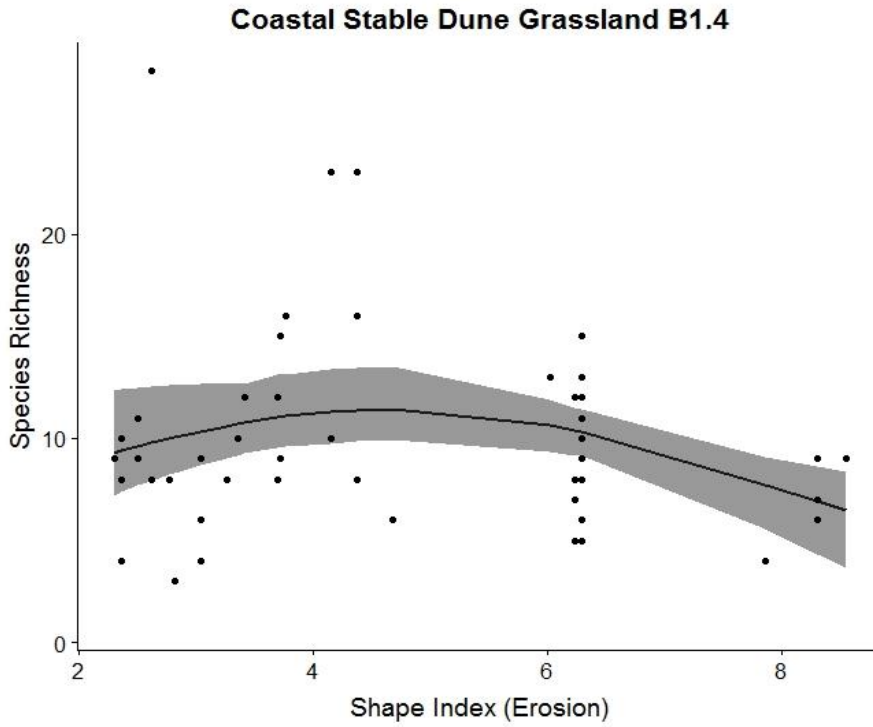


Figure A3. Effect of coastal erosion on species richness of coastal stable dune grassland (B1.4). Grey bands represent the 95% confidence intervals computed as 0.025 and 0.975 quantiles from 500 bootstrap samples.

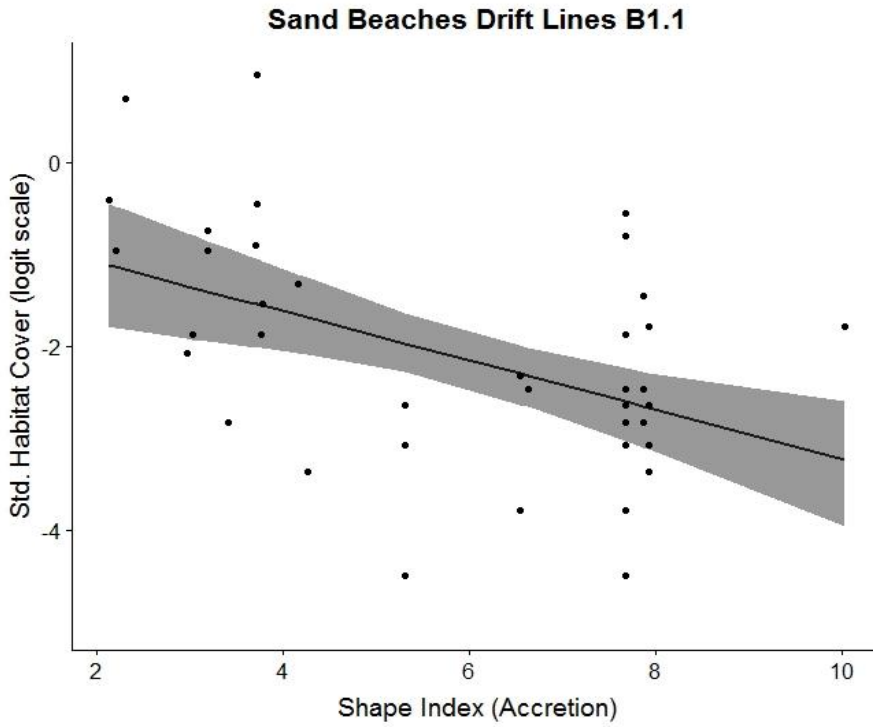


Figure A4. Effect of coastal erosion on vegetation cover (standardized and logit-transformed) of sand beaches drift lines (B1.1). Grey bands represent the 95% confidence intervals computed as 0.025 and 0.975 quantiles from 500 bootstrap samples.

Effects of coastal accretion

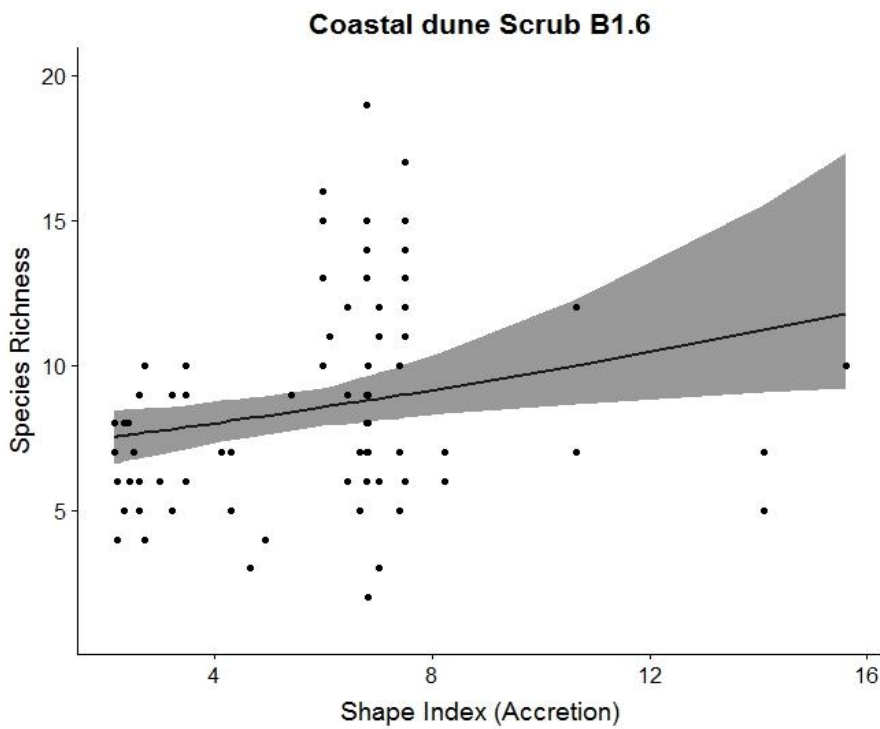


Figure A5. Effect of coastal accretion on species richness of coastal dune scrub (B1.6). Grey bands represent the 95% confidence intervals computed as 0.025 and 0.975 quantiles from 500 bootstrap samples.

Appendix B

Effects of coastal erosion

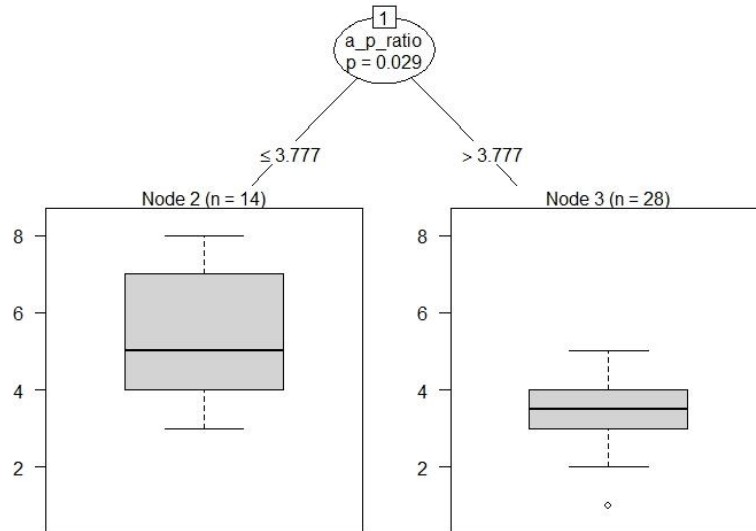


Fig. B1 – Regression tree output for the model: species richness $\sim SI_{\text{change}}$ in B1.1. Two groups of plots were identified according to the difference in species richness by the regression tree. In B1.1, species richness was significantly higher in stable-to-low erosion coastal sectors (represented by node 2 group) than in high erosion ones. Groups were divided at the SI_{change} threshold of 3.777.

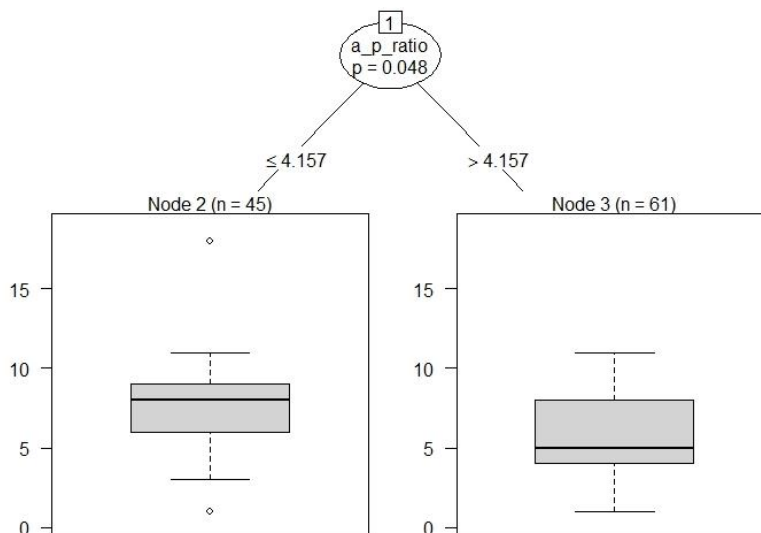


Fig. B2 – Regression tree output for the model: species richness $\sim SI_{\text{change}}$ in B1.3. Two groups of plots were identified according to the difference in species richness by the regression tree. In B1.3, species richness was significantly higher

in stable-to-low erosion coastal sectors (represented by node 2 group) than in high erosion ones. Groups were divided at the SI_{change} threshold of 4.157.

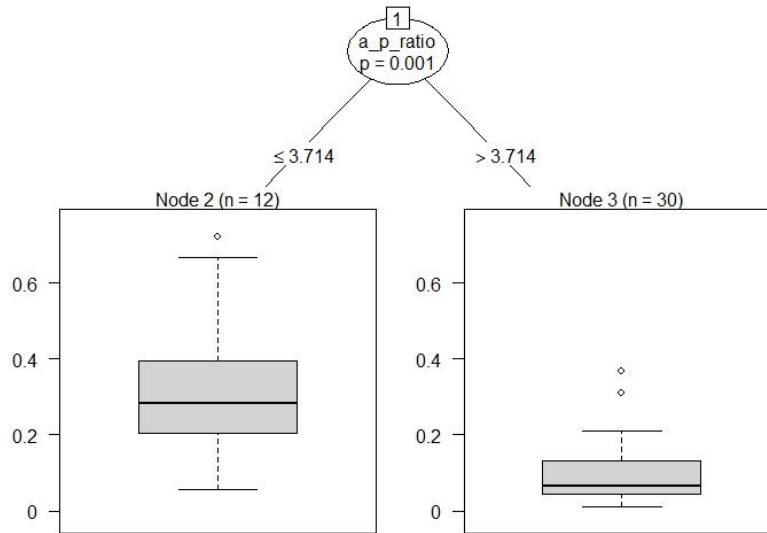


Fig. B3 – Regression tree output for the model: vegetation cover $\sim SI_{\text{change}}$ in B1.1. Two groups of plots were identified according to the difference in cover values by the regression tree. In B1.1, plant cover was significantly higher in stable-to-low erosion coastal sectors (represented by node 2 group) than in high erosion ones. Groups were divided at the SI_{change} threshold of 3.714.

Effects of coastal accretion

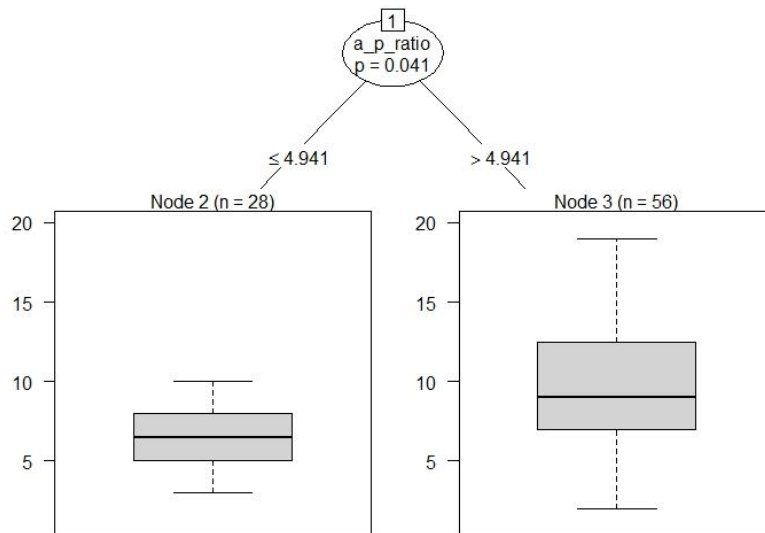


Fig. B4 – Regression tree output for the model: species richness $\sim$ SI_{change} in B1.6. Two groups of plots were identified according to the difference in species richness by the regression tree. In B1.6, species richness was significantly higher in high accretion coastal sectors (represented by node 3 group) than in stable-to-low accretion ones. Groups were divided at the SI_{change} threshold of 4.941.

Appendix C

Results of proportion tests performed comparing the occurrence frequencies of focal species recorded in coastal sectors associated to stable-to-low and high erosion intensity. The null hypothesis is that the frequency of occurrence does not change according to the increasing intensity of coastal erosion. *Prop_{low}*: occurrence frequency (occurrences/number of plots) of focal species in coastal sectors associated to stable-to-low erosion. *Prop_{high}*: occurrence frequency (occurrences/number of plots) of focal species in coastal sectors associated to high erosion. *Chi-sq.*: value of the Chi-sq. statistic. *d.f.*: degree of freedom. *Conf. Int. Diff_{prop}*: Confidence Interval of the difference in proportions.

