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E VITA

ANALYSIS OF DIVERSITY PATTERNS OF NATIVE AND ALIEN SPECIES IN COASTAL PLANT COMMUNITIES: FROM LOCAL TO GLOBAL SCALE

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Table of contents

Supplementary Materials

Appendix A: Supplementary Materials to Chapter 1 - Diversity patterns of alien and native plant species in Trieste port area: exploring the role of urban habitats in biodiversity conservation

Appendix B: Supplementary Materials to Chapter 2 - Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline

Appendix C: Supplementary Materials to Chapter 4 - Disentangling plant diversity in sand dune ecosystems: a global perspective from patterns to processes

Abstract

Coastal ecosystems are deemed one of the most productive ecosystem in the world hosting habitat and species of great ecological and conservation values. As a direct consequence of urbanization and globalization, these ecosystems are undergoing several threats among which biological invasions represent one of major concern. A clear and comprehensive understanding of the invasion process in these habitats is still lacking; in this thesis, I explored the diversity patterns of native and alien species along with the main ecological determinants shaping coastal plant communities from local to global scale. In more detail, I investigated alien and native diversity patterns both in a disturbed site (Trieste port area) and in natural sites (northern Adriatic sand dunes habitats) at a local scale by using a probabilistic sampling design. Furthermore, I collated a global database of sand dune ecosystems consisting in 14,841 quadrats and phytosociological relevès across habitats and floristic kingdoms aiming at disentangling patterns of native and alien plant diversity and understanding which are their main determinants at the global scale. In urban areas, I found that habitat diversity enhances biodiversity and it could provide an effective filtering effect able to reduce the spread of alien species. For what concern natural ecosystems, my results highlighted the strong differentiation in community composition between native and alien species with the latter showing, on average, lower complementarity among habitats. Furthermore, in these habitats, the occurrence of alien species showed to be locally related to geomorphological variables and coastal dynamism more than climatic features. Additionally, functional traits reveal that alien species pool have higher values of performance-related traits such as Specific Leaf Area displaying also lower functional diversity. A potential signal of small-scale functional homogenization driven by the occurrence of alien species has been also detected, with deleterious effects for ecosystem functioning (loss of species endowed of unique traits composition and reduction in the functional space). The global scale study confirm that native species follow the well-known sea-inland gradient worldwide; on the contrary alien species show different patterns according to the floristic kingdom considered. The global model developed (Bayesian GLMM) confirmed that anthropogenic factors are the main drivers of alien species richness whilst native richness is explained by a combination of climate and habitat features. As a general conclusion, these findings suggest that in coastal environments plant diversity patterns remain constant across spatial scales, especially for native species: this is probably due to the same strong environmental gradients characterizing these natural ecosystems worldwide that make plant communities strongly spatially structured. In addition, a more diversified native community seem to cope better with alien species spread. Conversely, alien community does not present such a strong spatial structure both considering the species pool than the functional diversity patterns;

anthropogenic factors do play a key role in their spread both at local and global scale. At last, controlling and eradication programs may be planned where higher levels of alien β diversity are observed optimizing time and resources.

Riassunto

Gli ecosistemi costieri sono ritenuti tra i più produttivi al mondo e ospitano sia habitat che specie di elevato valore ecologico e conservazionistico. A causa dell'urbanizzazione e della globalizzazione, questo ecosistema è soggetto a diverse minacce tra le quali le invasioni biologiche rappresentano una delle maggiori fonti di preoccupazione. Una completa ed esaustiva comprensione del processo d'invasione in questi habitat non è ancora stata individuata; in questa tesi ho esplorato i pattern locali e globali di diversità di specie native ed aliene in comunità vegetali costiere assieme ai loro principali driver ecologici. In particolare, ho indagato alla scala locale i pattern di diversità usando un campionamento probabilistico per un sito disturbato (l'area portuale di Trieste) e per siti naturali (habitat dunali della costa settentrionale adriatica). Inoltre, ho prodotto un database aggregando 14841 plot e rilievi fitosociologici in ambiente dunale includendo dati sia relativi a diversi habitat che a differenti regni floristici con lo scopo di esplorare i pattern di diversità specifica vegetale in specie aliene e native a scala globale e di comprenderne i principali determinanti. Relativamente all'area urbana, ho osservato una elevata biodiversità in presenza di patch che ospitano comunità più naturali, le quali forniscono anche un efficace effetto filtro capace di ridurre la diffusione di specie aliene. Per quanto riguarda gli ecosistemi naturali, i risultati indicano la forte differenziazione nella composizione della comunità tra habitat per le specie native, al contrario le specie aliene mostrano mediamente una minore complementarietà. Inoltre, la loro occorrenza a scala locale, sembra essere più influenzata da variabili geomorfologiche e legate alla dinamica costiera che climatiche. Per di più, queste sembrano possedere un uso delle risorse più efficiente rispetto alle specie native, come evidenziato dall'analisi dei tratti funzionali, ma una minore diversità funzionale. Inoltre, le specie aliene, mostrano anche una maggiore ridondanza funzionale che, con l'aumentare della loro diffusione, potrebbe condurre la comunità nativa ad un'omogeneizzazione funzionale, con conseguente perdita di specie native dotate di tratti funzionali unici ed una riduzione della nicchia funzionale della comunità. Alla scala globale, specie native ed aliene mostrano pattern opposti rispetto all'habitat considerato. I modelli sviluppati (GLMM bayesiano) mostrano come fattori antropogenici possano essere considerati tra i principali driver di ricchezza specifica nelle aliene, mentre la ricchezza delle specie native sembra essere più influenzata da una combinazione di caratteristiche climatiche e di habitat. In conclusione, questi risultati suggeriscono che i pattern di

diversità sono costanti attraverso le diverse scale spaziali, specialmente per le specie native, principalmente negli ecosistemi naturali dove sono presenti forti gradienti ambientali. Di conseguenza, le comunità confermano di essere fortemente strutturate lungo i principali gradienti ambientali; inoltre, comunità più diversificate sembrano contrastare più efficacemente la diffusione di specie aliene. La comunità delle aliene mostra una minore complementarietà rispetto a quella delle native, queste specie infatti sono più ubiquitarie e meno strutturate spazialmente lungo questi gradienti ambientali considerando sia la composizione specifica che i pattern di diversità funzionale. I fattori antropogenici confermano di avere un ruolo chiave nella diffusione di specie aliene; i risultati ottenuti mostrano, dunque, che i programmi di controllo ed eradicazione possono essere pianificati ove una maggiore β diversità di specie aliene è osservata ottimizzando così sia tempo che risorse.

Core papers related to this thesis published or prepared in the course of the PhD

Paper 1

Tordoni E, Napolitano R, Nimis P, Castello M, Altobelli A, Da Re D, Zago S, Chines A, Martellos S, Maccherini S, Bacaro G (2017) Diversity patterns of alien and native plant species in Trieste port area: exploring the role of urban habitats in biodiversity conservation. Urban Ecosystems 20: 1151–1160. doi: 10.1007/s11252-017-0667-0

Paper 2

Tordoni E, Napolitano R, Maccherini S, Da Re D, Bacaro G Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline. (*Under review* in Ecological Research)

Paper 3

Tordoni E, Petruzzellis F, Nardini A, Savi T, Bacaro G Make it simpler: alien species decrease functional diversity of coastal plant communities (*Under review* in Journal of Vegetation Science)

Paper 4

Tordoni E, Bacaro G, Weigelt P, Janssen J, Acosta ATR, Bagella S, Bergmeier E, Buckley HL, Ciccarelli D, Forey E, Hennekens SM, Lubke RA, Mahdavi P, Peet RK, Peinado M, Sciandrello S, Kreft H Disentangling plant diversity in sand dune ecosystems: a global perspective from patterns to processes (*In prep.*)

Side papers published in the course of the PhD

Paper 5

Bacaro G, Maccherini S, Chiarucci A, Jentsch A, Rocchini D, Torri D, Gioria M, **Tordoni E**, Martellos S, Altobelli A, Otto R, Escudero CG, Fernandez-Lugo S, Fernandez-Palacios JM, Arévalo JR (2015) Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands. Community Ecology 16(2): 223-234. doi: 10.1556/168.2015.16.2.10

Paper 6

Bacaro G, Rocchini D, Diekmann M, Gasparini P, Gioria M, Maccherini S, Marcantonio S, **Tordoni E**, Amici V, Landi S, Torri D, Castello M, Altobelli A, Chiarucci A (2015) Shape matters in sampling plant diversity: Evidence from the field. Ecological Complexity 24: 37-45. doi: 10.1016/j.ecocom.2015.09.003

Paper 7

Simeone MC, Grimm GW, Papini A, Vessella F, Cardoni S, **Tordoni E**, Piredda R, Franc A, Denk T (2016) Plastome data reveal multiple geographic origins of Quercus Group Ilex. PeerJ 4: e1897. doi. 10.7717/peerj.1897

Paper 8

Bacaro G, Altobelli A, Camelletti M, Ciccarelli D, Martellos S, Palmer MW, Ricotta C, Rocchini D, Scheiner SM, **Tordoni E**, Chiarucci A (2016) Incorporating spatial autocorrelation in rarefaction methods: implications for ecologists and conservation biologists. Ecological Indicators 69: 233-238. doi: 10.1016/j.ecolind.2016.04.026

Paper 9

Marcantonio M, Martellos S, Altobelli A, Attorre F, **Tordoni E**, Ongaro S, Rocchini S, Da Re D, Chiarucci A, Bacaro G (2017) How does spatial scale affect species richness modelling? A test using remote sensing data and geostatistics. Annali di Botanica 7: 11-24. doi. 10.4462/annbotrm-13804

Preface

This thesis explores the diversity patterns of native and alien coastal plant communities along with the relationships with their ecological determinants across spatial scales (from a local to a global perspective).