EUNIS	Species	<i>Prop_{low}</i>	<i>Prop_{high}</i>	<i>Chi-sq.</i>	<i>d.f.</i>	<i>p-value</i>	<i>Conf. Int. Diff_{prop}</i>
Sand beaches drift lines (B1.1)	<i>Cakile maritima maritima</i>	1	0.96	0.51	1	$p > 0.05$	$-0.03 \leq \text{Diff}_{prop} \leq 0.1$
	<i>Salsola kali</i>	1	0.78	3.5	1	$p > 0.05$	$0.06 \leq \text{Diff}_{prop} \leq 0.37$
	<i>Polygonum maritimum</i>	0.14	0.1	0.11	1	$p > 0.05$	$-0.18 \leq \text{Diff}_{prop} \leq 0.25$
	<i>Chamaesyce peplis</i>	0.64	0.14	10.92	1	$p = 0.0009$	$0.21 \leq \text{Diff}_{prop} \leq 0.78$
Shifting coastal dunes (B1.3)	<i>Ammophila arenaria australis</i>	0.31	0.24	0.55	1	$p > 0.05$	$-0.11 \leq \text{Diff}_{prop} \leq 0.24$
	<i>Elymus farctus farctus</i>	0.53	0.79	7.64	1	$p = 0.0057$	$-0.43 \leq \text{Diff}_{prop} \leq -0.07$
	<i>Anthemis maritima</i>	0.62	0.57	0.25	1	$p > 0.05$	$-0.14 \leq \text{Diff}_{prop} \leq 0.24$
	<i>Pancratium maritimum</i>	0.33	0.08	10.69	1	$p = 0.0011$	$0.09 \leq \text{Diff}_{prop} \leq 0.4$
	<i>Medicago marina</i>	0.07	0.1	0.33	1	$p > 0.05$	$-0.14 \leq \text{Diff}_{prop} \leq 0.07$
	<i>Cyperus capitatus</i>	0.29	0.13	4.06	1	$p = 0.04$	$0.0005 \leq \text{Diff}_{prop} \leq 0.31$

Results of proportion tests performed comparing the occurrence frequencies of focal species recorded in coastal sectors associated to stable-to-low and high accretion intensity. The null hypothesis is that the frequency of occurrence does not change according to the increasing intensity of coastal accretion. *Prop_{low}*: occurrence frequency (occurrences/number of plots) of focal species in coastal sectors associated to stable-to-low accretion. *Prop_{high}*: occurrence frequency (occurrences/number of plots) of focal species in coastal sectors associated to high accretion. *Chi-sq.*: value of the Chi-sq. statistic. *d.f.*: degree of freedom. *Conf. Int. Diff_{prop}*: Confidence Interval of the difference in proportions.

EUNIS	Species	<i>Prop_{low}</i>	<i>Prop_{high}</i>	<i>Chi-sq.</i>	<i>d.f.</i>	<i>p-value</i>	<i>Conf. Int. Diff_{prop}</i>
Coastal dune scrub (B1.6)	<i>Juniperus oxycedrus</i>	0.28	0.37	0.66	1	$p > 0.05$	$-0.3 \leq \text{Diff}_{prop} \leq 0.12$
	<i>Pistacia lentiscus</i>	0.5	0.55	0.21	1	$p > 0.05$	$-0.28 \leq \text{Diff}_{prop} \leq 0.17$
	<i>Phillyrea angustifolia</i>	0.68	0.61	0.41	1	$p > 0.05$	$-0.14 \leq \text{Diff}_{prop} \leq 0.29$
	<i>Lonicera implexa implexa</i>	0.46	0.14	10.29	1	$p = 0.0013$	$0.11 \leq \text{Diff}_{prop} \leq 0.53$

Chapter 3

Modeling plant invasion on Mediterranean coastal landscapes: An integrative approach using remotely sensed data

Modeling plant invasion on Mediterranean coastal landscapes: An integrative approach using remotely sensed data

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Abstract

Although many hypotheses explaining invasion success have been formulated, invasion drivers are usually tested in isolation. This work aims to analyze the combined influence of propagule pressure (P), abiotic (A) and biotic (B) factors (PAB) on determining the invasion process of an exotic plant *taxon* (*Carpobrotus* sp.) in Mediterranean coastal landscapes. Specifically, we used a binomial Generalized Additive Model for exploring the relation between the occurrence of the invasive species and a set of PAB proxy variables derived from high-resolution remote sensed imagery (LiDAR - Light Detection and Ranging - and orthophotos). We evaluated the predictive power of the model by computing the mean of the AUC scores obtained through a 5-fold cross-validation and visual inspection of the Hosmer-Lemeshow plot. The integrated PAB approach efficiently captured the different roles played by the drivers of invasion in affecting the presence of the species. Invasion does not proceed homogeneously across the coastal landscape, but is promoted wherever the combined action of the PAB factors is favorable for establishment of the invader. Moreover, the use of remotely sensed data allowed us to model the invader-landscape relationship on a large geographic extent and to highlight the coastal sectors that are most likely to be invaded in the future.

Keywords: *Carpobrotus* sp., Generalized Additive Model, Invasion Species Distribution Model, Light Detection and Ranging, CORINE Land Cover map.

1.Introduction

As invasions can cause damage to natural habitats, annual economic losses and implicate public health care problems, forecasting alien species expansion is a key issue in conservation biology (Hulme, 2009; Pimentel et al., 2005; Zimmermann et al., 2010). In this regard, Species Distribution Models (SDMs) are widely recognized as a powerful approach for conservation planning (Araujo et al., 2005; Elith & Burgman, 2002; Guisan & Thuiller, 2005; Tulloch et al., 2016) as well as a sound tool for prediction of the invasion probability at different scales. Being based on statistical relationships between species occurrence (dependent variable) and environmental predictors (explanatory variables), SDMs are particularly suitable both for assessing species-environment relationships and for predicting the species distribution (Elith & Leathwick, 2009; Zimmermann et al., 2010). Detaching the correlations between observed spatial patterns of species occurrence and ecological variables can further enhance our knowledge about the biology of an invasion event (Rouget et al., 2001). In particular, invasive Species Distribution Models (iSDMs) have been implemented for exploring the role of invasion drivers (Bellard et al., 2016; Thuiller et al., 2005; Vicente et al., 2010), for prediction of the potential invasive species distribution (e.g. Ficetola et al., 2007) and for early detection of invasion hotspots for optimizing eradication efforts (Leishman & Gallagher, 2015).

However, among the main constraints of SDMs, spatial biases in existing data occurrence and lack of spatially predictor variables do not allow to represent effectively the habitat characteristics of species (He et al., 2015).

In this regard, emerging and existing remote sensing technologies constitutes a cost-effective way for conducting recurrent observations over vast areas (Turner et al., 2003) and for providing spatial data that can be used in iSDMs as surrogates of both proximal explanatory variables (Gibson et al., 2004; Rotenberry et al., 2006; Vicente et al., 2010) and response variables (Andrew & Ustin, 2009). The availability of remotely sensed datasets, with a wide range of spectral and spatial resolutions, is constantly increasing, and so is the use of remotely sensed response and explanatory variables supporting and improving the performance of predictive models (Andrew & Ustin, 2009; He et al., 2015). However, it has been pointed out that remotely sensed variables do not often match the ecological processes affecting species distribution (Bradley et al., 2012) and, at the same time, little consideration has been given to the theoretical framework beyond SDMs (Austin, 2002, 2007). For these reasons, new approaches able to combine different remotely sensed data and techniques while also accounting for underlying ecological theory are needed to make the most of remote sensing potential (Cord et al., 2013).

So far, many hypotheses have been formulated to explain alien invasion success. Numerous studies attribute it to the interaction between alien species capacity to be invasive and the susceptibility of each site to be invaded (Colautti et al., 2004). More recently, integrative approaches accounting for the relative and combined effect of different driving factors have also been proposed (Barney

& Withlow, 2008). In general, it can be said that the extent and the intensity of alien invasion are affected by a simultaneous action of multiple mechanisms (Gurevitch et al., 2011; Wilson et al., 2007) that could be generalized in three main components: propagule pressure (P), abiotic (A) and biotic (B) factor (hereon PAB) (for a review see Catford et al., 2009). All theories of invasion ecology agree that propagule pressure, intended as the supply and frequency of introduction of plant propagules, represents a trigger driver (Colautti et al., 2006; Crawley et al., 1996; Simberloff & Holle, 1999). This factor promotes arrival and establishment of the alien species but the characteristics of the invaded environmental frame (abiotic filter) and the recipient community (biotic filter) are still essential to guarantee the invasion success over time. Indeed, invasion will fail if the invading species cannot survive the conditions of a site or its environmental filters (Weiher & Keddy, 1995). Furthermore, an alien species entering into a new range can either gain or lose biotic interactions capable of facilitating or constraining invasion (Mitchel et al., 2006). In this context, the use of an integrative approach in order to provide an efficient frame for better understanding of the complexity of invasion processes calls for a simultaneous evaluation of the influence of propagule pressure, abiotic and biotic factors (Catford et al., 2009). Although the role of these main drivers is well recognized in invasion ecology and the importance of an integrative approach for dealing with invasion processes is well acknowledged, few studies have investigated the simultaneous effect of these drivers on successful invasions (Barney & Withlow, 2008; Gurevitch et al., 2011). In particular, studies based on the above mentioned integrated methodology are needed to predict invasion vulnerability (Eschtruth & Battles, 2009).

This study is among the first works supported by multi-source remote sensed imagery, aimed at modeling the occurrence of a highly invasive plant in coastal ecosystems accounting for the simultaneous effect of propagule pressure, abiotic and biotic factors. We assume that invasion is not equally promoted across the coastal landscape, but it occurs wherever the combined influence of propagule pressure, abiotic and biotic factors is favorable to the invader establishment. In order to implement the iSDM, we derived both the response and the explanatory variables from high-resolution remotely sensed imagery (LiDAR - Light Detection and Ranging- and aerial orthophotos). As target species, we selected *Carpobrotus* sp., which is one of the most invasive plant *taxon* (Weber, 2003), and, being a neophyte, has probably not yet expanded into all its potentially suitable areas.

2. Materials and Methods

2.1. Target species

Invasion by *Carpobrotus* sp. (*Aizoaceae*) comprises one of the most severe threats to numerous terrestrial plant communities in coastal habitats (Vilà et al., 2006). To date, the genus *Carpobrotus* is considered as one of the major invaders in the Mediterranean basin (Sintes et al., 2007). *Carpobrotus* sp. is a South African succulent perennial *taxon* that was introduced in the western Mediterranean basin since the early 1800s (De La Cour, 1813) and in Italy in the 1900s (Santoro et al., 2011). Its introduction was promoted in order to stabilize dunes (Vilà et al., 2006) and as an ornamental plant (Traveset et al., 2008). The taxonomic identity of the invasive *Carpobrotus* sp. in Europe has long been a subject of debate. Two species are most often included in the European floras: *C. edulis* (L.) L. Bolus and *C. acinaciformis* (L.) L. Bolus, which may also hybridize, making their recognition difficult (Suehs et al., 2004). In this study, we refer to the *taxon* as *Carpobrotus* sp.

Invasion by the species has negative impacts on the diversity and functioning of the Mediterranean coastal plant communities (Santoro et al., 2012b; Jucker et al., 2013). *Carpobrotus* sp. is a highly competitive clonal alien *taxon* that forms wide monodominant evergreen carpets affecting negatively natural diversity in Mediterranean coast (Sintes et al., 2007; Suehs et al., 2004). In particular, *Carpobrotus* sp. has been recognized to have undesirable direct impacts on native plants, with negative competitive effects on germination, survival, growth and reproduction of the native species (Conser & Connor, 2009; Novoa et al., 2014; Santoro et al., 2012b; Vilà et al., 2006). Moreover, *Carpobrotus* sp. has been considered as a major driver of soil condition shifts and soil geochemical processes disruptions in invaded coastal systems (Novoa et al., 2014; Santoro et al., 2011).

2.2. Study area

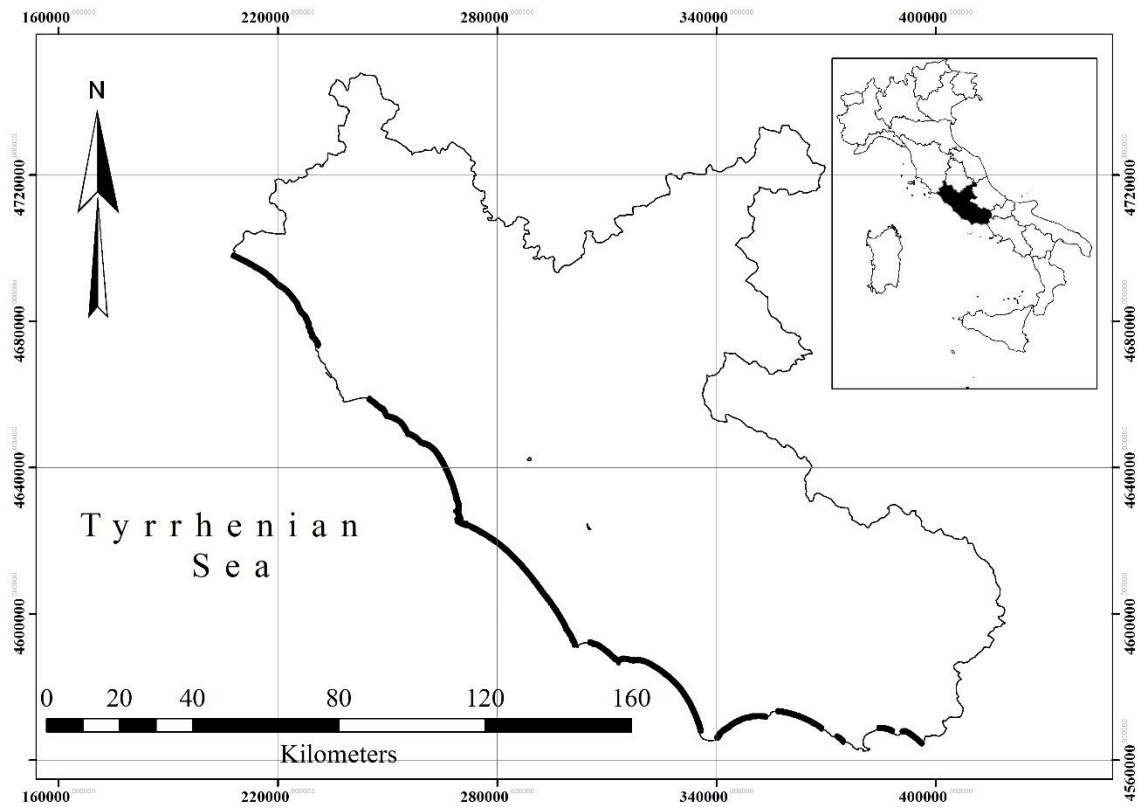


Figure 1: Study area is shown in black. Coordinate system: UTM(WGS84).

The study was conducted along 250 km of the Italian Tyrrhenian coast within the limits of the Lazio region (Fig. 1), the coastline of which consists mainly of sandy beaches. Recent dunes (Holocene) generally occupy a narrow strip along the seashore. They are not very high (usually less than 8-10 m) and relatively simple in structure. The compressed vegetation zonation follows the sea-inland environmental gradient: from the pioneer communities of the upper beach and embryo dunes to the shrubby communities of Mediterranean maquis (Acosta et al., 2003a; Prisco et al., 2012).

2.3. Land cover and *Carpobrotus* sp. map

We produced a fine scale (1:5000; minimum mapping unit = 0.5 ha) land-cover map of the Lazio coast. Given that the dune ridges in Central Italy are generally very narrow (Carranza et al., 2008), we mapped a 500 m wide strip starting from the coastline inland. The map was derived from

panchromatic digital aerial orthophotos with 1 m resolution taken in 2008 and accurate field work performed during spring 2012 and 2013. Land cover was manually interpreted on screen in an ArcGIS environment (ArcGIS 10.1; ESRI, 2011). The legend matches CORINE land cover expanded to a fourth level of detail for natural and semi-natural areas (for details see Acosta et al., 2005). The adopted spatial resolution and legend are the most accurate that can be produced through aerial photos for the analyzed coastal areas and are adequate for describing the heterogeneity and pattern of dune ecosystems (Acosta et al., 2005; Malavasi et al., 2014). Ten land cover types were identified and mapped (Appendix A). Particular attention was given to the detection of *Carpobrotus* sp. patches. The species forms thick and large mats developing up to 40 cm in depth and up to 20 m in width, making it accurately identifiable from aerial photos (Carranza et al., 2010). The identification of the species patches was further aided by the use of Bing Bird's Eye Images. Bird's Eye imagery is collected at a 45-degree angle from low-flying aircraft, offering greater depth and higher-resolution imagery (0.3 m resolution). The land-cover map accuracy was assessed by comparing the attribution of each class in the map with the data obtained by the field surveys. We calculated the KHAT statistic (Congalton & Green, 1999), which ranges from 0 to 1. A KHAT value of 1 indicates a perfect correspondence between the two compared classification schemes, while value of 0 suggests that a given classification is no better than a random assignment of classes in a map. The obtained map presents a global accuracy of 0.77.

2.4. Mapping of Propagule pressure, Abiotic and Biotic factors

Table 1 – GIS-derived proxy variables (predictors) for propagule pressure (P), abiotic (A) and biotic (B) factors. For a detailed description of the land cover types see Appendix A.

Proxy variables (predictors)	Description	Factors
ART, AGR (percentage)	- percentage of artificial (ART) and agricultural (AGR) land cover classes within each moving window	P
Distance from nearest major road (m)	- Euclidean nearest distance (m) from highways and primary roads	
Elevation (m)	- m above sea-level value	A
Slope (degree)	- maximum change in elevation from each cell and its eight neighbors.	
Curvature (adim.)	- second order derivative from the digital terrain model. Positive curvature values indicate that the surface is upwardly convex. Negative curvature values indicate that the surface is upwardly concave. Curvature values equal to 0 indicate that the surface is flat.	
Sea distance (m)	- Euclidean distance (m) from the shoreline	
AFF, SN (SHV and SWV), WET, BPV, HDV, WDV (percentage)	- percentage of the focal land cover class within each moving window. AFF: Afforestation, SN: Semi-Natural (herbaceous and woody vegetation), WET: Wetlands, BPV: Beach Pioneer Vegetation, HDV: Herbaceous Dune Vegetation, WDV: Woody Dune Vegetation	B

Three sets of proxy variables (predictors) representative of propagule pressure (P), abiotic (A) and biotic factors (B) that may affect *Carpobrotus* sp. invasion were mapped in an ArcGIS environment. 13 raster grid maps with 5 m resolution, each one representing one proxy variable, were obtained for the whole study area (Tab. 1).

It is already known that the rate of spreading of alien plant propagules introduced into a new region (Colautti et al., 2006) is related to both the amount of urban, industrial and arable lands (Carboni et al., 2010; Carranza et al., 2010; Chytrý et al., 2008; Chytrý et al., 2009; Malavasi et al., 2014) and to the distance from human infrastructure (Le Maitre et al., 2004; Vicente et al., 2010). As proxies of propagule pressure (P) occurring at each individual site (pixel), we mapped the percentage of artificial (ART) and agricultural (AGR) lands and the nearest distance from the major roads. The percentage of artificial land and agricultural fields were computed using a moving window procedure on the land cover map rasterized at a 5 m resolution performed in FRAGSTAT (McGarigal et al., 2012). The implemented moving window operates by moving a

fixed-area of 50 m radius over the map one pixel at a time, calculating the percentage of the selected cover type (agricultural or artificial) within the window and by returning that value to the center pixel (for details see McGarigal & Cushman, 2005). In this way, we mapped continuous surfaces where each pixel accounts for the percentage of the selected cover type (ART and AGR) in a 50 m radius of the surrounding area. The map describing the distance from the major roads was obtained by measuring the straight-line Euclidean distance of each pixel cell (the center) from the closest highway or primary road (road data retrieved from <https://planet.openstreetmap.org/>; OpenStreetMap contributors, 2016).

The abiotic characteristics (A) of the invaded ecosystem also constrain the expansion of invading species (Catford et al., 2009). In coastal dune ecosystems, the variables that best describe the ecological conditions along the sea-inland stress gradient include the sea distance, dune elevation, slope, and curvature features (Bazzichetto et al., 2016; Kim & Yu, 2009). We mapped abiotic factors (A) occurring in each site as the former four proxy variables. Elevation, slope and curvature variables were extracted from a 2 m resolution Digital Terrain Model (DTM) derived from Airborne LiDAR imagery, acquired in the context of the PST-A mission (Piano Straordinario di Telerilevamento Ambientale; Ministero dell'Ambiente e della Tutela del Territorio e del Mare) in 2008. Airborne LiDAR is particularly effective for collecting accurate elevation data over large areas as well as for analyzing the vegetation distribution in areas characterized by micro-topographical relief, such as coastal dunes (Bazzichetto et al., 2016; Ward et al., 2013). The use of LiDAR imagery allows the emergence of ecologically meaningful explanatory variables for species distribution modeling and it may play a key role in improving the performance of SDMs (He et al., 2015). The map describing the sea distance was computed calculating the straight-line Euclidean distance between each cell (the center) and the shoreline derived from the land cover map (Malavasi et al., 2016b).

The biotic factors (B) regulating the behavior of invading species also depend on the characteristics of the recipient habitats. As proxies of biotic factors (B) existing in each site we mapped the percentage of natural and semi-natural cover types (natural and semi-natural cover types classification follows Malavasi et al., 2013). By using a moving window procedure on the land cover map rasterized at 5 m resolution, we obtained seven continuous maps where each cell expresses the percentage of each natural and semi-natural cover type in the 50 m radius neighborhood. Specifically, we included the following land cover categories: afforestation (AFF); semi-natural, comprising herbaceous and woody dune vegetation (SN); inland wetland and marshes (WET); beach with pioneer annual vegetation (BPV); herbaceous dune vegetation growing on fore dune (HDV); woody dune vegetation growing on fixed dune (WDV) (Tab. 1).

2.5. Target species sampling

To fit the statistical model, we have at first generated point-wise presence/absence data from the *Carpobrotus* sp. cover map. Presences (n = 2,189) were sampled as the centroids inside the patches

of *Carpobrotus* sp. Absences were sampled generating 4,000 points distributed randomly in the entire study area excluding the areas occupied by the patches of *Carpobrotus* sp. Sampling procedure was implemented in an ArcGIS environment. We extracted the PAB factor values for each of the presence/absence points by intersecting their geographic coordinates with the relative PAB raster grid map.

2.6. Species Distribution Model

As the relation between *Carpobrotus* sp. and the selected predictors appeared to be non-linear, we performed a binomial Generalized Additive Model (GAM) with a logit link function to investigate the relative importance of each PAB predictor in determining *Carpobrotus* sp. occurrence (R package: mgcv; Wood, 2011). The power of GAM has been successfully tested for modeling species distribution in the environmental space (Araujo et al., 2005; Austin, 2007). The non-parametric nature of GAMs allows fitting splines defined by the data that can accurately outline complex response curves, outperforming other statistical methods, such as GLMs, which constrain the species-environment relationship to a linear, quadratic or cubic form (Segurado & Araujo, 2004; Thuiller et al., 2005). A logit link function was used to transform the conditional mean and model it as a linear function of the covariates (Hosmer & Lemeshow, 2000). We set the presence/absence of the invading plant as the response variable and the PAB predictors as covariates. Smoothers were outlined using Penalized Splines. The number of basis dimension (k) was set according to the smoothers' effective degrees of freedom (e.d.f.) for each predictor in order to balance the trade-off between bias and variance. The smoothing parameter estimation was performed through the Restricted Maximum Likelihood (REML) method, which is less prone to undersmoothing and convergence problems than other available methods (for theoretical see Reiss & Ogden, 2009; for empirical comparisons see Marra & Wood, 2011). Concurvity was tested among smooth terms in order to exclude those whose trend was expressed redundantly by other smooth terms (Wood, 2006).

2.7. Model Evaluation

The model prediction accuracy was evaluated using the following methodologies: the area under the ROC (relative operating characteristic) curve (AUC) (Pearce & Ferrier, 2000), the spatial sorting bias index (SSB) (Hijmans et al., 2012) and the Hosmer-Lemeshow plot (Hosmer & Lemeshow, 2000).

The computation of the AUC index provides an estimation of the model capacity to relate predicted presences to actual occupied sites and predicted absences to sites recorded as unoccupied (Pearce & Ferrier, 2000). AUC values that range between 0.5 and 0.7 indicate a poor discrimination; values between 0.7 and 0.9 represent a reasonable discrimination; and AUC greater than 0.9 indicates a very good discrimination (Pearce & Ferrier, 2000). As the values of AUC are affected by the spatial extent to which models are carried out (Lobo et al., 2008), analyses were conducted on a 300 m wide strip (from the shoreline inland) to select the appropriate spatial extent for modeling the

distribution of *Carpobrotus* sp. along the dune system of the study area (Acosta et al., 2008). We cross-validated the model partitioning the data randomly into five groups. Four out of the five data-groups were used to fit the model while the fifth was used to evaluate it. A corresponding AUC value was obtained for each cross-validation run. Subsequently, we computed the mean among the single AUC values resulting from each cross-validation. In this context, cross-validation was used for both estimating the generalization performance of the model and obtain a robust measurement of its predictive capacity through the averaging of the single AUC values (LeDell et al., 2015; Refaeilzadeh et al., 2009).

Spatial sorting bias occurs when the distance between training-presence and testing-presence sites tends to be smaller (“attraction” of testing-presence sites to training-presence sites) than the distance between training-presence and testing-absence sites (“repulsion” of testing-absence sites to training-presence sites) (Hijmans, 2012). Since this phenomenon commonly leads to inflated cross-validation results when evaluating the model power of prediction (Hijmans, 2012), we accounted for spatial sorting bias quantifying the spatial sorting bias index (SSB) (R package: *dismo*; Hijmans et al., 2016):

$$SSB = D_p/D_a$$

where D_p is the mean distance of testing-presence site to the nearest training-presence site and D_a is the mean distance of testing-absence site to the nearest training-presence site. The SSB index ranges from 0 (extreme spatial sorting bias) to 1 (no spatial sorting bias).

AUC values are often criticized as a misleading parameter (e.g. Lobo et al., 2008) and wider use of calibration plots is encouraged (e.g. Lawson et al., 2014). Therefore, we used the approach of Hosmer and Lemeshow (2000), i.e., grouping the data according to the fitted probabilities and comparing the model prediction with observation in each group (Hosmer & Lemeshow, 2000). We used 10 equally sized groups, having thus app. 10% of the data with the lowest fitted probabilities in the first group, next 10% in the second, and so on. For each group, we estimated the “observed” probability as the average of the binary responses in the group, and the “predicted” probability as the average of the fitted probabilities in the group. Instead of performing the Hosmer-Lemeshow’s chi-squared test, which was proposed for logistic regression and has limitations (see Agresti, 2013), we rather inspected visually the plot of the whole range of predicted (abscissa) vs observed (ordinate) probabilities. The points distributed along the $y=x$ line indicate a good model fit. This plot enables one to evaluate the fit in different parts of the probability range (i.e. the range of the fitted values).

3.Results

3.1.Influence of PAB factors on *Carpobrotus* sp.

According to the GAM model, each PAB factor has a specific and significant role on *Carpobrotus* sp. invasion (Tab. 2).

Among the propagule pressure predictors (P), the percentage of artificial land cover (ART) and the nearest distance from major roads showed a significant association with the presence of *Carpobrotus* sp. On the contrary, the agricultural class (AGR) did not exhibit a significant relation with the occurrence of *Carpobrotus* sp. Among abiotic factors (A), elevation, sea distance and slope were significantly related to the presence of *Carpobrotus* sp., while the curvature was not. All the biotic predictors (B) except the woody dune vegetation (WDV) were significantly related to the presence of *Carpobrotus* sp.

Table 2 – GAM model outcome (response variable: *Carpobrotus* sp. presence/absence; predictors: PAB proxy variables): number of basis dimension (k); effective degrees of freedom of the smoother (e.d.f.). The percentage of beach pioneer vegetation (BPV) was excluded from the model due to the high value of concurvity exhibited by this predictor (estimate = 0.64) ('***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$; '.' $p < 0.1$). For a detailed description of the predictors and the land cover types see Table 1 and Appendix A, respectively.

Predictors	k	e.d.f.	Chi-sq	p-value
P (Propagule pressure)				
Distance from major roads	9	4.545	36.391	***
Artificial	5	3.164	261.266	***
Agricultural	5	1.936	2.485	$p > 0.05$
A (Abiotic)				
Elevation	9	3.709	88.292	***
Sea distance	9	5.334	146.039	***
Slope	9	6.297	61.895	***
Curvature	9	4.876	8.800	$p > 0.05$
B (Biotic)				
Afforestation	5	1.893	12.436	**
Semi-Natural	5	2.557	52.473	***
Wetlands	5	1.731	8.457	*
Herbaceous Dune Vegetation	5	2.730	41.512	***
Woody Dune Vegetation	5	2.831	7.818	$p > 0.05$

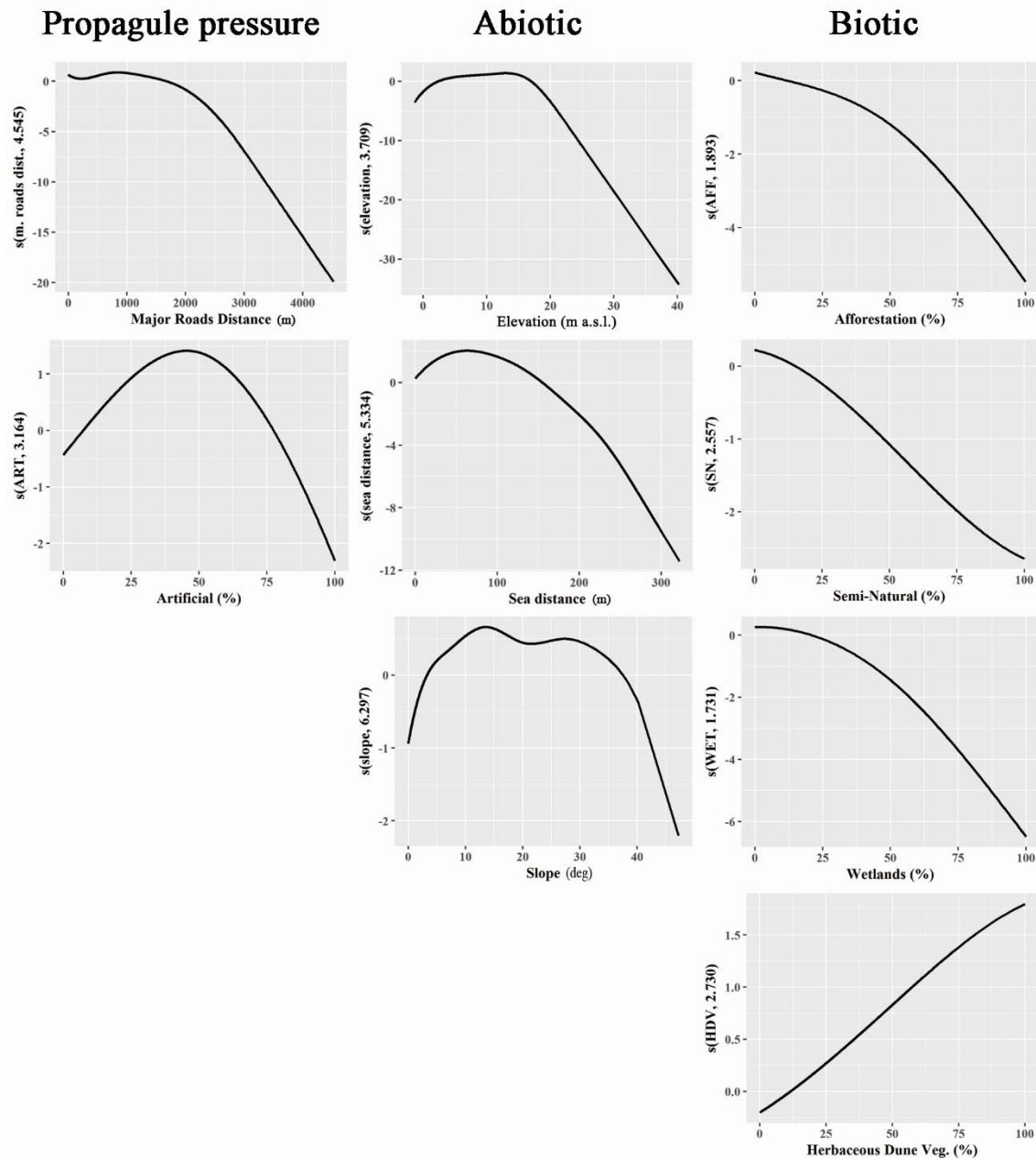


Figure 2 – Smoothing curves outline the relationship between *Carpobrotus* sp. occurrence and the PAB predictors. On the y-axis: smoothing function for each PAB predictor along with the effective degrees of freedom of the smoother (in brackets). On the x-axis: PAB predictor along with the corresponding unit of measurement: percentage (%); meter (m); degree (deg).