In the introduction, I briefly discussed the coastal zone characteristics and, more in detail, the two ecosystems investigated throughout this thesis, namely disturbed coastal sites (as those occurring in urban areas) and natural sites (coastal sand dunes). Furthermore, I addressed the issue of biological invasion and community invasibility related to coastal ecosystems along with the main ecological drivers determining alien species spread and their impacts on native communities.

In the first thesis chapter, I explored the diversity patterns of native and alien species in Trieste port area focusing on the potential role of different urban ecosystems in coping with alien species spread (paper 1).

In the second chapter, I focused on sand dune environments; specifically, I assessed the diversity patterns of native and alien plant species and the main ecological drivers responsible for the occurrence of exotics (paper 2).

The third chapter explore the functional diversity patterns in coastal plant communities characterizing sand dune ecosystems, with a specific focus on the relationships between native and alien species (paper 3).

Finally, in the fourth chapter, a global scale analysis of species richness diversity patterns of native and alien plants in coastal environments along with their main ecological determinants was presented for the first time in the ecological literature (paper 4).

The final chapter provides a general overview and synthesis on the key findings across the four case studies of the thesis, linking them to the current ecological knowledge and suggesting also potential conservation actions and directions for future research.

General introduction

The coastal domain: a fragile environment under pressure

Coastal zones act as a bridge between the marine environment and the inland (Maun 2009) and are deemed the planet's most productive and valued ecosystems (Crossland et al. 2005). Global coastline length has been estimated in approximately 1.5 million km of which about 16% are constituted by sandy beaches (Martínez et al. 2013). Coastal ecosystems are widely distributed across the globe spanning from the polar regions to the tropics, encompassing a wide range of habitats (e.g. beaches, cliffs and saltmarshes, among others), climate and biomes (Snead 1972; Van der Maarel 1993a, b). In the last decades, there has been a steady increase in human population living close to the coastline (Curr et al. 2000; Brown et al. 2013) and, at present, about 41% of the global population is living within 100 km of the shoreline (World Resource Institute 2005). In addition, around 65% of cities with populations greater than 5 million along with larger urban settlements tend to be more concentrated in low elevation coastal zones (McGranahan et al. 2007). Furthermore, coastal zones are much more densely populated and exhibit also greater levels of population growth and urbanization (Small and Nicholls 2003; McGranahan et al. 2007; Smith 2011) compared to their surroundings. This is mainly attributed to historical and logistical reasons (e.g. trades and transports), to their ability to provide subsistence resources, and socio-cultural aspects (Neumann et al. 2015). For all these reasons, coastal zones are deemed one of the most disturbed areas in the world where humans are progressively acting with a greater rate of exploitation-related factors (e.g. eutrophication, pollution, land reclamation), that are increasingly impacting on the sustainability of the coastal environments (Crossland et al. 2005). Moreover, coastal ecosystems are undergoing tremendous environmental and socio-economic changes that are expected to increase in the near future. Among the several potential threats they are currently facing, it is worth to mention sea-level rise; an increase in extreme natural events such as inundations and storm flooding, enhanced coastal erosion, seawater intrusion into fresh groundwater, encroachment of tidal waters into estuaries and river systems, and elevated sea-surface and ground temperatures (McLean et al. 2001). Despite the major issues mentioned above, coastal zones host also habitat and species of great ecological and conservation values, especially in sandy beaches and dunes. These exhibit a great range of adaptations because of the complex interactions of atmospheric, marine, and terrestrial elements across the land-ocean boundary (Ibanez and Ducrotoy 2002). As pointed out in Maun (2009): "coastal zones are becoming increasingly topical (and politically sensitive) as they face relentless pressures from urban expansion, recreational development and sea level rise due to climatic change".

Coastal sand dune ecosystem

Coastal dunes are eolian landforms derived from sedimentary deposits that develop in coastal situations thanks to the interplay between water erosion and winds. They mostly originate from cliff and coastal erosion, sediments transported by river through overflow events along with input from tides and storm surges (Maun 2009). Despite the wind is the primary agent responsible for sand dune formation, vegetation also has an important role at finer spatial scale acting chiefly on wind features such as speed and direction, and in fixing the windblown sand grains (Danin 1996).

Several ecosystems services are provided by coastal dunes, it is worth to remind protection against erosion, waves and sea-level rise, water purification and storage, and socio-cultural services (Defeo et al. 2009; Everard et al. 2010; Barbier et al. 2011). Whereas these last aspects of sandy beaches are generally well acknowledged, minor attention has been paid to their great ecological diversity (both in terms of biodiversity than geomorphological and environmental heterogeneity; Martínez et al. 2008). Species vegetating in sandy beaches (*psammophytes)*, present special adaptations that allow them to survive in this extreme environment. For instance, their cells can tolerate higher salt concentration and the root system are generally deep and extensive with the capability to stabilize and enhance sand deposition, thus preventing or stopping inland dune migration. Furthermore, short life spans, presence of hairs, sclerophyllous or succulent leaves, and cushion-type or prostrated life forms allow them to survive in stressful conditions (Acosta and Ercole 2015). Accordingly, these ecotone environments host both habitat (e.g. more than ten habitats of community interest according to European Directive 92/43/EEC) and species of great ecological and conservation values such as keystone species and endemism; despite the species richness is quite low due to the harsh environmental conditions naturally present in these environments. Consequently, vegetation is often structured in a constant framework following a well-known sea-inland gradient, the so called "*zonation*", repeatable across sites and biomes reflecting their azonality features, regardless of species composition (Acosta et al. 2007; Ellenberg and Leuschner 2010). Unfortunately, these ecosystems are seriously threatened both by shoreline erosion (O'Shea and Kirkpatrick 2000) and habitat loss and fragmentation (EEA 2012) from one side and anthropogenic factors such as urbanization, trampling and touristic pressure (Buffa et al. 2012) on the other, to the point that a new term was coined (*coastal squeeze*, Defeo et al. 2009) to describe the current status of these environments. In addition, coastal sand dunes are also one of the most invaded ecosystems in Europe (Chytrý et al. 2008a). At last, it is worth to mention also the role that symbiotic association such as arbuscular mycorrhizas that enhance water and nutrient supply along with the aggregation of sand particles (Maun 2009). Their role in biological invasion is still controversial, indeed some results indicate facilitation of invasion whereas others its inhibition (see Shah et al. 2009 for a detailed literature review). All these aspects will be duly addressed below.

The sea-inland gradient

Coastal dunes are characterized by a well-known sea-inland gradient originated from the peculiar abiotic conditions occurring in a relatively small area. At a broader scale, climate-related factors (e.g. high summer temperature and droughts), solar radiation and dynamic geomorphological processes, among others, may be accounted for major drivers of species diversity (Forey et al. 2008; Rubio-Casal et al. 2010). At a finer resolution, several limiting factors can be listed among which it is worth to remind marine aerosol, salt spray, soil fertility, soil salinity, pH, and sand burial; with their effect strongly depending from the spatial localization on the beach (Oosting and Billings 1942; Clark 1986; Maun 2009). A shared definition of the habitats originating from the zonation (see below) has been proposed and applied at international scale and it has been used consistently in this thesis to classify and analyze sampled vegetation. The *drift line* and *upper beach*, that is the part of the beach closer to the sea, are generally characterized by great amount of organic matter (Sykora et al. 2003). These are also one of the most disturbed zones of the beach where storms and tides exert the strongest impacts. The species vegetating here (e.g. *Cakile maritima*), that are the first to start the sand accumulation process, are mostly annual, nitrophilous and very resistant to salt spray and disturbances in general being endowed of good dispersal ability, seeds dormancy and buoyancy (Grime 2006; Acosta et al. 2009). Major threats are represented by trampling, tourism and sand beach leveling for touristic purposes. *Mobile (shifting) dunes or "white dunes"* are mainly characterized by perennial plants specialized in withstand sand burial, sand accumulation and wind blasts (e.g. *Elymus farctus* and *Ammophila arenaria*). Establishment and survival is warranted by the production of adventitious roots such as rhizomes and stolons that facilitate their colonization and spread, these species have also a crucial role to build and stabilize sand dunes (Maun 2009). Along with the pressures cited above, this habitat is seriously threatened by shoreline erosion and biological invasions; indeed, it is the first zone where it is possible to find alien species ("exotic" or "non-native" species). *Fixed dunes or "grey dunes"* occurred right behind the shifting dunes where the substrate is more stable, thus hosting denser perennial communities thanks also to lower levels of marine aerosol and sand burial. Aridity represents the main limiting factor along with the high temperatures on the soil surface (Provoost et al. 2004), which however decline rapidly according to soil depth (Maun 2009). This can be considered among the most threatened habitat in Europe where the coastal squeeze is having the heaviest effects to the point that is deemed of priority importance according to EU regulations. Major concerns derive from touristic pressures, shoreline erosion, nitrification and biological invasions

(Acosta and Ercole 2015). The term grey dunes in Italy refers only to the habitat present in the north Adriatic coastline. *Interdunes* or *dune slacks* are humid or dry depressions characterized by sizeable fluctuations of table water during the year; on average, this habitat tends to host greater species richness compared to mobile dunes (Miller et al. 2010). *Saltmarshes* are constituted by wet habitats generally associated with tidal flats or salt pans that can be temporarily or permanently inundated by salty or brackish water. Salinity gradient is the major limiting factor; accordingly, plants have evolved specific adaptations to survive in this stressful habitat such as the capability to tolerate low soil water potential and to exclude or tolerate negative effects of toxic ions like Na+ (Munns 2002; Bazihizina et al. 2012). Vegetation characterizing this environment is mainly constituted by the so called *halophytes*, that is succulent Chenopodiaceae such as *Sarcocornia fruticosa*. These species cope with high salinity through different mechanisms; some accumulate salt in salt bladders (e.g. *Atriplex*), thus preventing its concentration in the mesophyll; others exclude it by means of roots or leaves (e.g. *Tamarix*). Furthermore, seeds can both germinate with high salt concentration or even remain viable until new inputs of freshwater are provided to the ecosystem (Khan and Gul 2002). Unfortunately, even this stress prone environment is subjected to biological invasions (e.g. Morais et al. 2012) and to the consequent biological alterations (e.g. Silliman and Bertness 2004). Thus, understating the diversity patterns of these coastal environments in the light of biological invasions is still a conundrum in plant ecology. To date, not many studies addressed this topic in a quantitative way and, above all, considering all the facets of both taxonomic and functional diversity (e.g. β diversity).