The relation between the predicted occurrence of *Carpobrotus* sp. and the percentage of artificial land cover (ART) exhibited a parabolic trend, with the maximum presence of the species around 50% ART coverage. The occurrence of *Carpobrotus* sp. negatively relates with the distance from major roads, with the invader especially occurring in areas within 1 kilometer from these.

The shape of the left-side tails of the smoothers for the sea distance and the elevation indicate that the presence of *Carpobrotus* sp. in low areas close to the shoreline is predicted to be low. On the contrary, the species occurrence is predicted to be high in dune sectors approx. 50 m from the shoreline and in areas with elevation less than 15 m. The probability of finding *Carpobrotus* sp. is higher in the central section of the slope smooth predictor function. On the contrary, the species occurrence is limited both in extremely high and low slopes.

The relation between biotic factors and *Carpobrotus* sp. exhibited linear trends. Among the biotic predictors, the herbaceous dune vegetation (HDV) was the only variable positively associated with the presence of *Carpobrotus* sp. On the contrary, the probability of finding the species declined with the increasing coverage by the remaining biotic predictors (AFF, WET, SN).

3.2. Model performance

The fitted model explained the 57.4% of the deviance. The mean AUC score was 0.94, with AUC scores obtained for each cross-validation run being always over 0.93. The spatial sorting bias index (SSB) was 0.98, excluding AUC scores inflated by the model cross-validation.

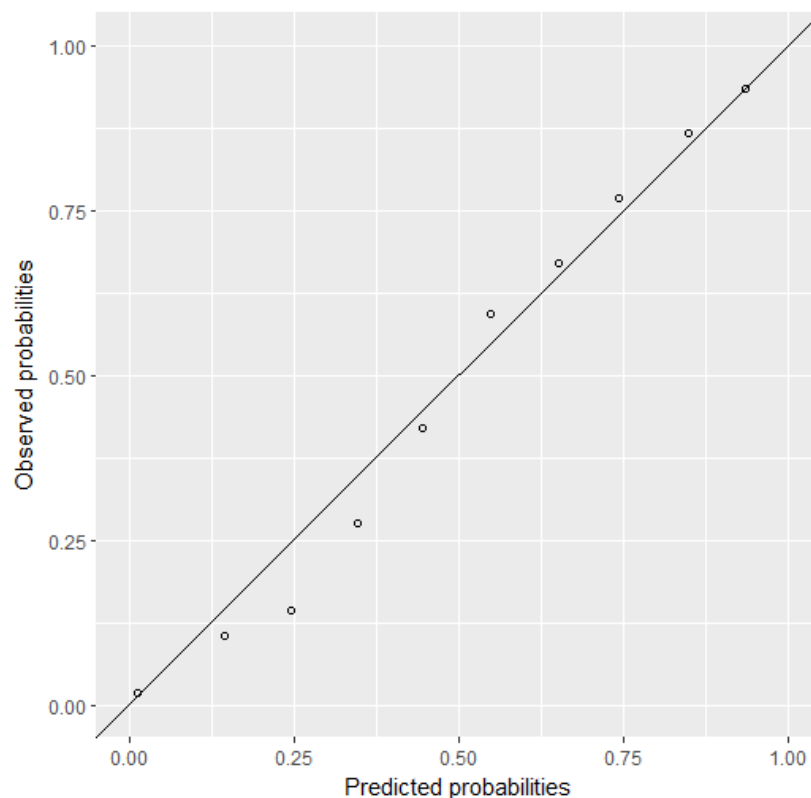


Figure 3 – Hosmer and Lemeshow plot. Predicted probabilities of *Carpobrotus* sp. occurrence (X-axis) plotted versus the observed probabilities of *Carpobrotus* sp. occurrence (Y-axis) along with the plan bisector.

In the Hosmer-Lemeshow plot, the points were distributed regularly over the probability range, and they were aggregated along the $y=x$ line (Fig. 3). This confirms a good agreement between predicted and observed probabilities of *Carpobrotus* sp. occurrence, with no considerable lack of fit in any part of the probability range.

4. Discussion

We effectively predicted the occurrence of *Carpobrotus* sp. along a Tyrrhenian coastal dune system using a Generalized Additive Model that integrates propagule pressure (P), abiotic (A) and biotic (B) factors into a single experimental design. The relations between the invader and the PAB factors were found to be non-linear and GAM successfully captured these relations. The predictive performance of the model, according to the obtained mean AUC score, can be considered good (following Thuiller et al., 2005). The high values of the mean AUC and of the spatial sorting bias index (~ 1) supported by the visual inspection of the Hosmer-Lemeshow plot indicate that the model can predict accurately both the presence and the absence of *Carpobrotus* sp.

We observed that the influence of each PAB factor on the invasion by *Carpobrotus* sp. varies across the coastal landscape. In fact, its expansion is mediated by the context-specific contribution of each PAB factor. The occurrence of *Carpobrotus* sp. was favored substantially in discontinuous urbanized areas and in the proximity of roads. The presence of the invader is also delineated by the abiotic and biotic conditions with the alien invader tending to establish in areas characterized by both moderate environmental stress (abiotic factor) and a low cover of the native vegetation (biotic factor) (see Appendix B for figures).

4.1. Propagule pressure

In the analyzed coastal landscape, the propagule pressure factor is significantly related to the presence of *Carpobrotus* sp., which appears favored by the proximity of roads and the presence of human settlements, as reported for other alien plants (Arévalo et al., 2005; Le Maitre et al., 2004). While roads most likely support long-distance dispersal processes, artificial areas promote the introduction of *Carpobrotus* sp. propagules at a limited spatial scale. On the other hand, the parabolic relation between *Carpobrotus* sp. occurrence and the percentage of land covered by artificial structures suggests that the probability of invasion is higher in discontinuous urban areas rather than in proximity of heavily urbanized ones. In this regard, the common practice of planting *Carpobrotus* sp. as ornamental in summerhouses with gardens directly facing coastal dunes provides a local input of propagules that constantly supports invasion (Carboni et al., 2010; Malavasi et al., 2013; Sobrino et al., 2002). Farming does not seem to be a likely invasion pathway for *Carpobrotus* sp. (Carboni et al., 2010), even though agricultural practices have been previously considered to be connected to plant invasion on coastal dunes (Arévalo et al., 2005; Elmore et al., 2003). In fact, farmlands offer few public accesses to the beach, thus representing a barrier for touristic exploitation and reducing the likelihood of *Carpobrotus* sp. establishment on dune systems (Carboni et al., 2010).

4.2 Abiotic factor

Abiotic factors also play a key role in promoting *Carpobrotus* sp. invasion along the analyzed dune system. The invader particularly occurs in a specific sector of the dune system, delineated by the dune morphology and sea distance. *Carpobrotus* sp. avoids the highly stressful conditions of the coastal area, typical for the shoreline (Drius et al., 2016; Santoro et al., 2011; Traveset et al., 2008). Contrary, it prefers sites located at intermediate elevation and distances from the shoreline, which portray milder environmental conditions.

4.3 Biotic factor

Biotic predictors are significantly associated with the presence of *Carpobrotus* sp. invading mainly the herbaceous dune vegetation (HDV), usually open areas intermingled with low vegetation cover (Carranza et al., 2011; Maltez-Mouro et al., 2010). Generally, the presence of open and sparse vegetation is considered to be one of the main factors in promoting invasion as plants, like other sessile organisms, need space to exploit resources (Catford et al., 2009). Moreover, direct human disturbance depleting vegetation cover (e.g. trampling, sand removal, or mechanical cleaning; Malavasi et al., 2013, 2016b) exerts a strong pressure on herbaceous dune vegetation and, in turn, promotes invasion. Contrary, *Carpobrotus* sp. occurrence is lower in natural and semi-natural densely vegetated cover types, in particular in woody vegetation, such as Mediterranean maquis (WDV), *Pinus* spp. plantations with dense canopy (AFF) and semi-natural areas with woodlands (SWN) (Malavasi et al., 2013) as close woody vegetation may be associated with a higher biotic resistance of these plant assemblages to alien invasion (Eschtruth & Battles, 2009). Besides, the environmental properties of the semi-natural herbaceous vegetation (SHN) probably do not match the ecological requirements of *Carpobrotus* sp. as this cover type is typical for abandoned meadows and pastures colonized mainly by ruderals developing on nitrogen rich soils. Similarly, *Carpobrotus* sp. also avoids wetlands (WET) probably because of the unsuitability of this invasive plant to grow in ecosystems strongly regulated by flooding regimes (Keddy, 2010).

5. Conclusions

The integration of propagule pressure, abiotic and biotic factors into a single experimental design efficiently caught the simultaneous effect of different drivers in determining the presence of a highly invasive plant in Mediterranean coastal dunes and identified areas prone to invasion. The combined influence of the above mentioned factors is not homogeneous across the landscape, with invasion succeeding wherever the synergistic action of the PAB factors is favorable to the establishment of the invader. In this context, the PAB modeling approach allowed to partition and disentangle the effect of propagule pressure, abiotic and biotic factors, providing valuable insights on the invasion process. The implemented analysis could be extended for investigating and modeling invasion processes across a large ensemble of landscapes and spatial scales, providing a sound tool for the risk assessments required by the recent EU regulation on invasive alien species (EEC, 2014; Sitzia et al., 2016).

The utilization of high-resolution remotely sensed data for mapping both the invasive species (response variable) and the PAB predictors to build the iSDM allowed analysis of the relationship between alien species occurrence and the invaded environment and thus to model

the former relation on a broad geographic extent. Furthermore, fine resolution of remotely sensed data allowed us to investigate ecological processes on dune systems characterized by a complex and finely grained mosaic of plant communities that coexist in a relatively small space. As the availability of remote sensing datasets is increasing constantly, we hope that further studies using remote sensed data will be conducted in the future. In this perspective, the proposed approach provides a cost-effective methodology widely applicable to other invasion events and therefore suitable for planning efficient conservation policies aimed at controlling expansion of exotic plants at the local scale.

Appendix A

List of the ten mapped land cover types along with their CORINE Code, CORINE Description, detailed description of the main characteristics and abbreviations.

CORINE Code	CORINE Description	Detailed description	Abbreviation
1.	Artificial areas	Artificial areas including urban fabrics; industrial and commercial units; mine, dump and construction sites; artificial vegetated areas.	ART
2.	Agricultural areas	Agricultural land, including arable land, permanent crops, pastures and heterogeneous agricultural areas.	AGR
3.1.2.1.	Afforestation	Afforestation on coastal dunes with <i>Pinus</i> spp. plantations.	AFF
3.2.3.1.	Woody Dune Vegetation	Mediterranean maquis growing on fixed dune.	WDV
3.2.4.1.	Semi-natural Woody Vegetation	Bushy vegetation with scattered trees represented by fore dune woodland degradation or forest regeneration/recolonization.	SWV
3.2.4.2.	Semi-natural Herbaceous Vegetation	Abandoned meadows and pastures with different degree of degradation or recolonization.	SHV
3.3.1.1.	Beach Pioneer Vegetation	Upper beach colonized by pioneer annual vegetation.	BPV
3.3.1.2.	Herbaceous Dune Vegetation	Fore dune colonized by herbaceous vegetation intermingled to open sectors.	HDV
3.3.1.6.	Vegetation invaded by <i>Carpobrotus</i> sp.	Patches of <i>Carpobrotus</i> sp.	INV
4.1.1.	Wetlands	Inland wetlands and marshes.	WET

Appendix B

The output map derived from the SDM of *Carpobrotus* sp. is overlapped to a basemap of two sites included in the study area.



Figure a represents a typical urbanized sector of the Lazio coast, where discontinuous urban areas are in close proximity to the dune system. In such context, the invasion by *Carpobrotus* sp. is highly favored. In Figure b, on the other hand, *Carpobrotus* sp. shows different invasion patterns depending on the structure of the dune. While in the left side of the figure (towards the West) the dune system is well developed and *Carpobrotus* sp. occurrence is predicted to be high, in the right side of the figure (towards the East) the dune is absent and the model predicts the absence of the invasive taxon.