Alien species and the invasion process in plant communities

The concept of biological invasion date back since to Darwin (1859); however, it is only since Elton (1958) and, more recently, thanks to the seminal papers written by Richardson and Pyšek, among others, that this field has become one of the more cutting-edge branch of modern plant ecology (Hulme et al. 2013). Due to the increase of interest in this topic, the need of shared terminology among scientists was crucial. Great efforts have been made in this sense by Richardson et al. (2000) and Pyšek et al. (2004). Table 1 schematically reports the substantial and internationally adopted terminology after Richardson et al. (2000) and Pyšek et al. (2004). An alternative classification is based on residence time, and it groups alien species in archaeophytes and neophytes (introduced before or after ca. 1500, respectively; Pyšek et al. 2004). It has been widely recognized that biological invasions represent one of the main threats to global biodiversity, second only to habitat loss and fragmentation (Sala et al. 2000; Millennium Ecosystem Assessment 2005). Biological invasions have been observed for different taxa such as vascular plants (e.g. Vitousek et al. 1997; Kühn and Klotz 2006), vertebrates (Jeschke and Strayer 2005) and even viruses (La Deau et al. 2007).

Species type	**Definition**
Alien species	Plant taxa resulting from intentional or accidental human introduction in a given area, according to their invasion status
Casual species	Plant taxa not forming self-sustaining populations, human-mediation needed
Naturalized species	Plant taxa forming self-sustaining populations without direct human intervention
Invasive Alien Species (IAS)	Naturalized species that may spread far away from their parent plants, producing large number of propagules and having also the potential capability to alter ecosystem features

Table 1 Glossary providing used terminology in this thesis (after Richardson et al. 2000; Pyšek et al. 2004)

Species have been migrating and spreading and new introduction were common since ages, however, worldwide globalization allowed the blast of several pathways of introduction and exponentially increase the rate of invasion according to trades and transport network development (Hulme 2009). For instance, in the Galápagos Islands, the rate of invasion was estimated in one new vascular plant species approximately every 10000 years on average, to date this rate is about 1.2 species per year (Tye 2006). Saul et al. (2017) showed that intentional pathways of introduction such as ornamental horticulture are the dominant ones in two major IAS databases (IUCN’s Global Invasive Species Database and the DAISIE European Invasive Alien Species Gateway, respectively) for plants and vertebrates, moreover global patterns in the distributions of IAS are determined by the role of colonial history, economic development and trades (Turbelin et al. 2017). Propagule pressure, that is the number of individuals (or viable propagules) released into a region where they are not native (Lockwood et al. 2005), is strongly related to the presence of human-disturbed habitat such as urban areas (Aronson et al. 2014), gardens (Mayer et al. 2017), roads (Bacaro et al. 2015) or any factor related to human presence or activities in general (O'Shea and Kirkpatrick 2000; Thuiller et al. 2006). Generally, the invasion process is conceptualized as a “*continuum*” (Richardson and Pyšek 2012), constituted by a series of filters through which a species must pass through (arrival with a lag phase

– invasion – consolidation). The position of a species along the continuum is dynamic and, above all, it is worth to highlight that is more a population than the proper species that can be deemed invasive (e.g. Essl et al. 2009 for *Ambrosia artemisiifolia* invasion history in Central Europe). Biogeographical and climate constraints have been claimed among the major drivers of alien species at global scale (Richardson and Pyšek 2012), hence on average islands are more invaded than mainland since tend to harbor more exotics both per unit area and as a proportion of total species richness (Lonsdale 1999; but see Vilà et al. 2010); undisturbed tropical forests are less invaded than temperate mainland regions (Rejmánek et al. 2013); mesic environments seem to be more susceptible than extreme ones with some exceptions; within temperate region, there is a decrease in naturalized species with latitude along with an increase according to their geographical ranges (Sax 2001). Other factors related to invasion include landscape heterogeneity (Deutschewitz et al. 2003), spatial patterns (Van Rensburg et al. 2002; Davies et al. 2005), and geomorphological processes (Dimitrakopoulos et al. 2017). At a finer scale, three main features have been claimed as the major responsible of plant invasion: resource availability (e.g. Davis et al. 2000; Stohlgren et al. 2006); disturbances (chiefly for the establishment process, Davis and Pelsor 2001; Leishman and Thomson 2005), propagule pressure along with the interactions with resident biota such as competition, mutualism and herbivory (Lockwood et al. 2005; Leishman et al. 2014). Taylor et al. (2016) suggest that propagule pressure may become less important than biotic interactions as invasions proceed along the continuum. Minimum residence time has been also accounted for invasion extent at regional scale (Wilson et al. 2007; Pemberton and Liu 2009). Additionally, habitat features play also a crucial role in determining the level of invasion at this scale as observed for European flora (Chytrý et al. 2008a, b). Specifically, anthropogenic and coastal habitats host the greatest proportion of aliens showing greater composition similarity within regions than across habitats. However, it has been clearly established by several studies that the invasion rate and extent is strongly context-dependent (e.g. Daehler 2003; Funk et al. 2016) resulting from the interplay among several drivers that increase the performance of IAS over that of native species (Rejmánek et al. 2013). Under a functional point of view, in general exotics tend to have larger size, higher growth rate and higher values of resource-acquisition traits such as Specific Leaf Area. They have also higher C input (Van Kleunen et al. 2010) and transpiration rates (Funk 2013). All this, associated with thinner leaves and less amount of structural carbohydrates, reduces energetic costs given the same growth rate warranting a more rapid response to unforeseen events. In addition, according to the so called leaf economics spectrum (LES, Wright et al. 2004), IAS seem to be prone to a “fast-return” strategy (Penuelas et al. 2010; Funk 2013). Although relationships between alien and native species can be mainly explained by Stohlgren’s theory (Stohlgren et al. 2006) and Davis’ theory of community invasibility (Davis et al. 2000), it exists a so called “invasion paradox” (Fridley et al. 2007) where the relationship between native and alien species seems to vary across spatial scales, specifically negative at neighborhood scales whilst positive at the landscape or biome scale. Furthermore, competitive inhibition of IAS increases with their functional similarity to resident abundant species (Hooper and Dukes 2010) and the potential effect of an invader in the recipient community increase according to its abundance and functional distinctiveness (how much of its functional niche diverge from those of the native community, Strayer et al. 2006); this issue will be thoroughly investigated in the third chapter of this thesis. Given the pervasive nature of alien species and the variety of potential damaging effects on recipient ecosystems, it is mandatory to fully comprehend the patterns and mechanisms responsible of the alien plant invasion. This is the main topic and the more general research question that I tried to answer in this thesis.

Main impacts on natural ecosystems

In general terms, alien species have strong impacts on ecosystem services and socio-economic sectors in particular in agriculture, fisheries and forestry (Pimentel et al. 2001), for instance only in Europe this cost has been estimated in ca. 12.5 € billions/year (Kettunen et al. 2008). Other consequences consist for instance in direct loss of crops and reduced yields (direct costs) or reduction in ecosystem services (indirect costs to natural, societal or cultural values). Furthermore, there are also some direct impacts on human health (e.g. allergic reactions and injures through stinging or biting) and indirect ones (e.g. vectors for diseases). For what concern natural ecosystems, patterns and extent of alien species are generally poorly documented (McGeoch et al. 2010). These have strong negative effects as already demonstrated in some studies (e.g. Vilà et al. 2011) chiefly modifying species composition, reducing native species richness and β diversity (Stohlgren et al. 2006; Hejda et al. 2009; Powell et al. 2011; Socolar et al. 2016), thus leading the native community to a potential biotic homogenization (e.g. Lososová et al. 2012; La Sorte et al. 2014 but see Moles et al. 2012) and to an increase in species pool similarity (Winter et al. 2009) through the loss of β diversity that is often associated with the simultaneous extinction of specialist native species and the gain of exotic or generalist native species (McCune and Vellend 2013). Main consequences of biotic homogenization could imply the potential loss of adaptive potential along with reduced resilience to disturbances (Olden et al. 2004). Another issue derives from the so called "invasion debt", that is the time delayed invasion of species already introduced to a region (Seabloom et al. 2006; Essl et al. 2011; Rouget et al. 2016) so that the full invasion potential of an alien species may be completely realized only after many decades. In addition, IAS can even influence abiotic factors in a site; hence, the most dangerous exotics are the "transformers" (Richardson et al. 2000), these represent around 10% of the IAS and have the capability to alter ecosystem features. For instance, IAS can alter flux rates of ecosystem through greater litter decomposition compared to natives thus increasing N fluxes (Ehrenfeld 2010; Wang et al. 2015). They generally have also higher biomass, therefore taller plants change light and moisture regimes and create thicker layers, even though habitat physical alterations are mostly due to size, morphology, and density (Davis 2009). In addition, these have even the capability to change the disturbance regimes such as fire regime (Brooks et al. 2004) and flooding regime (Catford and Jansson 2014). In sand dune environments, not all habitats suffer the same level of invasion hosting mainly neophyte species (Carboni et al. 2010). Probably, the main cause of the high invasibility of these ecosystems might be related to the strong propagule pressure undergoing in these habitats that is generally associated with anthropogenic factors such as urbanization and tourism (Malavasi et al. 2014).