Appendix C

R code used for implementing and for evaluating the iSDM.

```
library(mgcv)
library(dismo)
library(raster)

# Data preparation -----
----

# Reading the dataset, whose structure is as follows:
#   Point      Latitude      Longitude      Pres
#   1          2342342        2342342        1
#   2          3566536        7647373        1
#   3          4287654        2345677        0
#   ...
> data_set <- read.table("dataset.csv", header=T, sep=";")
> coord_pres <- data_set[data_set[,4]==1,2:3]
> coord_abs <- data_set[data_set[,4]==0,2:3]
# Creation of RasterLayer objects from source file
> elevation <- raster::raster(x = "Directory/elevation_raster")
> artificial <- raster::raster(x = "Directory/artificial_raster")
...
> predictors <- raster::stack(elevation, artificial, ...)
# Extraction of the predictors values at the location of each
# presence/absence point from the raster objects
> pres_val <- raster::extract(predictors, coord_pres)
> abs_val <- raster::extract(predictors, coord_abs)
# Creation of the main data frame (df)
> p_a <- c(rep(1, nrow(pres_val)), rep(0, nrow(abs_val)))
> df <- data.frame(cbind(p_a, rbind(pres_val, abs_val)))

# Model fit -----
----

# Fit the binomial GAM with link logit, setting the basis dimension
k
> (model <- mgcv::gam(p_a ~ s(elevation, bs='ps', sp=0.6) +
                      s(artificial, bs='ps', sp=0.6, k=0.5) +
                      s(...),
                      family=binomial(link=logit), data = df,
                      method='REML'))

# Check model assumptions
> (mgcv::gam.check(model))
# Check concurvity
```

```

> (mgcv::concurvity(model, full = T))

# Model evaluation using mean AUC score -----
----
# (For details, see Hijmans & Elith, 2017)
# Separating presence and absence data
> pres_data <- df[df[,1]==1, 2:14]
> abs_data <- df[df[,1]==0, 2:14]
# Dataset partitioning
> k <- 5
> group <- dismo::kfold(pres_data, k)
> eval <- list()
# AUC computation through the 5-fold cross-validation
> for (i in 1:k) {
+   train <- pres_data[group != i,]
+   test <- pres_data[group == i,]
+   model
+   eval[[i]] <- dismo::evaluate(test, abs_data, model)
+}
# Extraction of the AUC scores from the "eval" list and computation
of
# their mean
> auc <- sapply(eval, function(x){slot(x, 'auc')})
> mean(auc)

# Computation of the Spatial Sorting Bias index -----
# (For details, see Hijmans & Elith, 2017)
# Generate training and testing samples for presences
> nr <- nrow(coord_pres)
> s <- sample(nr, 0.25 * nr)
> pres_train <- coord_pres[-s, ]
> pres_test <- coord_pres[s, ]
# Generate training and testing samples for absences
> nr <- nrow(coord_abs)
> s <- sample(nr, 0.25 * nr)
> abs_train <- coord_abs[-s, ]
> abs_test <- coord_abs[s, ]
# Compute SSB index
> sb <- dismo::ssb(pres_test, abs_test, pres_train)
> sb[,1] / sb[,2]

# Production of the iSDM map -----
----
> hope <- raster::predict(predictors, model)

```

```
> hope_map <- raster::writeRaster(x = hope, filename = "hope",  
                                  format="GTiff")
```

References:

Hijmans, R. J., & Elith, J. (2017). Species distribution modeling with R. Available at:
<ftp://ftp.gr.xemacs.org/mirrors/CRAN/web/packages/dismo/vignettes/sdm.pdf>

Chapter 4

Plant invasion risk: A quest for invasive species distribution modelling in managing protected areas

Plant invasion risk: a quest for invasive species distribution modelling in managing protected areas

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Abstract

Preventing biological invasions in areas of conservation concern represents the most cost-effective strategy to minimize the impact of Invasive Alien Species (IAS) on native communities. In this context, invasive Species Distribution Models (iSDMs) are a sound tool for predicting invasion risk in protected areas. Although their potential to support invasive species managers is widely acknowledged, evidence of iSDMs providing actual conservation solutions is still scarce. With this work, we propose an iSDM-based methodology that accounts for the role of multiple invasion drivers to assess the risk posed by IAS in protected areas. Using a binomial Generalized Additive Model, we predicted the occurrence of a highly invasive plant in Mediterranean dune systems. According to the predicted IAS occurrence, we quantified the invasibility of protected sites inside the study area, classified each site in low to medium-high invasibility categories, and identified site-specific management perspectives. Our results encourage the use of iSDMs as a means of evaluating the risk posed by IAS in protected areas, and, at the same time, represent an attempt to fill the gap between theory and practice in conservation decision-making.

Keywords: biological invasion; conservation planning; invasive species distribution model; site invasibility; remote sensing.

1. Introduction

A key topic in conservation biology is the preservation of natural areas with a concurrent reduction of time and costs needed for their conservation (Margules & Pressey 2000). In 1992, the European Parliament promulgated the Habitat Directive (92/43/EEC) which aimed to “...contribute towards ensuring biodiversity through the conservation of natural habitats and of wild fauna and flora in the European territory...” by means of specific measures such as the establishment of a functional system of protected areas (PAs), namely the Natura 2000 network (EEC 1992). This network is composed of Sites of Community Importance (SCIs) and Special Protection Areas (SPAs), in which European conservation strategies are implemented for maintaining plant communities and wildlife species at a “favourable conservation status”.

Nowadays, the Natura 2000 network constitutes one of the most valuable conservation tools against the loss of biodiversity in Europe (Kati et al. 2015). Nonetheless, the biodiversity of sites included in the network is affected by several threats. Among them, the introduction of Invasive Alien Species (hereafter, IAS) is one of the most severe, preceded only by habitat loss and fragmentation (Foxcroft et al. 2013). IAS cause severe impacts on native communities and affect the functioning of ecosystems, with expected consequences on human health (Ricotta et al. 2010; Aerts et al. 2017; Hattab et al. 2017). Moreover, actions aimed at minimizing the impact of IAS on native communities imply high economic investments (Pimentel et al. 2002). In this context, the European Commission adopted a recent Regulation “on the prevention and management of the introduction and spread of invasive alien species” (EC Regulation 1143/2014) which came into force in 2015. According to the EU Regulation (hereafter, IAS Regulation), Member States are committed to undertake specific actions related to challenging research, monitoring and surveillance aimed at early detection of invasive species and predict their spread into non-native regions.

Preventing the arrival of IAS is claimed as the most effective strategy to deal with biological invasions (Leung et al. 2002; Sitzia et al. 2016). To achieve this aim, invasive Species Distribution Models (iSDMs), based on the statistical relationship between invasive species (presence/absence or abundance data) and the invaded environment (environmental predictors), have been effectively applied to predict the distribution of IAS and to identify areas that are likely to be invaded (Muñoz & Real 2006; Andrew & Ustin 2009; Vicente et al. 2010; Gallardo et al. 2017). iSDMs have the potential to support conservation decision-makers in defining possible actions aimed at IAS monitoring and containment (Guisan et al. 2013). Nevertheless, although iSDMs are widely considered as powerful tools for managing IAS (Addison et al. 2013; Crall et al. 2013; Underwood et al. 2004), their implementation for mapping the risk posed by biological invasion remains sparse (Guisan et al. 2013). In fact, iSDMs are currently underused for conservation purposes, mainly due to the lack of resources (time and/or money) available to conservation managers (Addison et al. 2013; Guisan et al. 2013). In this regard, the recent evolution of remote sensing and the increasing availability of spatial data has provided modellers with new ecologically meaningful environmental variables suitable for modelling species distribution (Franklin et al. 2013; He et al. 2015). For this reason, the contribution of remote sensing could be crucial for overcoming the lack of resources to collect adequate (quality/quantity) data for implementing iSDMs, which is one of the main

objections raised by conservation managers against the use of predictive models (Addison et al. 2013; Gil et al. 2013).

When implementing an iSDM, attention must be given to the theoretical background underlying the ecological processes that influence species distribution (Austin 2007), as ill-informed models (e.g., based on inappropriate ecological assumptions) can lead to suboptimal conservation outcomes (Addison et al. 2013). Relying on an accurate theoretical framework, iSDMs should provide a sound tool for supporting decision-making and resource allocation in conservation (Catford et al. 2009). As biological invasions are complex processes whose success (or failure) is driven by multiple factors (Barney & Withlow 2008; Colautti et al. 2006; Pyšek & Richardson 2006), integrative approaches should be adopted to effectively model the simultaneous influence of different invasion drivers in determining IAS occurrence and spread (Catford et al. 2009; Gurevitch et al. 2011; Malavasi et al. 2018; Theoharides & Dukes 2007).

Although biological invasions represent a potential threat for the biodiversity in Europe and the IAS Regulation has explicitly highlighted the urgency of identifying management tools for reducing IAS impacts, few studies have attempted to propose model-based methodologies for preventing the expansion of invasive species in Natura 2000 sites (but see Dimitrakopoulos et al. 2017). Overall, an urgent need to bridge theory and practice in the application of iSDMs for conservation issues has been claimed (Guisan et al. 2013).

In response to the need for early warning tools claimed by the IAS Regulation, the present work aims at providing an iSDM-based methodology that accounts for the role of multiple drivers to assess the invasion risk posed by IAS on protected sites. In particular, the method aims at estimating the potential distribution of IAS for using model predictions of the invasive species occurrence to quantify site vulnerability to plant invasion (invasibility). The model framework presented here relies entirely on multi-source remotely sensed data, including high-resolution aerial orthophotos and Light Detection and Ranging (LiDAR) imagery. We test the proposed methodology for assessing the invasion risk posed by the non-native plant *Carpobrotus* sp. (*Aizoaceae*) in coastal Natura 2000 sites in central Italy. Currently, invasion by the South African *Carpobrotus* sp. constitutes one of the most severe threats to coastal plant communities of the Mediterranean basin (Vilà et al. 2006). *Carpobrotus* sp. is a succulent perennial *taxon* that has documented negative impacts on the diversity and functioning of Mediterranean coastal plant communities (Conser & Connor 2009; Campoy et al. 2018).

The proposed approach could be extended to other invasion events to support conservation managers who aim to minimize the impact of invasive species on native communities in other conservation networks.

2. Material and Methods

2.1. The selected Natura 2000 sites

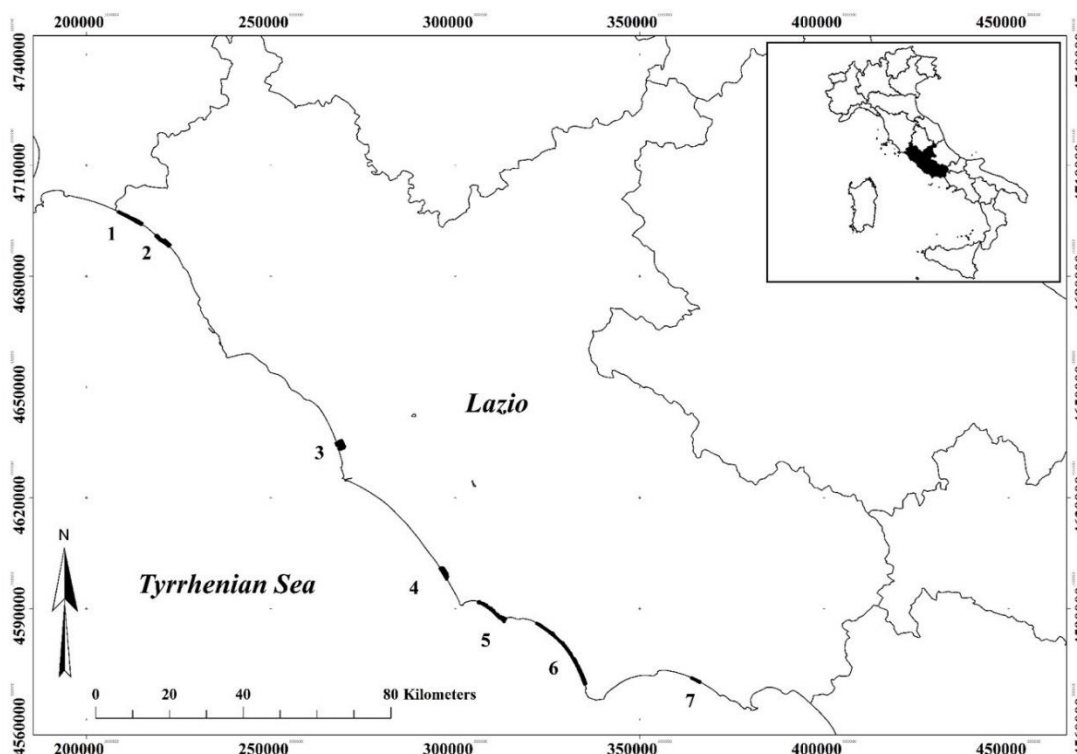


Figure 2 - Study area. Analyzed Sites of Community Importance (SCIs) are shown in black: (1) Litorale a Nord-Ovest delle Foci del Fiora (IT6010018), (2) Litorale tra Tarquinia e Montalto di Castro (IT6010027), (3) Macchia grande di Focene e Macchia dello Stagneto (IT6030023), (4) Lido dei Gigli (IT6030045), (5) Litorale di Torre Astura (IT6030048), (6) Dune del Circeo (IT6040018), (7) Duna di Capratica (IT6040021). Coordinates system: UTM(WGS 84).

The study was carried out on the Tyrrhenian coast of central Italy (Lazio administrative region) (Fig. 1). In this area, sandy dunes are relatively simple in structure and occupy a narrow strip (< 500 m) that extends parallel to the shoreline (Acosta et al. 2003a). In this study, we considered seven SCIs hosting representative areas of coastal dunes that are included in the Natura 2000 network. Specifically, proceeding from north to south, we analyzed the following SCIs: Litorale a Nord-Ovest delle Foci del Fiora (site 1), Litorale tra Tarquinia e Montalto di Castro (site 2), Macchia grande di Focene e Macchia dello Stagneto (site 3), Lido dei Gigli (site 4), Litorale di Torre Astura (site 5), Dune del Circeo (site 6), Duna di Capratica (site 7).

2.2. The selected IAS: *Carpobrotus* sp.

The introduction of *Carpobrotus* sp. in the Mediterranean basin dates back to the early 1800s (De La Cour, 1813). Its spread was promoted for dune stabilization and for gardening purposes (Vilà et al., 2006; Maltez-Mouro et al. 2010). *Carpobrotus* sp. is characterized by a fast clonal growth that results in the formation of wide and thick monodominant carpets (Sintes et al. 2007). Invasion by *Carpobrotus* sp. causes negative effects on the germination, survival and growth of native species, ultimately altering the composition and diversity of coastal plant communities (Campoy et al. 2018). Moreover, *Carpobrotus* sp. produces substantial changes in soil properties that prevent re-colonization by native species (Santoro et al. 2011; Novoa et al. 2014).

2.3. Invasion status in the selected Natura 2000 sites

We extracted information about the status of *Carpobrotus* sp. invasion in the selected Natura 2000 sites from a fine-scale land cover map produced through the photo-interpretation of 1 m resolution aerial orthophotos acquired in 2008 (for details about the land cover map see section 2.4.1.). Sites were affected by different levels of *Carpobrotus* sp. invasion (Tab. 1). Site 2 was the only SCI not invaded by *Carpobrotus* sp. The analysed protected areas were characterized by different invasion status (intended as the proportion of area occupied by *Carpobrotus* sp. in each site), which were independent from the extent of the SCIs (Tab. 1). In particular, the extent of the area occupied by *Carpobrotus* sp. varied from a minimum of 0.06 ‰ in site 3 to a maximum of 15.1 ‰ in site 4.

Table 2 - Analyzed Natura 2000 coastal sites along with their site identification (id) as reported in figure 1; extent (in hectares - ha.); total area covered by *Carpobrotus* sp. cover type in each SCI (expressed in hectares - ha.); invasion status (proportion of area covered by *Carpobrotus* sp. land cover type expressed in per mille - ‰). N.I.: not invaded by *Carpobrotus* sp. The extent of the area occupied by *Carpobrotus* sp. land cover type in each site was derived from a fine-scale land cover map in an ArcGIS environment (for details about the land cover map, see section 2.4.1.).

id	Site name (European code)	SCI area (ha.)	<i>Carpobrotus</i> sp. land cover type (ha.)	Invasion status (‰)
1	Litorale a N-W delle Foci del Fiora (IT6010018)	185.44	0.05	0.27
2	Litorale tra Tarquinia e Montalto di Castro (IT6010027)	199.78	N.I.	-
3	Macchia grande di Focene e Macchia dello Stagneto (IT6030023)	317	0.02	0.06
4	Lido dei Gigli (IT6030045)	220.55	3.33	15.1
5	Litorale di Torre Astura (IT6030048)	201.01	0.48	2.39
6	Dune del Circeo (IT6040018)	440.98	3.58	8.12
7	Duna di Capratica (IT6040021)	30.16	0.09	2.97

2.4. IAS distribution model implementation and PA invasibility assessment

It is widely recognized that the outcome of an invasion event should be analyzed as a function of the combined influence of three basic aspects: propagule pressure (P), abiotic (A) and biotic (B) factors (hereafter, PAB; see Catford et al. 2009). Propagule pressure is regarded as the frequency of introduction of plant individuals in a non-native region (Colautti et al. 2006), the abiotic factor stands for the environmental filters posed by the invaded environment (Catford et al. 2009), and the biotic factor can be intended as the interaction arising between the invasive species and the recipient native communities (Theoharides & Dukes 2007).