Coastal urban ecosystem

Nowadays, urbanization is occurring rapidly and it is deemed one of the biggest threat to the coastal environment (see for instance Lee et al. 2006 for a coastal wetland). Since the emergence of cities, the growing urban context has gradually lead to long-term environmental changes (Kaniewski et al. 2013). Currently, urbanization is claimed as one of the primary driver of habitat loss (McKinney 2002); hence, urban sprawl often may modify habitat configuration and connectivity potentially impacting also species dispersal (Bierwagen 2007). In addition, it could lead to biotic homogenization of resident communities (McKinney 2006; Kühn and Klotz 2006; Socolar et al. 2016) reducing their complementarity (e.g. β diversity, La Sorte et al. 2014). However, recent studies showed off that recently established exotics may account for higher β diversity than natives (Ricotta et al. 2012 considering phylogenetic β diversity; Martin and Wilsey 2015 for a tallgrass prairie), suggesting a short-term process of heterogenization before the proper establishment. For a long time, urban areas have been recognized as environments of low ecological values and poor in species richness (Guneralp and Seto 2013). However, recently it has been observed how natural habitats can persist in highly human-affected areas (Kühn et al. 2004; Cornelis and Hermy 2004; Alvey 2006; Aronson et al. 2015), even hosting species of great conservation value (Gustafsson 2002; Vähä-Piikkiö et al. 2004; Rebelo et al. 2011). As highlighted in McKinney (2002), plant species vegetating in urban environment can be classified in three major recognizable classes. *Urban avoiders* that is those species that are very sensitive to human disturbances and habitat destruction and, therefore, they are also the first that tend to disappear (e.g. late-successional taxa). *Urban adapters* intended as those species, such as early-successional ones coming from nearby ecosystems, that are endowed of peculiar features that make them well suited to cope with stresses (e.g. wind-pollination, scleromorphic leaves; Knapp et al. 2008). Accordingly, it has been observed that urban habitats are primarily colonized by ruderals species (*sensu* Grime's CSR classification, Grime et al. 1988) that are generally highly resistant to disturbances (intended as "the mechanism which limits plant biomass by causing its partial or total destruction", Grime 2006), and tend to be characterized by short life-spans (generally annual or short-lived perennial), early flowering strategy along with large seed production (Deutschewitz et al. 2003; Kühn et al. 2004; Grime 2006). Therefore, as pointed out in Ricotta et al. (2017), pre-adaptations to disturbed anthropogenic habitats is a key feature that contribute to the early introduction into similar habitats in other regions. At last, *urban exploiters* represent a peculiar class of species that are often dependent to human resources. Plant species belonging to this group tend to be extremely resistant to several limiting factors such as pollution, trampling, and to the high level of aridity due to the presence of hard surface that may promote run off. Species belonging to this class has been claimed as the most homogenized biota in the world for what concerns birds and butterflies (Blair 2001). Due the great heterogeneity of urban habitats (Ortega-Álvarez and MacGregor-Fors 2009) and the contemporary presence of increasing availability of long-distance anthropogenic vectors for dispersal, cities often represent the introduction epicenters for alien plant species (e.g. Vitousek et al. 1997; McLean et al. 2017) and one of the most invaded ecosystem in the world making these ecosystems prone to biological invasions (Pyšek et al. 1998; Shochat et al. 2010). Further concerns derive from human-related activities in the shoreline, mainly for touristic purposes such as land reclamation and engineering structures (e.g. sea walls, groins, breakwaters; Burke et al. 2001). All this can modify sediment supply and transport along the coastline, resulting in increased local and displaced erosion (e.g. Pethick 2001; Nordstrom et al. 2009). Therefore, the encroachment of human facilities has dramatically reduced the space for natural landforms and vegetation; consequently, environmental gradients have been largely truncated, fragmented or compressed (Buffa et al. 2012).

Aims

Due to the numerous pressures occurring in coastal zones worldwide along with the contemporary presence of numerous habitats and species of great ecological and conservation values, these ecosystems represent perfect model systems to study the complex interactions between native and alien species and the main mechanisms of invasibility in the communities under investigation. Moreover, for the reasons explained above, there is also a constant need to update the conservation status of these environments. This thesis aims at providing a better comprehension of ecosystem functioning in coastal environments from local to global scale, by achieving the following general goals:

1) The first general aim is to understand diversity pattern of native and alien plant species in disturbed coastal plant communities (Chapter 1, Appendix A). Specifically, I aim at:

a) exploring diversity pattern in an urban coastal site like Trieste port area;
b) focusing on the potential role of urban ecosystems and urban green areas in buffering alien species spread; given that cities and port areas in particular, are often the starting point of the invasion process.

2) The second general aim is to analyze plant diversity patterns in natural sites such as sand dune ecosystems considering both taxonomic (Chapter 2, Appendix B) and functional features (Chapter 3). In particular, the following specific aims were addressed:

a) assess diversity patterns in sand dune ecosystems of northern Adriatic coastline and explore the relationships between native and alien species along with the main drivers of species diversity in the light of biological invasions;
b) investigate the functional aspects of sand dune communities for what concerns both functional traits and functional diversity testing also a potential signal of functional homogenization caused by alien species.

3) The third general goal is to grasp the global patterns of plant species diversity in coastal habitats (Chapter 4, Appendix C). To do so, a global plant database has been collated and analyzed with the following specific aims:

a) explore the global patterns of native and alien plant diversity on coastal sand dune ecosystems across habitats and floristic kingdoms;
b) detect the main environmental and anthropogenic determinants of the variation in species richness in native and alien species in these ecosystems and their relationships.

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Chapter 1

Diversity patterns of alien and native plant species in Trieste port area: exploring the role of urban habitats in biodiversity conservation

Tordoni E, Napolitano R, Nimis P, Castello M, Altobelli A, Da Re D, Zago S, Chines A, Martellos S, Maccherini S, Bacaro G (2017) Urban Ecosyst 20: 1151–1160. doi: 10.1007/s11252-017-0667-0

Abstract

Nowadays, urban areas play a crucial role in biodiversity conservation and habitat protection despite the constant pressures on which these habitats are subjected. They may even host relatively new plant communities due to the peculiar ecosystem where they vegetate. The port of Trieste (NE Italy) is characterized by a mixed mosaic of intensely human impacted areas (where commercial activities are still ongoing) flanked by abandoned areas where vegetation persists or has spontaneously recovered. In this study, we sampled the whole port area through a stratified random sampling by placing multiscalar nested plots in four different habitats (*strata*) previously identified by photo-interpretation. Plant species richness and abundance were assessed in each plot. Each species was then classified as native or alien and patterns of species richness and complementarity were compared among habitats. Results show that there is a significant difference in species richness patterns among habitats, while observed patterns are likely to vary at different spatial scales. As expected, urban plots account for most of the alien species in the sampling, while wooded plots cope better with invasion, accounting for a lower alien/native ratio. These results highlight how habitat diversity enhances biodiversity in urban areas and how it could provide an effective filtering effect able to reduce the spread of alien species. In addition, we provide further evidence for the use of multi-scale approaches in order to study the complex relationships between spatial heterogeneity and plant species richness.

Keywords: Alien species, Quantitative methods, Rarefaction curves, Spatial scale, Species richness, Urban flora.

Introduction

Nowadays, urbanization is occurring at a rapid pace being deemed as one of the main causes of biotic homogenization (McKinney 2006; Kühn and Klotz 2006), also affecting local alpha and beta-diversity (Socolar et al. 2016). Urban ecosystems evolve over time and space, emerging as the outcome of dynamic interactions between socio-economic and biophysical processes operating over multiple scales. To date, preserving large, intact areas of natural habitat is a key means for preserving biodiversity. However, this may not be feasible in highly urbanized territories, where there is little natural habitat available. For a long time, urban areas have been seen as degraded environments, characterized by species of low ecological value where natural ecosystems are usually absent (Guneralp and Seto 2013). However, in the last decade, several studies demonstrate how small and fragmented natural habitats can persist in highly human-affected areas, accounting for relatively high levels of biodiversity in terms of species richness (Kühn et al. 2004; Cornelis and Hermy 2004; Alvey 2006; Aronson et al. 2015). It has already been highlighted how urban environment may host species of local or regional conservation value (Rebelo et al. 2011; Vähä-Piikkiö et al. 2004) and even red-listed plant species (Gustafsson 2002). A significant variation in these patterns has been observed both across cities (Kühn et al. 2004; Aronson et al. 2014) than within cities (Sushinsky et al. 2013, Beninde et al. 2015). Urban ecosystems are characterized by a high heterogeneity, which is attributable to the presence, in a small extent, of different land uses (Savard et al. 2000, Ortega-Álvarez and MacGregor-Fors 2009). Moreover, it has been observed that some taxa are able to form atypical assemblages in cities, as species which are typical of different ecosystems coexist in an "artificial" environment (McKinney 2006). Consequently, these remnants can be easily considered as "hotspots" for species richness (*sensu* Knapp et al. 2008; Croci et al. 2008) and, accordingly, for biodiversity conservation compared to their rural surroundings. Nevertheless, human-altered environments, such as cities, are more often the introduction epicenters for alien plant species, in particular for Invasive Alien Species (hereafter IAS, Vitousek et al. 1997, Pyšek 1998). High human pressure and the contemporary presence of numerous pathways of introduction and spread (e.g. transport, human activities) alongside other factors such as "heat island effect", ensure a high dispersion rate of the propagules and the reduction of competition with native species, making these ecosystems prone to biological invasions (Hulme 2003; Chytrý et al. 2008; Bacaro et al. 2015). Within urban environments, port areas represent preferential places from where alien species move into new ecosystems, as shipping routes represent one of the main pathways of introduction and colonization (Molnar et al. 2008; Adhikari et al. 2015). The IAS in port areas have been extensively explored with regard to the introduction of marine species, especially fish and jellyfish (e.g. Galil 2000; Bax et al. 2003) while few descriptions of patterns and distributions of plant IAS are reported in these peculiar areas. Considering the strong dependence between biodiversity metrics such as species richness and spatial scale (Wiens 1989; Crawley and Harral 2001; Stohlgren 2007), a multiscalar approach should be applied in the analysis of biodiversity patterns. As far as we know, this relationship is not constant and varies with both spatial grain (the size of the sampling unit) and spatial extent (the maximum distance among them, or simply the extension of the study area), as pointed out by Rahbek (2005), among others. In the last two centuries, Trieste (NE Italy) has developed behind its harbor, wedged in the foothills of the Karst plateau. The singularity of Trieste's port area lies in its conformation. It is a mixed mosaic of intensely human impacted areas (where commercial activities are still ongoing) flanked by abandoned patches, where vegetation has been naturally restored. For these reasons, it can be considered an interesting environment where to assess biodiversity patterns within urban area, with a special focus on alien species component of plant communities. As a consequence, the main aims of this paper are: i) to investigate the plant diversity in the Trieste port area through quantitative methods; ii) to explore diversity patterns of native and alien species and assess their relationships within this environment. Both objectives aim at describing the important role of urban ecosystems and their mosaic as biodiversity hotspots, as well as highlighting their possible role in the context of plant invasion mechanisms.

Materials and methods

Study area

Vegetation data used in this study were collected in the port area of Trieste (centroid coordinates: 45.6640° N-13.7987° E, *datum*: WGS 84); the whole sampling area covers a surface of 3.48 km^2; being located at sea level (Fig. 1). The main natural vegetation types recognizable in the surveyed green areas of the port may be attributed to a Mediterranean scrubland. They correspond to the phytosociological class *Quercetea ilicis* in the northernmost portion, while in the southern part, which is characterized mostly by marine clays and silts, there are remnants of an old wetland, which was reclaimed after the Second World War to build part of the current industrial area of Trieste. Here it is possible to find fragments of the typical vegetation of salt marshes (closer to the sea) and swamps, which belong to classes *Juncetea maritimi*

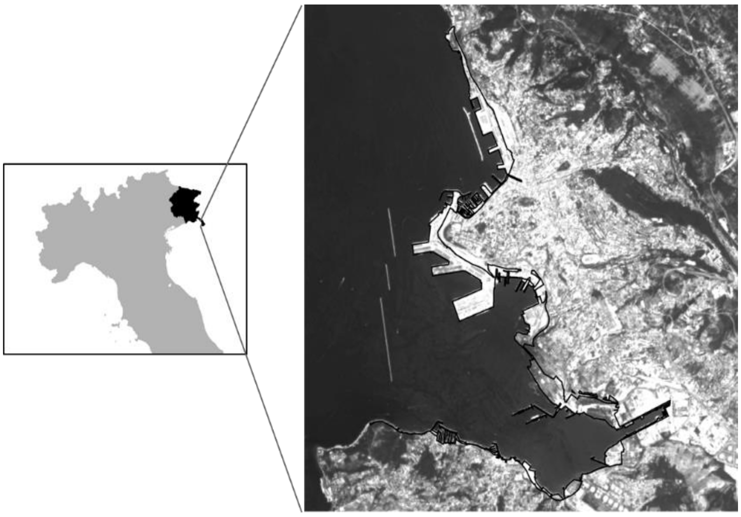

Fig. 1 Satellite image representing the city of Trieste (right part). Black line represents the perimeter of the study area (Port Area)

and *Phragmitetea,* although plant communities are severely altered by the high anthropic pressure and the strong modifications of habitats and soils.

Sampling Design and Data Collection

Vegetation data were collected by means of a probabilistic sampling. Specifically, the sampling design was based on a hierarchical stratified random sampling. At first, manual photo-interpretation and digitalization of the whole port area was performed using regional orthophotos (year 2011, spatial resolution 50 cm, source IRDAT FVG). Then the sampling area was classified by habitat type (four classes: urban, meadow, shrubland and woodland), later verified on the field. The urban habitat encompasses those environments that are typical of cities, such as roadsides, railway lines, brownfields and all those niches where human pressure is higher. The identification of the other three habitats was based on the percentage of the vegetation cover (later verified on the field). The selection of sampling units worked as follows: firstly, a grid of 1 x 1 km was superimposed to habitat map of the port area. Subsequently, a total of 100 random sampling units (plots) were selected, with the number of sampling units being proportional to the area of habitat types in each grid cell. This sampling procedure ensures a representative coverage of the whole territory, avoiding sampling points to be clustered. Each sampling unit was identified in the field by means of a high precision GPS (Leica Nexteq T6, accuracy < 2 m). A nested multiscalar plot with four spatial scales (linear dimension: 0.5 m, 1 m, 2 m, 4 m) was then materialised in the field and the vegetation was sampled. The complete inventory of plant species occurring in each sampling unit was listed for each plot scale along with the percentage coverage of each species (visual estimate) for the largest spatial scale (16 m^2). Data were collected during the period June-September 2015. Nomenclature and taxonomy follow Pignatti (1982) and Conti et al. (2005). All species were classified as native or alien, according to the inventory of the Italian alien flora (Celesti-Grapow et al. 2009). Moreover, alien species were further classified into archaeophytes and neophytes (introduced before or after ca. 1500, respectively; Pyšek et al. 2004).

Analysis of Plant Diversity Patterns for Alien and Native species

Differences in plant species richness (for both alien and native) were statistically evaluated for each plot scale and habitat using non-parametric Kruskal-Wallis rank sum test. Where the test resulted significant, an adjusted *posteriori* pairwise comparison was performed (using the “kruskalmc” function in the R package “pgirmess”; Giraudoux 2016). Plot-based rarefaction curves (hereafter SAC, Gotelli and Colwell 2001) were computed at each spatial scale, considering the whole dataset and native and alien species separately. The analytic solution proposed by Kobayashi was used (1982, for details see Chiarucci et al. 2008) using the R “vegan” package (Oksanen et al. 2016). For an analysis of spatial autocorrelation in the species distribution patterns, SACs were compared with Spatially-Constrained Rarefaction curves (hereafter SCR, Chiarucci et al. 2009; Bacaro et al. 2012) using the R code provided in Bacaro et al. (2012) which allows to consider spatial autocorrelation of the samples in the calculation of rarefaction curves. This recent methodology proved to be more effective in comparing biodiversity patterns among areas with different extent (Bacaro et al. 2016). The ratio between the plot-based rarefaction curve of alien and native species was finally calculated and used to describe how patterns of these two groups vary among plots for an increasing sampling effort. All spatial scales were analyzed in this way. Species diversity patterns were also compared using additive partitioning techniques (Lande 1996; Gering et al. 2003, Crist et al. 2003): partition of alpha, beta and gamma diversity elements across different scales (plot scale, habitat scale and whole sampling area) was performed for each group (native and alien species). Each of these diversity component, was expressed as a proportion of the total species richness. For calculation of diversity elements at different spatial scales, samples were nested from lower hierarchical level within higher units, so that the spatial component increases constantly from i=1 to i=*l*, where *l* is the spatial scale investigated. Species richness in the whole sampling area was partitioned into the inventory diversities at the various spatial scales (α plot, α habitat), that added up to the differentiation diversities for the corresponding spatial scales (β plot, β habitat), give the total diversity of the whole sampling area (γ). According to the above, $\bar{\alpha}$ reflects the average diversity found within plots. Values at higher sampling levels have been obtained as:

$$\beta_l = \gamma - \bar{\alpha}_l \qquad [1]$$

where *l* are the levels of sampling with samples in lower hierarchical levels nested within higher level units. For each lower sampling level as:

$$\beta_i = \alpha_{i+1} - \alpha_i \qquad [2]$$

Finally, additive partition was calculated as:

$$\gamma = \alpha_i + \sum_{j=i}^{l} \beta_j \qquad [3]$$

Departures from random expectations of species richness values were evaluated through null model testing, according to a nested hierarchical sampling design. 999 permutations of the raw matrix were performed to assess significance in the deviation from randomness in the observed patterns. In term of species assemblages, plot-to-plot differences in species composition for the whole recorded set of species and for the alien group alone were analyzed using the Non-metric MultiDimensional Scaling procedure (hereafter NMDS; Kruskal and Wish, 1978); it is worth to remind that this analysis may be quite sensitive to the input parameters and few changes may lead to quite different patterns. Before performing NMDS, abundance data were log-transformed and the Bray-Curtis dissimilarity metric was calculated. All statistical analyses were conducted using R 3.3.2 (R Foundation for Statistical Computing, Vienna, Austria) except NMDS, that was computed using Primer 6 software (Clarke and Warwick, 2005).

Results

In total, 234 species were collected: 203 native species (86.75% of the whole sample) and 31 alien species, corresponding to 13.25% of the total species richness (according to Celesti-Grapow and Accogli 2010, the Italian national average is 13.4% whereas the percentage for the Friuli Venezia Giulia Region is 11.6%). Mean species richness values at different spatial scales are shown in Table 1. The most represented Families were *Poaceae* (18%), *Asteraceae* (17%), *Fabaceae* (12%) and *Rosaceae* (7%). *Dactylis glomerata* subsp. *glomerata* was the most frequent species (62% of the sampled plots), followed by *Rubus ulmifolius* (60%) and *Daucus carota* subsp. *carota* (55%). Among alien species, the most abundant were *Sorghum halepense* (27%), *Robinia pseudoacacia* (26%), *Senecio inaequidens* (25%) and *Ambrosia artemisiifolia* (18%).