We modelled and mapped the probability of occurrence of *Carpobrotus* sp. on coastal dunes of the Lazio region, accounting for the concurrent effect of propagule pressure, abiotic and biotic factors and by using multi-source remotely sensed imagery for deriving both the response variable (*Carpobrotus* sp. presence/absence) and the PAB predictors (for details see Bazzichetto et al. 2018). We implemented the *Carpobrotus* sp. distribution model on a 300 m wide strip parallel to the seashore that is an appropriate spatial extent for modelling the distribution of *Carpobrotus* sp. along the dune system of the study area (Acosta et al. 2008). First, the *Carpobrotus* sp. distribution model was implemented inside the 300 m wide coastal strip. Then, a risk assessment of *Carpobrotus* sp. invasion was carried out in each selected SCI belonging to the Natura 2000 network. In particular, model predictions of *Carpobrotus* sp.

occurrence were used to map the potential distribution of the invasive species on a raster grid map for the whole Lazio dune system. Then, the map was used as input for conducting the invasion risk assessment in the analysed protected sites (Thuiller et al. 2005; Jiménez-Valverde et al. 2011). A flowchart reporting the overall process implemented is reported in figure 2.

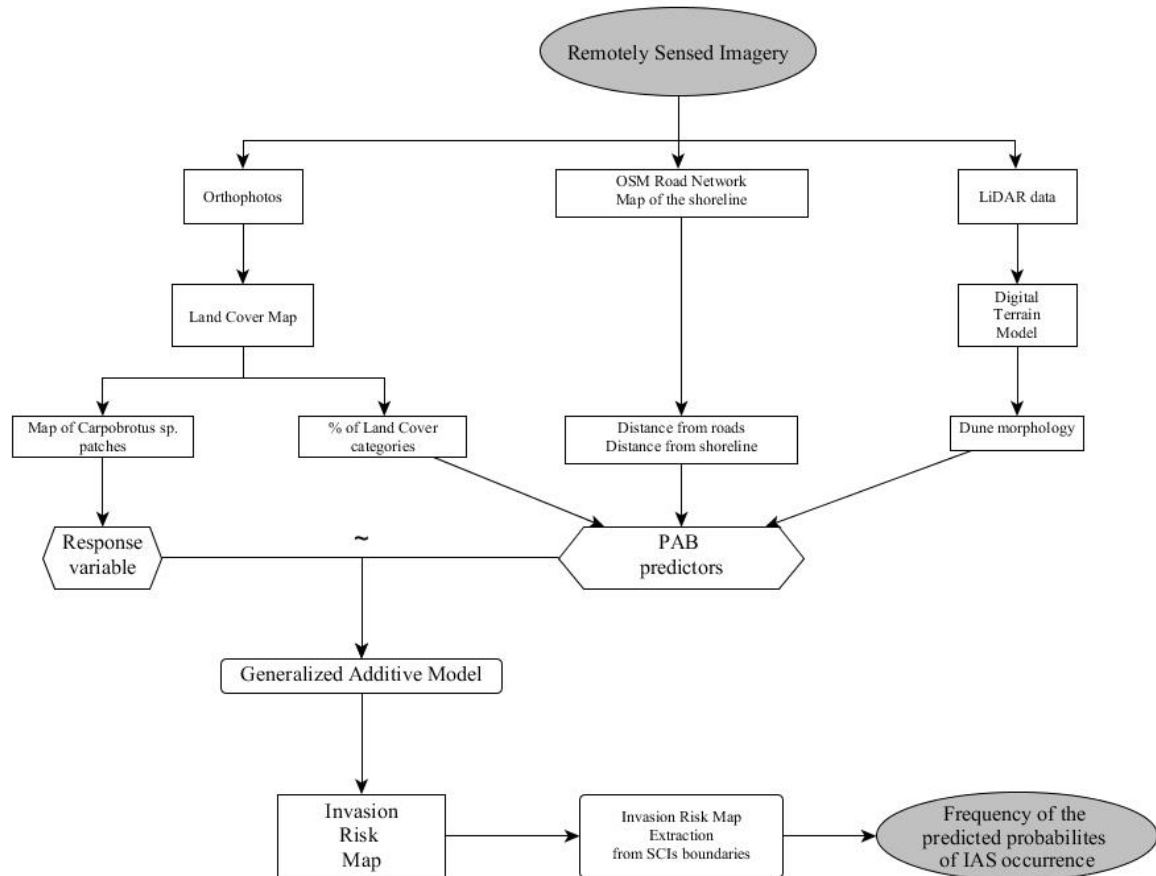


Figure 2 – Flowchart synthesizing the procedure implemented for assessing the invasion risk posed by *Carpobrotus* sp. in the Natura2000 sites. OSM; OpenStreetMap.

2.4.1. Remotely sensed imagery processing

A set of panchromatic aerial orthophotos with 1 m resolution taken in 2008 were manually interpreted on screen in an ArcGIS environment (ArcGIS 10.1; ESRI 2011) to produce a fine-scale land cover map (1:5000) that covered a 500 m wide coastal belt along the study area (for details see Bazzichetto et al. 2018). Ten land cover categories were mapped. The legend matches CORINE land cover expanded to a fourth level of detail for natural and semi-natural areas (for details see Acosta et al. 2005; Appendix A). Particular attention was given to the detection of *Carpobrotus* sp. patches. As the species can form monodominant patches represented by thick and large mats with characteristic shadow, tone/color and texture, its accurate identification from remote is facilitated (Carranza et al. 2010). The accuracy of the land cover map was assessed by comparing the attribution of each class in the map with the data obtained by the field surveys (performed from 2012 to 2013 using a GPS). We calculated the KHAT statistic (Congalton & Green 1999), which ranges from 0 to 1. A KHAT value of 1 indicates a perfect correspondence between the two compared classification schemes, while value of 0 suggests that a given classification is no better than a random assignment of classes

in a map. The obtained map presents a global accuracy of 0.77. Moreover, the detection of the *Carpobrotus* sp. cover type was further supported and updated using Bing Bird's eye images, which were collected in 2013 at a 45-degree angle from low-flying aircraft and offer high spatial resolution (0.3 m resolution).

Each mapped land cover category (except for the *Carpobrotus* sp. cover type) was converted to a raster grid map with 5 m resolution to derive a set of topographical variables that were used as surrogates of propagule pressure and biotic factors in the analyses.

Airborne LiDAR imagery taken in 2008 during the "PST-A mission - Piano Straordinario di Telerilevamento Ambientale; Ministero dell'Ambiente e della Tutela del Territorio e del Mare" were processed to derive a 2 m resolution Digital Terrain Model (DTM). The obtained DTM was used to extrapolate a set of morphological variables that have already been used to delineate the abiotic conditions along the sea-inland environmental gradient (Bazzichetto et al. 2016).

2.4.2. PAB proxy variables

A set of proxy variables representative of propagule pressure (P), abiotic (A) and biotic (B) factors were mapped for the whole study area (for details on the proxy variables, see Appendix B).

Percentage of artificial (ART), agricultural (AGR) areas and distance from roads were mapped as surrogates of propagule pressure (Carboni et al. 2010; Carranza et al. 2010; Vicente et al. 2010). Percentage of artificial and agricultural land cover were derived from the 5 m rasterized land cover map by means of a moving window (50 m radius) procedure in FRAGSTATS (McGarigal et al. 2012). Distance from roads was computed as the Euclidean distance between the centre of each raster cell and the roads (road network data retrieved from <https://planet.openstreetmap.org/>; OpenStreetMap contributors 2016).

Dune elevation, slope and curvature were derived from the 2 m resolution LiDAR-DTM in an ArcGIS environment as surrogates of the sea-inland environmental gradient (Bazzichetto et al. 2016; Bazzichetto et al. 2018). Moreover, a raster grid map reporting the distance between the centre of each raster cell and the shoreline was built by computing the straight line Euclidean distance.

To account for biotic interactions between *Carpobrotus* sp. and the recipient community (Carranza et al. 2011), we mapped the percentage of the following natural and semi-natural land cover categories occurring in the study area: afforestation (AFF); semi-natural (SN; semi-natural herbaceous and woody dune vegetation); wetland and marshes (WET); beach with pioneer annual vegetation (BPV); herbaceous dune vegetation (HDV); and woody dune vegetation (WDV). The percentage of natural and semi-natural land cover types was derived from the 5 m rasterized land cover maps by means of a moving window (50 m radius) procedure implemented in FRAGSTATS (McGarigal et al. 2012).

For each PAB proxy variable, a raster grid map with 5 m resolution was derived. In particular, downscaling of the raster layers derived from the LiDAR-DTM was performed to match the spatial resolution of the other PAB layers (5 m).

2.4.3. SDM implementation

Carpobrotus sp. presence points were sampled at the centroids inside each mapped *Carpobrotus* sp. patch ($n = 2\,189$). Absence points were generated sampling randomly 4 000 points outside *Carpobrotus* sp. patches.

Values of propagule pressure, abiotic and biotic proxy variables were extracted from each PAB raster grid map at the location intersecting the geographic coordinates of *Carpobrotus* sp. presence/absence points.

The relationship between *Carpobrotus* sp. occurrence and the PAB factors was modelled using a binomial Generalized Additive Model (GAM) with link logit. We set the presence/absence of *Carpobrotus* sp. as the response variable and the PAB proxy variables as predictors. The major well-known problem of GAMs is how to set the degree of smoothness of the relationship between the response variable and the predictors (see Wood 2011). As GAMs allow for any kind of non-linear relationship, they may result in a simple general trend with high residual variance on one hand, or, on the other hand, in a very complex curve, strongly biased to the individual data points. The two principal factors affecting the degree of smoothness are the choice of smoothers (i.e. the type of basis functions), and the basis dimension (i.e. the number of basis functions used for each predictor). A generally recommended way to find an “optimal” smoothing to balance the trade-off between variance and bias is to use Penalized Splines as basis functions and then to set the basis dimension for each predictor according to the effective degrees of freedom of the smoother. For these reasons, we used Penalized Splines for fitting the smoothers and set the number of basis dimension (k) according to the effective degree of freedom of the smoothers. Another problem concerning GAMs is the concurvity among predictors, which means that two or more predictors may have similar relationships with the response variable, making some of them redundant. Concurvity can be considered as an analogical issue to collinearity in linear models. We tested concurvity among smoothers to exclude those predictors whose trend was redundant with others. GAM was implemented and concurvity was tested in R using the package *mgcv* (Wood 2011).

Model goodness-of-fit was assessed by computing the mean of individual AUC (Area Under the Relative Operating Characteristic Curve; Pearce & Ferrier 2000) values obtained by a 5-fold cross-validation of the model (following Hijmans et al. 2016).

2.4.4. Invasion risk map

An invasion risk map was built for the Lazio dune system by projecting the predicted probabilities of *Carpobrotus* sp. occurrence on a raster grid map with 5 m resolution (R package: *raster*; Hijmans et al. 2016). Then, for each SCI a specific invasion risk map was derived by overlaying the site boundaries to the invasion risk map generated for the whole Lazio dune system. For each SCI, we derived histograms describing the frequency of the predicted probabilities of *Carpobrotus* sp. occurrence. In particular, the continuous range of occurrence probabilities was discretized in ten classes (from 0 to 1, by 0.1) and the three most frequent ones were used to indicate the invasibility of each SCI. The most frequent classes were chosen instead of other summary measurements, such as the mean or the median of the

occurrence probabilities, as the latter would have led to misleading information on *Carpobrotus* sp. potential of invasion in the case of multimodal distribution.

To allow reproducibility, the complete R code to perform the whole analysis is provided in Appendix C.

3. Results

3.1. PAB influence on the IAS occurrence

The model explained 57.4 % of the deviance and depicted a significant role of propagule pressure, abiotic and biotic factors in determining *Carpobrotus* sp. occurrence along the analyzed coastal dune system (Tab. 2).

Among propagule pressure predictors, the percentage of artificial land (% ART) and the distance from roads exhibited a significant relationship with *Carpobrotus* sp. occurrence, while the percentage of agricultural land (% AGR) did not show any significant relationship. Concerning abiotic factors, *Carpobrotus* sp. occurrence was significantly affected by elevation, distance from the sea, and slope. In contrast, curvature was not significantly associated to the presence of *Carpobrotus* sp. All biotic predictors showed a significant relationship with the occurrence of *Carpobrotus* sp., except for Woody Dune Vegetation (% WDV) land cover ($p > 0.05$).

The mean AUC value obtained by the 5-fold cross-validation of the model was 0.94.

Table 2 - Model outcome. From left to right: propagule pressure (P), abiotic (A), biotic (B) predictors; smoothers' degree of freedom (k); significance of the PAB predictors. Deviance explained by the model is reported at the bottom of the table. As the percentage of Beach Pioneer Vegetation showed a high degree of concavity with other predictors (estimate = 0.64), this variable was excluded from the model. For a detailed description of the PAB proxy variables see Appendix B.

PAB proxy variables	k	p-value
Propagule pressure (P)		
Distance from roads	9	***
% ART	5	***
% AGR	5	$p > 0.05$
Abiotic (A)		
Elevation	9	***
Sea distance	9	***
Slope	9	***
Curvature	9	$p > 0.05$
Biotic (B)		
% AFF	5	**
% SN	5	***
% WET	5	*
% HDV	5	***
% WDV	5	$p > 0.05$
Deviance explained		57.4 %

3.2. Natura 2000 sites invasibility

The likelihood of *Carpobrotus* sp. invasion on the coastal dunes of the Natura 2000 sites ranges from a probability of 0 (which indicates low invasion risk as the invasive species is predicted to be absent) to 1 (which, in contrast, predicts the highest invasion risk posed by the IAS). All the analyzed sites are at risk of invasion by *Carpobrotus* sp.; their invasibility is not equivalent, but varies heterogeneously across the Tyrrhenian coastal landscape, with some sites being more vulnerable to invasion than others. The histograms describing the frequency of the predicted probabilities of *Carpobrotus* sp. occurrence (Fig. 3, 4) and, in particular, the three most frequent occurrence probability classes for each SCI (Tab. 3), both indicate the presence of two main invasion trends in the Natura 2000 coastal network. According to the former trends, SCIs can be grouped into sites that are characterized by low invasibility or medium-high invasibility. Figures representing site-specific invasion risk maps are reported in Appendix D.