Species Group	Plot linear dimension			
	0.5 m	1m	2 m	4m
Total	4.40 ± 2.2	6.50 ± 3.2	9.10 ± 4.2	13.5 ± 5.7
Native	3.85 ± 2.1	5.68 ± 3.0	7.90 ± 4.0	11.7 ± 5.3
Alien	0.54 ± 0.7	0.81 ± 0.9	1.20 ± 1.1	1.80 ± 1.4

Table 1 Species richness (Mean ± SD) at each spatial scale considering all species pooled and for native and alien species separately

Neophytes comprise 26 taxa (11.11%) and Archaeophytes 5 taxa (2.14%). Most aliens have American (53.33 % of the total alien flora) and Asiatic origin (30 %). Table 2 shows proportional representations of aliens, archaeophytes, neophytes and their ratio in city floras of Italy for which published data are available. Species richness strongly varied according to habitat, group and spatial scale (Table 3). For the whole species pool, comparisons of the mean ranks between habitats at larger scale showed that species richness is not significantly different ($\alpha = 0.05$) when urban habitat is compared to meadow (observed rank mean difference= 17.8; $p > 0.05$). Conversely, statistical differences were observed when woodlands and shrublands were compared to meadow, (observed mean difference woodlands *vs* meadows= 17.27, $p < 0.05$; shrubland *vs* meadow = 19.12, $p < 0.05$). At the smallest spatial scale (0.25 m^2) Kruskal-Wallis resulted significant (χ^2 (3) = 10.97, $p = 0.01$) with meadow *vs* urban habitat showing significant differences (observed rank mean difference = 26.66; $p < 0.05$). No differences were observed among habitats at the intermediate spatial scales (1 and 4 m^2). With regard to native species, we observed a significant result just at the smaller spatial scale where there is a difference among plots in meadow and urban habitat (observed rank mean difference = 27; $p < 0.05$). Alien species show significant differences outputs just at 16 m^2 and 4 m^2 and in both cases the difference was detected between woodland and meadow (observed rank mean difference is 23.4 and 19.6, $p < 0.05$, respectively).

City	Population	% Al	% Arch	% Neo	Ratio	Source
Ancona	101,331	11.9	4	7.9	0.51	Celesti-Grapow and Blasi (1998)
Cagliari	154,422	11.9	4.3	7.6	0.57	Celesti-Grapow and Blasi (1998)
Milano	1,344,906	25.6	4.2	21.4	0.20	Celesti-Grapow and Blasi (1998)
Palermo	674,565	14.3	4.7	9.6	0.49	Celesti-Grapow and Blasi (1998)
Roma	2,867,143	12.4	4.3	8.3	0.52	Celesti-Grapow and Blasi (1998)
Trieste	204,419	13.36	2.26	11.10	0.20	Martini and Altobelli (2009)
Trieste (port area cells grid)	-	15.10	2.56	12.54	0.20	Martini and Altobelli (2009)
Trieste (port area)	-	13.25	2.14	11.11	0.19	Present study

Table 2 Proportions of alien species, archaeophytes, neophytes and their ratio in city floras of the Italian peninsula for which published data exist. (Al: Alien, Arch: Archaeophytes, Neo: Neophytes)

Group	Plot linear dimension			
	4 m	2 m	1 m	0.5 m
Total	$\chi^2(3) = 9$*	$\chi^2(3) = 5$ ns	$\chi^2(3) = 8$ ns	$\chi^2(3) = 10$**
Native	$\chi^2(3) = 7$ ns	$\chi^2(3) = 4$ ns	$\chi^2(3) = 7$ ns	$\chi^2(3) = 10$***
Alien	$\chi^2(3) = 10$**	$\chi^2(3) = 10$*	$\chi^2(3) = 3$ ns	$\chi^2(3) = 1$ ns

Table 3 Output of the Kruskal Wallis test at each spatial scale for each species group (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant)

The highest values of species richness, considering all species pooled, have been detected in meadows and woodlands, and the same pattern has been confirmed also for native species. Conversely, alien species tend to have higher species richness in urban plots as expected even though meadows show similar values as well. SCR and SAC present similar patterns for each spatial scale (Fig. S1 in Appendix A for a comparison between SCRs and the classic rarefaction curves). The lack of any asymptotic trend characterizes all curves. The spatial scale of analysis does not affect patterns in species accumulation even when native and alien species are analyzed separately (Fig. 2), although SAC for alien species reach an asymptotic trend, which means that, on average the majority of the alien species pool in the sampled area have been sampled.

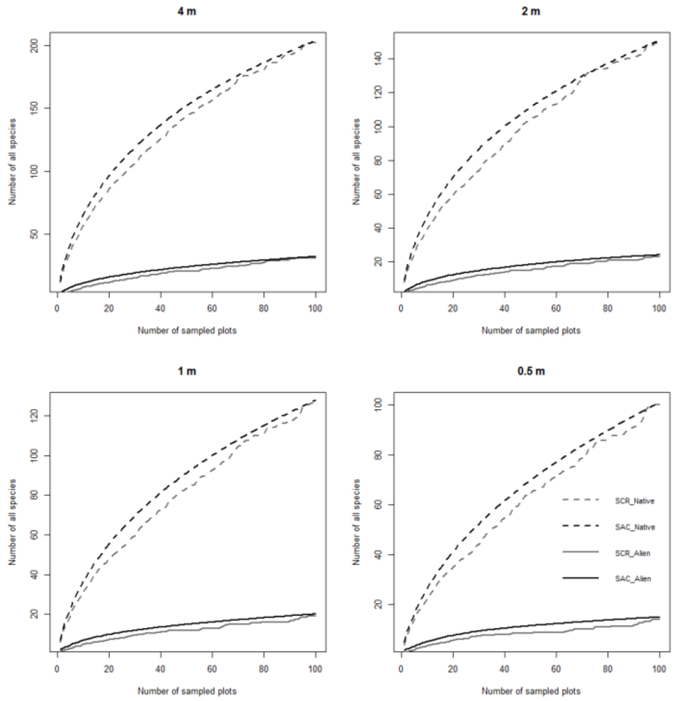

Fig. 2 Spatially-Constrained Rarefaction curves (SCR) and classical rarefaction curves (SAC) comparing native and alien species for each spatial scale investigated

When rarefactions were calculated for each habitat considering all the species pooled, observed patterns slightly differ according to scale (Fig. 3). In particular, it is worth noting as the woodland curve lies above the others at larger scales (but below at lower scales) and the urban curve is higher than shrubland curve at smaller scales. All SCR curves fall below the SAC (Fig. S2, S3; Appendix A), indicating that plant communities are spatially autocorrelated despite habitats being prone to fragmentation effects. The ratio between native and alien rarefactions results in slightly different outputs: this pattern varies among scales even though a general trend can be observed (Fig. 4). At the smallest scale, we can observe a smaller ratio that can be explained by the fact that less alien species are sampled by chance, given their low number in proportion to native species. On an increasing plot scale, a higher ratio occurred, with values more closely related to the actual rate of invasion expected for the region. Diversity element proportion (α and β) increased according to increasing grain sizes. All calculated values were significantly different from random expectations, meaning that these elements are highly spatially structured. When considered separately, native and alien diversity patterns were constant across scales (Fig. S4, S5; Appendix A). The partition of diversity according to habitat (Fig. 5) shows that urban environment accounts the highest proportion of alien species diversity at the plot level (α plot) for each scale investigated; on the contrary, woodland and shrubland habitats have the smallest mean percentage in aliens. It is worth noting how urban the habitat hosts a high proportion of native species compared to other environments considered in this study.

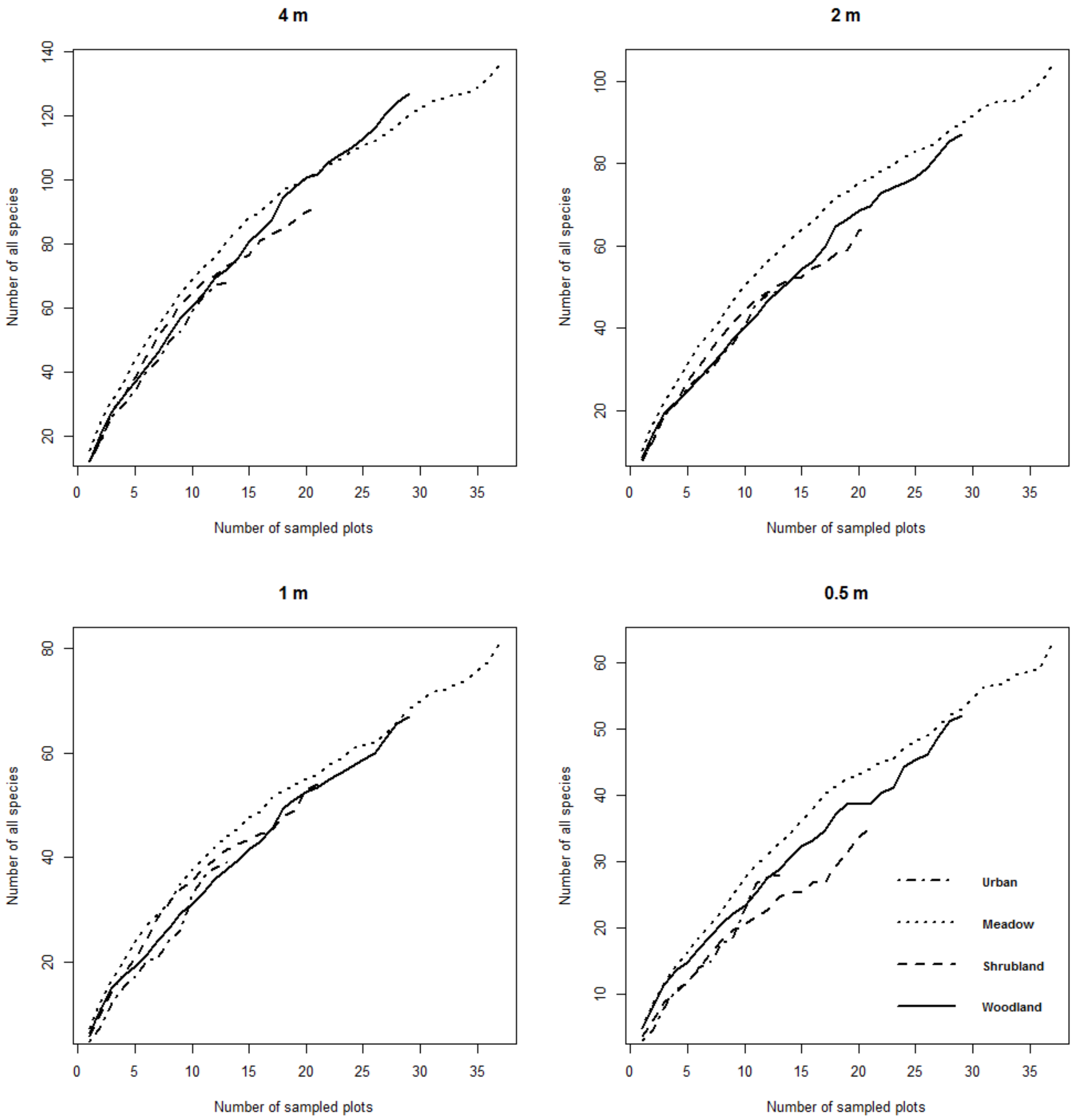

Fig. 3 SCR curves for all species pooled divided according to habitat type for each spatial scale investigated. The difference in expected species number for number of plot between the two curves ranged from fifteen to eight reducing the scale of observation, all these patterns are constant across scales