In low invasibility sites (1, 2, 3 and 5), the frequency of *Carpobrotus* sp. occurrence probabilities exhibits a marked skewness towards low or null risk of invasion by *Carpobrotus* sp. (Tab. 3; Fig. 3). In the former sites, the most frequent probability classes of *Carpobrotus* sp. occurrence are 0 and 0.1, which jointly covered approximately the 70% of the corresponding invasion risk maps. On the other hand, medium-high invasibility sites (4, 6 and 7) show a bimodal distribution of *Carpobrotus* sp. occurrence probabilities. In these sites, the frequency of *Carpobrotus* sp. occurrence probabilities is high in correspondence of both a first

peak occurring in low probability classes and a second peak occurring in high probability classes (Tab. 3; Fig. 4). While such pattern is particularly marked in sites 6 and 7, it is less marked in site 4.

Table 3 - Natura 2000 coastal sites along with the 1st, 2nd, 3rd most frequent probability classes of *Carpobrotus* sp. occurrence and the relative invasibility: low invasibility (LI) and medium-high invasibility (MHI). The proportion of the area covered by the three most frequent probability classes on the invasion risk map extent for each SCI is reported in brackets. P: probability of *Carpobrotus* sp. occurrence.

Site	1 st	2 nd	3 rd	Invasibility
Litorale a N-W delle Foci del Fiora (site 1)	<i>P</i> =0; (57%)	<i>P</i> =0.1; (10%)	<i>P</i> =0.2; (7%)	LI
Litorale tra Tarquinia e Montalto di Castro (site 2)	<i>P</i> =0; (57%)	<i>P</i> =0.1; (11%)	<i>P</i> =0.2; (8%)	
Macchia grande di Focene e Macchia dello Stagneto (site 3)	<i>P</i> =0; (77%)	<i>P</i> =0.1; (4%)	<i>P</i> =0.3; (3%)	
Litorale di Torre Astura (site 5)	<i>P</i> =0; (79%)	<i>P</i> =0.1; (9%)	<i>P</i> =0.2; (3%)	
Lido dei Gigli (site 4)	<i>P</i> =0; (41%)	<i>P</i> =0.1; (9%)	<i>P</i> =0.8; (8%)	MHI
Dune del Circeo (site 6)	<i>P</i> =0; (31%)	<i>P</i> =0.8; (12%)	<i>P</i> =0.9; (12%)	
Duna di Capratica (site 7)	<i>P</i> =0.8; (19%)	<i>P</i> =0.7; (13%)	<i>P</i> =0.9; (13%)	

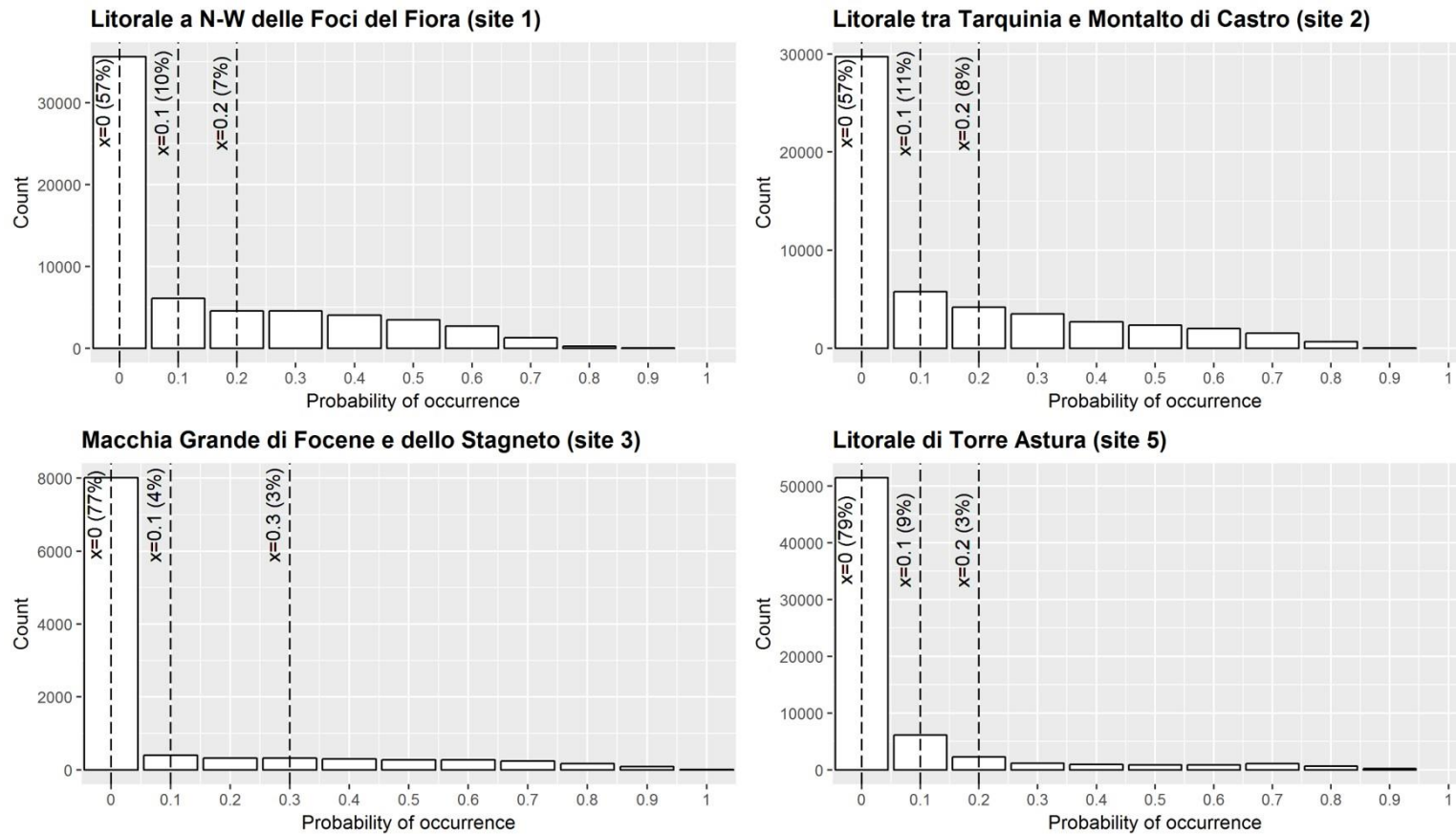


Figure 3 - Frequency of *Carpobrotus* sp. occurrence probability classes in sites characterized by low invasibility. Values of the three most frequent probabilities of *Carpobrotus* sp. occurrence are reported along the dashed lines (relative frequencies are shown in brackets).

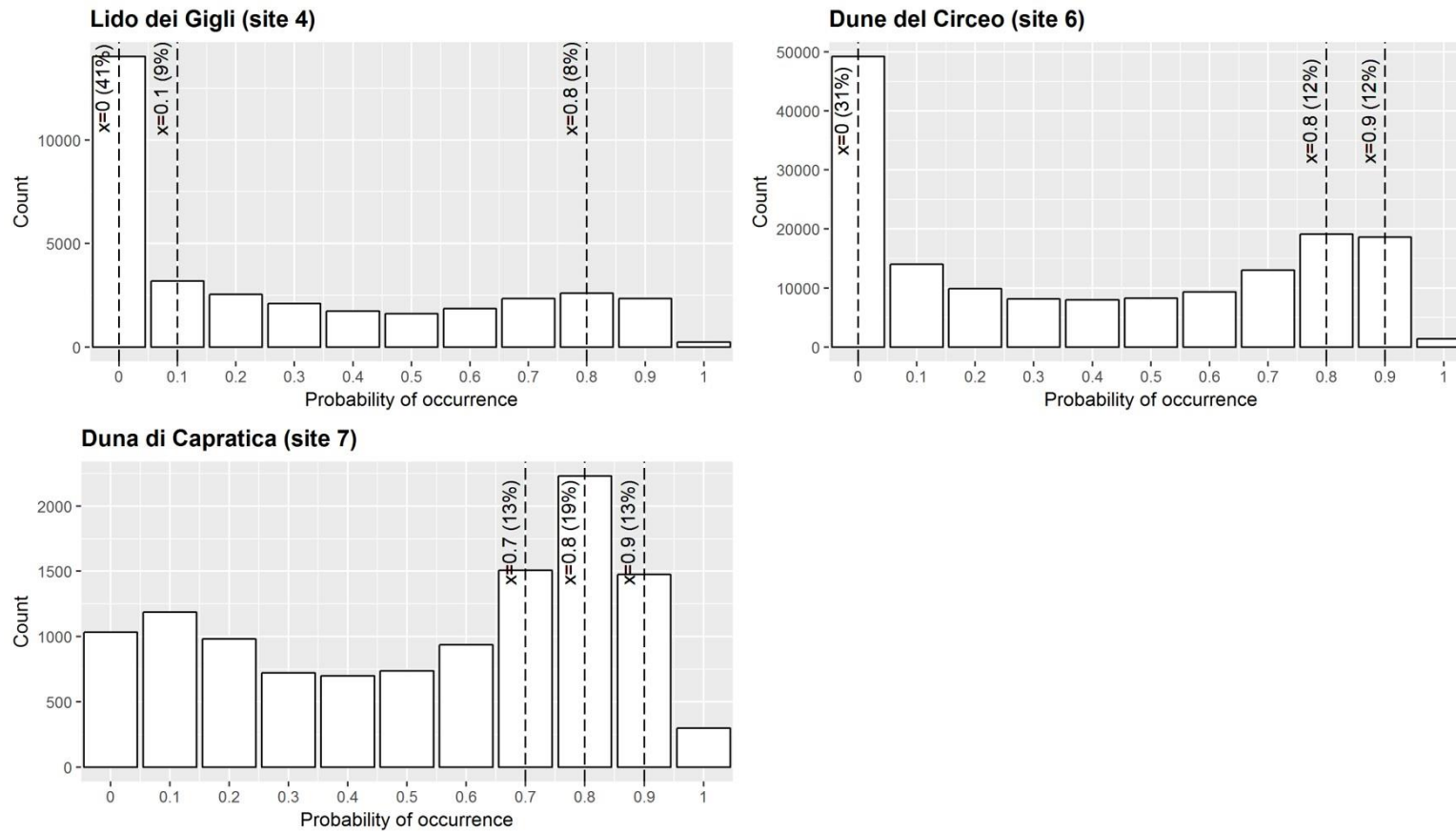


Figure 4 - Frequency of *Carpobrotus* sp. occurrence probability classes in sites characterized by medium-high invasibility. Values of the three most frequent probabilities of *Carpobrotus* sp. occurrence are reported along the dashed lines (relative frequencies are shown in brackets).

4. Discussion

In this study, we propose an iSDM-based methodology that accounts for the combined role of propagule pressure, abiotic and biotic factors to assess the invasion risk posed by IAS in protected areas; we test this approach using the highly invasive *Carpobrotus* sp. as study species to evaluate the invasibility of Natura 2000 coastal sites of central Italy. The integration of PAB factors into a single model framework enhanced our understanding of *Carpobrotus* sp. invasion in the study area (variance explained = 57.4 %) and allowed accurate prediction of the likelihood of *Carpobrotus* sp. invasion across the Natura 2000 coastal network. At the same time, the use of the predicted probabilities of *Carpobrotus* sp. occurrence for quantifying the invasibility of each SCI allowed identification of site-specific management perspectives. We underline that the improvement of knowledge about the influence of multiple drivers (PAB factors) on an invasion process, and the production of invasion risk maps that report the likelihood of IAS potential for invasion, both constitute essential steps for developing effective surveillance and monitoring strategies.

4.1. Influence of PAB factors on IAS occurrence

The model results highlight that, as the occurrence of *Carpobrotus* sp. on the dune system is significantly affected by the context-specific influence of the PAB factors, invasion does not proceed homogeneously across the coastal landscape, making some Natura 2000 sites more vulnerable to invasion.

In the analyzed Mediterranean dune system, propagule pressure has a prevalent role in promoting *Carpobrotus* sp. occurrence, as documented in the literature (Carboni et al. 2011; Carranza et al. 2010; Malavasi et al. 2014). Indeed, the presence of *Carpobrotus* sp. was significantly related to the distance from roads and the percentage of artificial land cover. In fact, roads (Pauchard & Alaback 2004; von der Lippe & Kowarik 2007) and population density (Spear et al. 2013; Dimitrakopoulos et al. 2017) have been identified as primary drivers in favouring invasive plant introduction in PAs from surrounding areas. Road networks are considered as potential reservoirs of invasive plant propagules and can contribute to propagule dispersion by creating corridors throughout the landscape (von der Lippe & Kowarik 2007; Parendes & Jones 2000). At the same time, population density (measured as the number of nearby households) was one of the most important factors affecting invasibility of PAs in Florida (Iacona et al. 2014).

The abiotic factor (expressed by the dune morphology) significantly shapes the likelihood of *Carpobrotus* sp. invasion along the sea-inland gradient, constituting an environmental filter to the spread of the invasive species, whose occurrence is consequently limited to a specific sector of the dune system. Indeed, it has been observed that *Carpobrotus* sp. preferentially occurs at intermediate elevations and distances from the shoreline (Bazzicheto et al. 2018).

In this conjunction of factors regulating invasion success (or failure), the biotic drivers are also significantly related to *Carpobrotus* sp. occurrence. As previously reported in the literature, *Carpobrotus* sp. establishes on dune sectors colonized by herbaceous dune vegetation or on other sparsely vegetated coastal areas (Carranza et al. 2011). In contrast, it avoids close vegetation formations that could be associated with a higher biotic resistance of the former plant assemblages to plant invasion (Carboni et al. 2010; Eschtruth & Battles, 2009).

4.2. Natura 2000 sites invasibility and management perspectives

The different level of invasibility characterizing the sites of the Natura 2000 coastal network mirrors the heterogeneous contribution of each PAB factor in determining *Carpobrotus* sp. occurrence in the analyzed PAs, as in the surrounding coastal landscape. In addition, the effect of PAB factors is known to be driven by landscape pattern and processes, which have a dramatic role in shaping the resulting plant invasion pattern in PAs (Braun et al. 2016; Foxcroft et al. 2011, 2013; Gurevitch et al. 2011). For this reason, information concerning sites invasibility itself needs to be supported by the knowledge on the invasion process occurring outside PAs of interest to implement effective conservation strategies aimed at reducing the impact of IAS in PAs (Pauchard & Alaback 2004).

We observed that the analyzed Natura 2000 sites can be schematically grouped into two different invasibility categories according to the likelihood of *Carpobrotus* sp. invasion predicted by the iSDM: low invasibility and medium-high invasibility sites.

In low invasibility sites (such as 1, 2, 3 and 5), the distribution of the predicted probabilities of *Carpobrotus* sp. occurrence is strongly skewed to low or null invasion risk (Tab. 3; Fig. 3). The prediction is coherent with the invasion status observed in those sites (Tab. 1) where the relative cover of *Carpobrotus* sp. was low (at the time of the survey). We hypothesized that the spread of *Carpobrotus* sp. is unlikely in low invasibility sites due to the overall unfavourable contribution of PAB factors to the occurrence of the invasive plant. To prevent the establishment and spread of IAS, early detection and eradication should be carried out in sites not yet or sparsely invaded and for which the model predicts a low risk of invasion.

To the other hand, invasion risk is higher in medium-high invasibility sites (such as 4, 6 and 7), which show bimodal trends of the predicted probabilities of *Carpobrotus* sp. occurrence (Tab. 3; Fig. 4). Indeed, we observed that *Carpobrotus* sp. is likely to invade from 10 % up to 45 % of the total amount of habitat potentially suitable for its establishment in medium-high invasibility sites. Thus, in the former SCIs the combined influence of the PAB factors is likely to highly promote *Carpobrotus* sp. establishment. Strategies that aim at controlling the spread of IAS in heavily invaded PAs should be particularly addressed in sites characterized by a medium to high risk of invasion. Furthermore, monitoring actions and resource allocation should be prioritized in sites that are not yet or just sparsely invaded, but for which the model predicts a high invasion risk, such as site 7.

Our results highlight the need to address site-specific management actions that consider the relative level of PA invasibility in areas where invasion does not occur homogeneously.

5. Conclusion

In this study, we propose an iSDM-based methodology that accounts for the role of multiple invasion drivers in assessing the risk posed by plant IAS to the biodiversity of protected sites. The presented approach matches the need for early warning mechanisms claimed by the IAS Regulation and promotes the use of predictive models for conservation tasks. Indeed, we highlight that the use of iSDMs supported by the PAB theoretical framework constitutes a sound tool that may efficiently support conservation decision-makers dealing with plant invasion in PAs.

The implementation of the iSDM allowed mapping of the invasion risk posed by a highly invasive alien plant and deriving a site-specific measure of invasibility. In this regard, the use of remotely sensed data for iSDM implementation provides a cost-effective approach for

conducting recurrent IAS monitoring on a broad geographic extent, overcoming the lack of resources claimed by conservation managers. For instance, the proposed methodology could be used in evaluating the efficiency of IAS management actions implemented over time.

In conclusion, we warmly encourage the spread of iSDM-based approaches in order to fill the gap between model theory and practice in IAS management, providing, at the same time, efficient solutions for conservation managers.

Appendix A

List of the ten mapped land cover types along with a detailed description of their main characteristics and abbreviations. The land cover map accuracy was evaluated through the KHAT statistic and field surveys. The map presents a global accuracy of 0.77.

Land cover type	Cover type description	Abbreviation
Artificial	Artificial areas including urban infrastructure; industrial and commercial units; mine, dump and construction sites; artificial vegetated areas.	ART
Agricultural	Agricultural land, including arable land, permanent crops, pastures and heterogeneous agricultural areas.	AGR
Afforestation	Afforestation on coastal dunes with <i>Pinus</i> spp. plantations.	AFF
Woody Dune Vegetation	Mediterranean maquis growing on fixed dune.	WDV
Semi-natural Woody Vegetation	Bushy vegetation with scattered trees represented by foredune woodland degradation or forest regeneration/recolonization.	SWD
Semi-natural Herbaceous Vegetation	Abandoned meadows and pastures with different degree of degradation or recolonization.	SHW
Beach Pioneer Vegetation	Upper beach colonized by pioneer annual vegetation.	BPV
Herbaceous Dune Vegetation	Foredune colonized by herbaceous vegetation intermingled to open sectors.	HDV
Areas invaded by <i>Carpobrotus</i> sp.	<i>Carpobrotus</i> sp. cover type.	INV
Wetlands	Inland wetlands and marshes.	WET

Appendix B

Propagule pressure (P), abiotic (A) and biotic (B) factors along with the corresponding proxy variables (predictors) used for implementing the iSDM. For a detailed description of the land cover types, see Appendix A.

Factor	Proxy variables (predictors)	Description
P	% ART, % AGR	- percentage of artificial (ART) and agricultural (AGR) land cover classes within each moving window (50 m radius).
	Distance from roads (m)	- Euclidean nearest distance (m) from motorways and primary roads.
A	Elevation (a.s.l. m)	- m above sea level value.
	Slope (degree)	- maximum change in elevation from each cell and its eight neighbours.
	Curvature (adim.)	- second order derivative from the digital terrain model. Positive curvature values indicate that the surface is upwardly convex. Negative curvature values indicate that the surface is upwardly concave. Curvature values equal to 0 indicate that the surface is flat.
	Sea distance (m)	Euclidean distance (m) from the shoreline.
B	% AFF, % SN (SHV and SWV), % WET, % BPV, % HDV, % WDV	- percentage of the focal land cover class within each moving window (50 m radius). AFF: afforestation, SN: semi-natural (herbaceous and woody vegetation), WET: wetlands, BPV: beach pioneer vegetation, HDV: herbaceous dune vegetation, WDV: woody dune vegetation.

Appendix C

*R code used for implementing the *Carpobrotus* sp. distribution model and for assessing the risk posed by the invasive species in the analyzed Natura 2000 sites.*

```
library(mgcv)
library(dismo)
library(raster)
library(rgdal)
library(ROCR)

# Data preparation -----
----
# Reading the dataset, whose structure is as follows:
#   Point      Latitude      Longitude      Pres
#   1          2342342        2342342        1
#   2          3566536        7647373        1
#   3          4287654        2345677        0
#   ...
> data_set <- read.table("dataset.csv", header=T, sep=";")
> coord_pres <- data_set[data_set[,4]==1,2:3]
> coord_abs <- data_set[data_set[,4]==0,2:3]
# Creation of RasterLayer objects from source file
> elevation <- raster::raster(x = "Directory/elevation_raster")
> artificial <- raster::raster(x = "Directory/artificial_raster")
...
> predictors <- raster::stack(elevation, artificial, ...)
# Extraction of the predictors values at the location of each
# presence/absence point from the raster objects
> pres_val <- raster::extract(predictors, coord_pres)
> abs_val <- raster::extract(predictors, coord_abs)
# Creation of the main data frame (df)
> p_a <- c(rep(1, nrow(pres_val)), rep(0, nrow(abs_val)))
> df <- data.frame(cbind(p_a, rbind(pres_val, abs_val)))

# Model fit -----
----
# Fit the binomial GAM with link logit, setting the basis dimension
k
> (model <- mgcv::gam(p_a ~ s(elevation, bs='ps', sp=0.6) +
                      s(artificial, bs='ps', sp=0.6, k=0.5) +
                      s(...),
                      family=binomial(link=logit), data = df,
                      method='REML'))

# Check model assumptions
```

```

> (mgcv::gam.check(model))
# Check concurvity
> (mgcv::concurvity(model, full = T))

# Model evaluation using mean AUC score -----
-----
# Split the dataset into k pairs of testing and training data -----
-----
> k <- 5
> group_ <- dismo::kfold(df, k)
> group_list <- lapply(1:k, function(i) list(train=df[group_!=i,],
                                             test=df[group_==i,]))

# Function that fits GAM and computes performance measures -----
-----
> perform <- function(dat){
+ mod <- mgcv::gam(p_a ~ s(elevation, bs='ps', sp=0.6) +
+               s(artificial, bs='ps', sp=0.6, k=5) +
+               s(...),
+               family=binomial(link=logit),
+               data = dat$train, method='REML')
+ prob <- mgcv::predict.gam(mod, newdata=dat$test, type="response")
+ pred <- ROCR::prediction(as.numeric(prob),
+ as.numeric(dat$test$p_a))
+ perf <- ROCR::performance(pred, measure = "tpr", x.measure =
+ "fpr")
+ auc <- ROCR::performance(pred, measure = "auc")
+ return(list(auc=auc@y.values[[1]], perf=perf))
+}

# Fit GAM and compute performance measures for each pair of training
and # testing data
> performances <- lapply(group_list, perform)

# Plot TPR-FPR curves -----
-----
> par(mfrow=c(2,3))
> plots <- lapply(performances, function(.) plot(.$perf))
> par(mfrow=c(1,1))

# Compute mean AUC -----
-----
> (mean_auc <- mean(sapply(performances, function(.) .$auc)))

```

```

# Production of the iSDM map -----
-----
> hope <- raster::predict(predictors, model)
> hope_map <- raster::writeRaster(x = hope, filename = "hope",
                                format="GTiff")

# Risk assessment -----
-----
# Reading site 1 boundaries
> site_1 <- rgdal::readOGR(dsn = "Directory/site_folder", layer =
                          "site_1")

# Extraction of the iSDM map that overlaps site 1
> site_1_map <- raster::mask(x = hope_map, mask = site_1)
# Extraction of the iSDM map values (probabilities of Carpobrotus
sp. occurrence) for site 1
> site_1_values <- raster::getValues(x = site_1_map)

```

Appendix D

Invasion risk maps are reported for protected sites characterized by low invasibility in Fig. D.1 and by medium-high invasibility in Fig. D.2. The potential distribution of *Carpobrotus* sp. was mapped using the predicted probabilities of occurrence of the invasive species. Such information was used as input to derive site-specific invasion risk maps.



Figure D.1 – Invasion risk maps reporting the predicted probabilities of *Carpobrotus* sp. occurrence in sites characterized by low invasibility (LI): site 1, site 2, site 3, site 5. Color bar: probabilities of occurrence range from 0 that indicates low invasion risk as the species is predicted to be absent (green) to 1 that indicates high invasion risk as the species is predicted to be present (red).

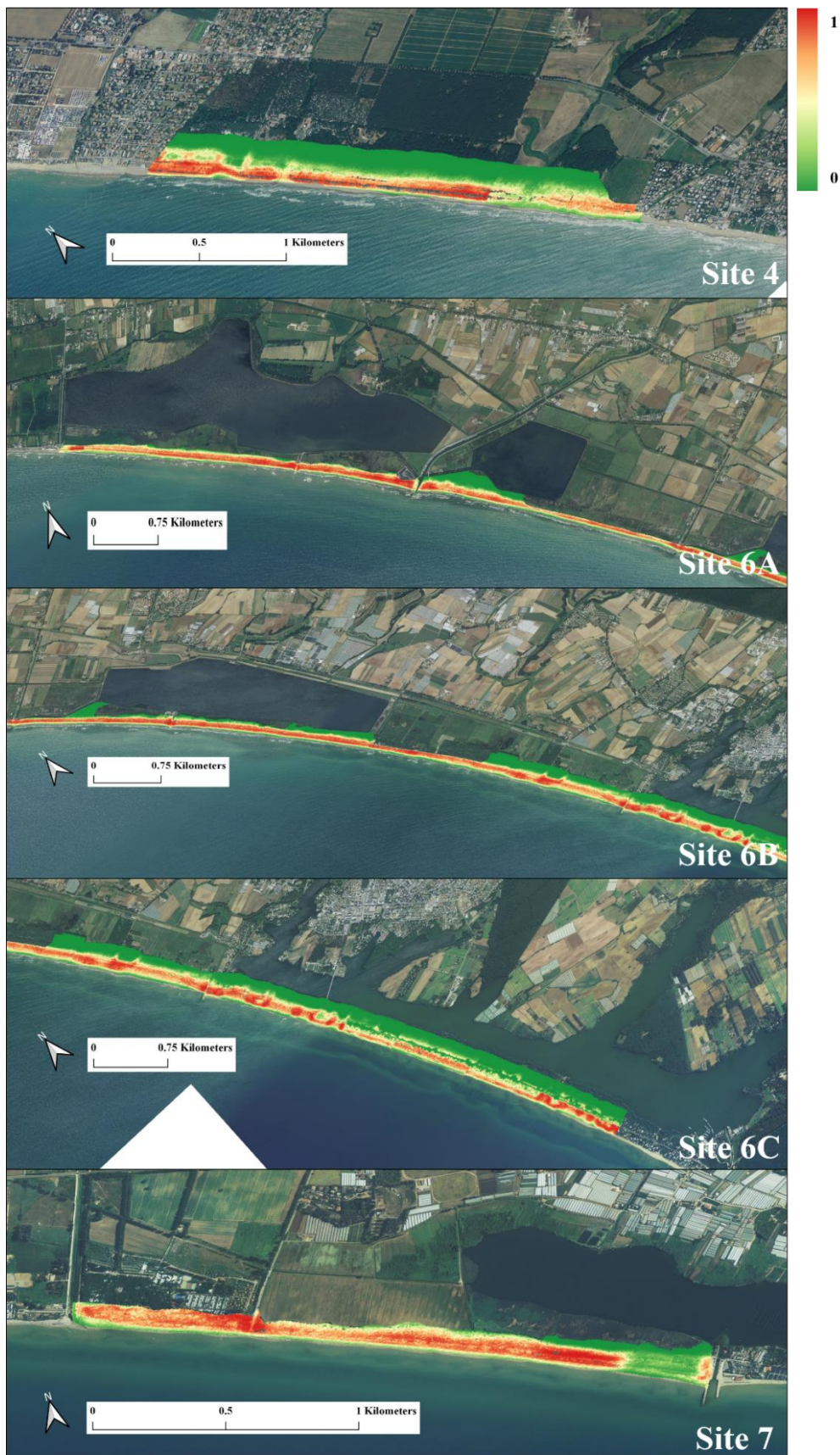


Figure D.2 – Invasion risk maps reporting the predicted probabilities of *Carpobrotus* sp. occurrence in sites characterized by medium-high invasibility (MHI): site 4, site 6 (divided in three frames A, B, C), site 7. Color bar: probabilities of occurrence range from 0 that indicates low invasion risk as the species is predicted to be absent (green) to 1 that indicates high invasion risk as the species is predicted to be present (red).

Conclusions and future perspectives

The research activities carried out during the three years of doctorate highlighted the potential of integrating field collected vegetation data and remotely sensed imagery for analyzing and monitoring plant diversity in coastal dunes.

The use of LiDAR derived Digital Terrain Model (DTM) allowed the accurate characterization of the morphological profile of coastal European Community-habitats (*sensu* EU Habitats Directive), while providing valuable information on the influence of dune morphology in determining the occurrence of plant communities along the coastal zonation. Furthermore, data derived from aerial imagery summarizing coastline dynamism over a 12-years period were successfully used to quantify the impact of coastal erosion and accretion on dune plant communities and to assess how sand redistribution affects the ecomorphodynamic process underpinning the functioning of coastal ecosystems.

At the same time, the integration of LiDAR and orthophotos allowed modelling the distribution of one of the most threatening exotic species (*Carpobrotus* sp.) in Mediterranean dune systems. In particular, remotely sensed data were fundamental for analyzing the relationship between *Carpobrotus* sp. and the invaded environment on a wide geographic extent. Remote sensing was also crucial for highlighting that invasion does not occur homogeneously along the analyzed Tyrrhenian dune system, being affected by the context-dependent contribution of propagule pressure, abiotic and biotic factors. Finally, modelling the distribution of *Carpobrotus* sp. allowed the invasibility of 7 Sites of Community Importance included in the Natura 2000 coastal network of the Lazio region to be assessed and a methodology for the identification of site-specific invasive species management strategies to be proposed.

This thesis showcases how remote sensing technologies can play a key role in supporting the monitoring and conservation of threatened ecosystems such as coastal dunes. All of the remotely sensed imagery used in this project were freely available, demonstrating that remote sensing can be a cost-effective tool for conducting ecological studies.

The increasing availability of remotely sensed datasets provides momentum for addressing new ecological questions and improving the management of biodiversity. Relying on a solid theoretical background, remote sensing techniques can be used to investigate the multifaceted nature of biodiversity. In this light, it is likely that remote sensing, benefitting from the integration with field-collected ecological data, will play a pivotal role in ecological and conservation sciences. As stated by Turner et al. in 2003, wishing for a future marked by the increasing collaboration between remote sensing experts and ecologists: “*The tools are there. Let us hope that users will soon follow*”.

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