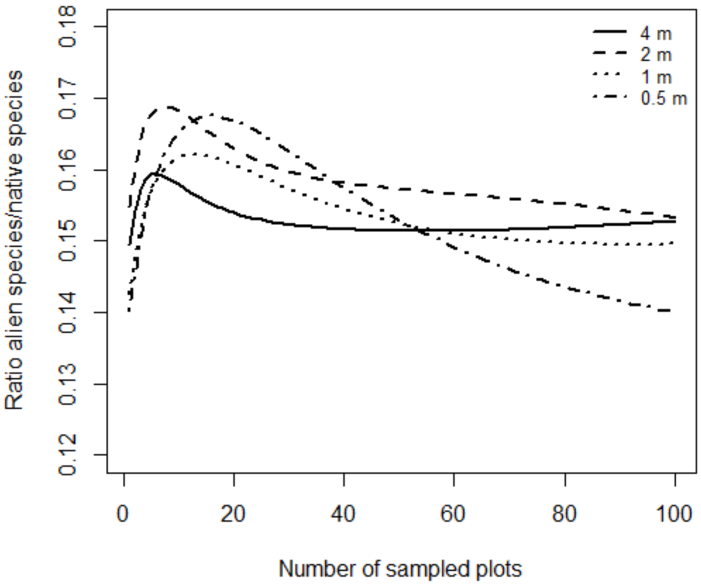

Fig. 4 Ratio between rarefaction curves calculated for alien and native species at each spatial scale investigated

The NMDS analysis for native species provides a fairly good representation of the data (Fig. 6a, stress = 0.23): it can be noted as urban plots set aside respect to the others, indicating their compositional differentiation. NMDS computed only on alien species (Fig. 6b, stress = 0.15) clearly shows the absence of specific pattern among different habitats, highlighting how the urban ecosystem may be prone to a diffuse propagule pressure by alien species, resulting in alien flora homogenization across the whole studied area. In addition, it provides further evidence of the high level of habitat plasticity that alien species are able to tolerate, thanks to their great adaptability to various types of environment.

Discussion

The role of green areas in urban ecosystem

Green areas inside cities play a key role in global efforts to protect and manage vulnerable ecosystems and biodiversity (Goddard et al. 2005). The correct management and conservation of these habitats may mitigate the rate of biodiversity loss and habitat destruction (Alvey 2006). Furthermore, they may provide benefits in terms of ecosystem services (e.g. Brack 2002). Here, we quantitatively evaluated plant diversity elements as well as their patterns in the context of the urban habitat mosaic induced by human activities in a peculiar area: the port of Trieste. The effect of the habitat on species richness has long been examined and it is well known to influence both natural and urban environments (Pyšek et al. 2002; Celesti-Grapow et al. 2006). Knapp et al. (2008) proved how plant species vegetating in urban environments are endowed with those functional traits that make them well suited to cope with stresses. In fact, they are usually wind-pollinated, zoochores and with scleromorphic leaves. As already reported by other authors (Deutschewitz et al. 2003; Kühn et al. 2004), these environments are primarily colonized by many R-strategy native species (Ruderals *sensu* Grime’s CSR classification, Grime et al. 1988) that could contribute to increase local alpha diversity.

These species are generally highly resistant to disturbances (intended as the mechanism which limits plant biomass by causing its partial or total destruction, Grime 2006), and tend to have short life-spans (generally annual or short-lived perennial), early flowering with a large amount of seeds (Grime 2006), all features that make these species well-adapted to urban ecosystem. Our findings mirror these studies very well; furthermore, we highlighted that the urban habitat shows high proportions of alpha diversities both in native and alien species compared to more natural habitats such as woodlands or shrublands, even though its flora may be primarily constituted by alien species, especially where urban heat island effect is more pronounced (McKinney 2006).

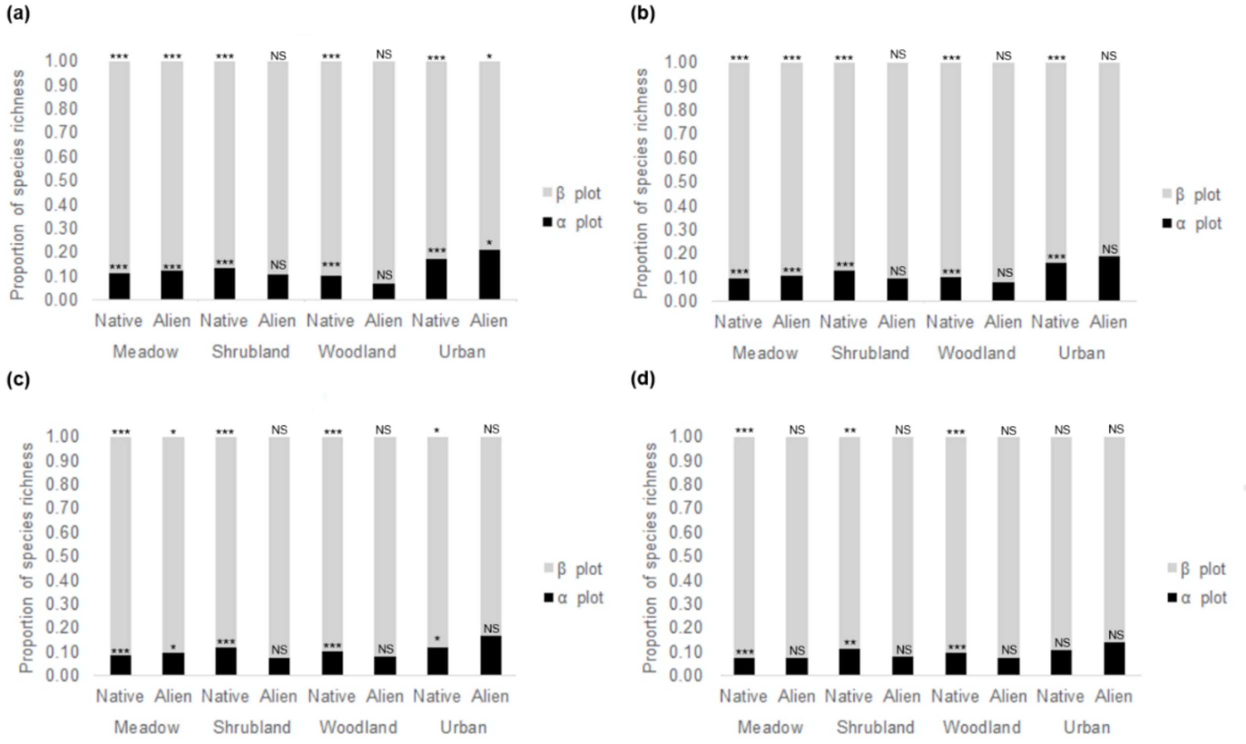

Fig. 5 Alpha and beta components of diversity (% of the total) for native and alien species for each habitat on a) 4 × 4 m, b) 2 × 2 m, c) 1 × 1 m, d) 0.5 × 0.5 m. The contributions to the total richness for each scale were determined by the additive partitioning of diversity method (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = Not Significant)

Thus, we expected to find a high proportion of alien species, as already demonstrated in many other studies (Ricotta et al. 2010, Kowarik et al. 2013; Aronson et al. 2015 among others). Indeed, the constant availability of propagules and the great connectivity present within cities, ensure the maintenance of established populations. Additionally, other factors such as landscape fragmentation, heat island effect, and the presence of hard surface that promote aridity due to run off, create conditions that allow the establishment and spread of those species, like alien plants, that are ecologically pre-adapted to cope with stresses and harsh conditions. On the other hand, the low alien percentages found in woodland and shrubland may be explained according to the theory of biotic resistance (Levine 2000). This states that resident species in a community reduces the success of exotic invasion (Levine et al. 2004) through biotic filters that may impede plant invasion such as competition from native species (mainly through shading effect considering that most of alien plants are sun-loving), pathogens and herbivores.

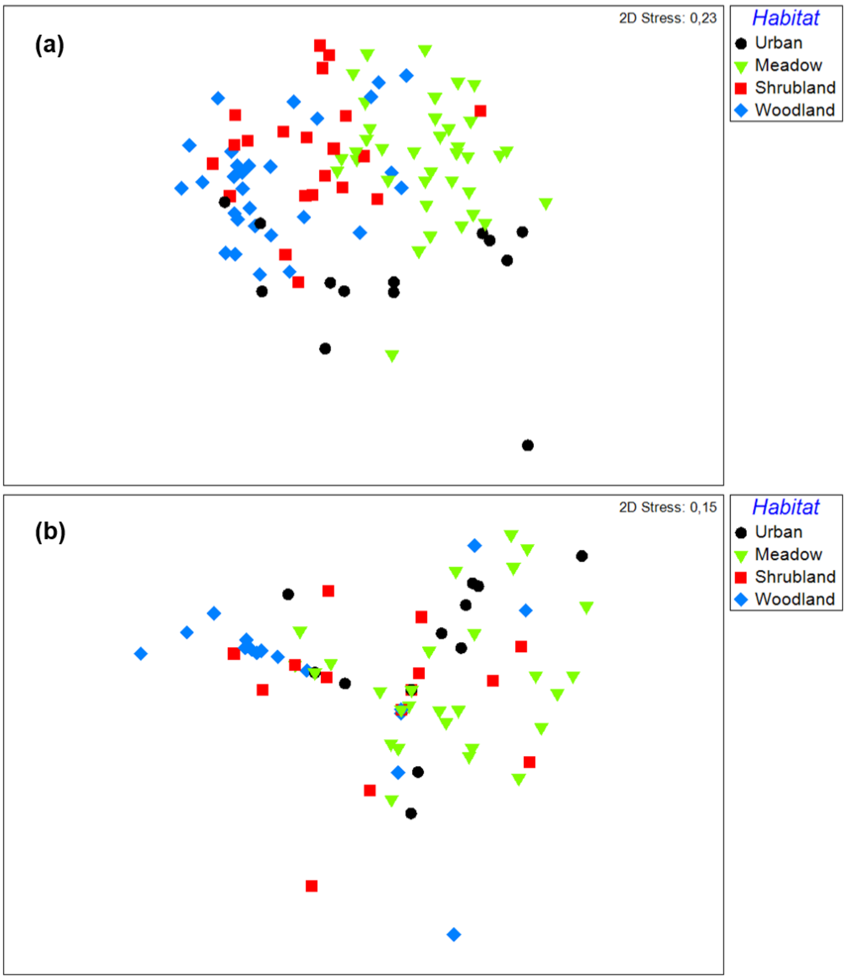

Fig. 6 NMDS based on Bray-Curtis dissimilarity matrix (log-transformed abundance data) for the largest spatial scale (16 m^2) for each habitat. a) Native species b) Alien species

The high steepness of the rarefaction curves suggests that further sampling efforts would have been necessary to capture the complete species pool of native species, conversely to what was observed for alien species. The ratio among rarefaction curves is an interesting tool to disentangle the relative contribution of typical groups such as alien *vs* native species (e.g. Pyšek et al. 2002). The high proportion of neophytes to the detriment of archaeophytes combined with the low archaeophytes to neophytes ratio (compared to other cities, see Table 2) demonstrates how in Trieste alien species have spread in relatively recent times. Our results concur with those obtained by Martini and Altobelli (2009) in a census of the flora of the city of Trieste, both considering the whole urban area and the grid cells only which encompass the port area. This allows us to make some considerations: firstly, that probabilistic sampling is efficient (in term of both costs and time) in capturing actual diversity patterns and plant variability within urban areas; secondly, that the rate of invasion in Trieste is very high, considering its small population and extension compared to other Italian cities for which data are available. This could be probably explained chiefly by the role of port areas as preferential pathway of introduction and spread of alien species, this is further confirmed by the very low proportion of the more ecologically specialized archaeophytes compared to other Italian cities.

Effects of scale on plant species richness

This study points out how assessing species richness with a multi-scale approach is desirable in order to study the complex relationships between spatial scale and plant species richness at different grain sizes. Similar evidences have been demonstrated by other authors in natural contexts (Crawley and Harral 2001; Palmer et al. 2006 for N- American flora; Chiarucci et al. 2012 for a network of protected areas). Our results suggest the need to use different spatial scales to detect a reliable rate of invasion in an area, since small scales are not able to capture the real amount of alien species due to sampling effects. Spatial heterogeneity is considered as the major driver in shaping species composition (Davies et al. 2005); this encompasses several factors such as ecological interactions mainly at the local scale, or geography-based factors such as topography or aspect on a larger scale (Fridley et al. 2004). Since urban development patterns affect spatial heterogeneity of urban ecosystems, we also argue that alternative urban patterns that emerge from human and ecological interactions play an important role in the dynamics and resilience of these peculiar areas.

Conclusion

Cities are highly anthropogenic ecosystems, further challenging the ecological understanding of how novel species assemblages support urban ecosystem services. As urban areas continue to expand in the coming decades, so will the size of the urban green habitat: however, the role of particular groups of species (native, alien, invasive) in the supply and demand for ecosystem services remains poorly understood (Haase et al. 2014). Additionally, understanding habitat function and habitat connectivity is a key target for city planners to design appropriate management and conservation strategies for urban biodiversity and ecosystem resilience. To our knowledge, this is one of the first attempts to explore plant diversity patterns in port areas: this evaluation assumes particular importance, since ports are deemed one of the main pathways for alien species introduction and spread. Our findings contribute to integrate an increasing literature about port floras shedding light on the role of port areas as potential hotspots for biodiversity conservation. We also explored the habitat-filtering role of green areas with respect to the spread of alien plant species and the prominent role that green areas seems to have in tackling alien plant invasion inside urban environment. These remnants of natural vegetation are fundamental to preserve native vegetation and ecosystem services, mainly considering the ongoing pressures occurring in our ecosystems such as urban sprawl, globalization and global warming. Under this scenario, alien species should be favored, and their spread and establishment may be enhanced; for these reasons, maintaining large green areas inside urban ecosystem could preserve local biodiversity against an increasing alien species pressure. Future investigations and sampling efforts are needed to better understand how native and alien species interact in urban habitats, specifically, it could be interesting to develop a system of horizon scanning (e.g. Sutherland and Woodroof 2009) for risk assessment and management, to foresee the arrival of new alien species, for instance through the study of the main shipping routes in port areas. Furthermore, the application of a multi-scale integrated approach in vegetation analysis may provide useful ecological insights to understand better these ecosystems, allowing the development of enhanced management strategies. There is a hope that an increased knowledge of how urban plant communities are structured will allow us to design cities that promote biodiversity and the survival of native plant species pool.

Acknowledgements

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Chapter 2

Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline

Tordoni E, Napolitano R, Maccherini S, Da Re D, Bacaro G Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline

(Ecological Research - *Under review*)

Abstract

Coastal sand dunes represent one of the most fragile ecosystems in the Mediterranean basin. These habitats naturally suffer the action of several limiting factors such as sand burial, marine aerosol and low soil fertility; on the other hand, they often host species of high conservation value. In the last decades, they have also experienced high level of biological invasion. In this study, we sampled psammophilous vegetation in two sites in northern Adriatic coast belonging to Natura 2000 network to describe diversity patterns and to identify the main ecological drivers of species diversity. Plant species richness and their abundance have been assessed in each plot. Differences in species composition for native and alien were compared through PERMANOVA analysis. Species complementarity was explored by partitioning beta diversity in its spatial components (richness and replacement). A Generalized Linear Model was also computed to assess the main environmental factors that may promote invasiveness in these ecosystems. For the investigated area, our results highlight the strong differentiation in community composition both in alien and native species: in particular alien species showed on average a lower complementarity among habitats compared to native species. Specifically, communities seem to be more diversified when larger spatial scales were considered. Beta diversity in both groups appears to be more dominated by the richness component respect to the replacement one. Furthermore, in these habitats, the occurrence of alien species showed to be related to geomorphological predictors more than climatic variables.

Keywords: Alien species, Beta diversity, Diversity partition, Generalized Linear Model, Natura 2000 network, PERMANOVA.

Abbreviations: GLMM – Generalized Linear Mixed Model; LCBD - Local Contributor of Beta Diversity; MAM – Minimum Adequate Model; PERMANOVA - Permutational Analysis of Variance; SAC - Species Accumulation Curve; SER **-** Spatially-Explicit Rarefaction.

Introduction

Coastal sand dunes are peculiar ecosystems that represent natural barriers against waves and windy storms. Three interacting factors are mainly responsible for the biota hosted in these habitats: waves, tides and sand particle size (McLachlan 2001; Šilc et al. 2017). Established plant communities naturally undergo several limiting factors such as sand burial, sand blasting, marine aerosol and soil fertility. Therefore, these environments are characterized by strong ecological gradients due to differences in the abiotic conditions that allow the establishment of a typical spatial arrangement of the plant community along a sea-inland gradient, typically described as “zonation” by plant ecologists, which can be easily reiterated in different sites. Across the globe and particularly in the Mediterranean basin, coastal ecosystems are deemed to be highly endangered (Kutiel et al. 2000) and they suffered heavy loss of biodiversity and habitat simplification (Dolan and Walker 2006), mainly due to a steady increase in human pressure in the last decades (Curr et al. 2000; Reidesma et al. 2006; Brown et al. 2013). Despite these environments naturally cope with stresses, recent alterations driven by anthropic disturbs (tourism, urbanization; O’Shea and Kirkpatrick 2000), shoreline erosion (Anderson et al. 2015), climate changes (Van der Meulen et al. 2004; Prisco et al. 2013), and biological invasion (Feagin et al. 2005; Prisco et al. 2013), seriously threaten these ecosystems. The latter factor has been widely demonstrated to heavily jeopardize worldwide biodiversity, along with habitat loss and fragmentation (DAISE 2009; EEA 2012). A growing body of literature is shedding light on the negative effects that alien species can have in natural ecosystems (e.g. Vilà et al. 2011). They can trigger cascade effects among which it is worth to remind the modification in local species composition (Gaertner et al. 2009; Hejda et al. 2009; Powell et al. 2011) and the alteration of nutrient cycle (Ehrenfeld 2010). These may lead even to extinction of native taxa with great ecological value, like endemism and keystone species, through competitive exclusion processes. This can be particularly evident in coastal ecosystems, which are one of the most invaded ecosystems in Europe (Chytrý et al. 2008) in which alien species are having the heaviest ecological impacts (see for instance Santoro et al. 2012). In fact, despite their adaptations in tackling stresses, these environments have little resilience capability since modest disturbs may cause long-term alterations and abrupt changes (Carter 1988; Lemauviel and Rozé 2003). Italy, being a peninsula, has about 7500 km of coastline. Among these, coastal dunes occupy only 40% of the total (3300 km, CNR 1999), even though most of them are exploited mainly for touristic purposes. In fact, since 1950s, sand dune ecosystems in

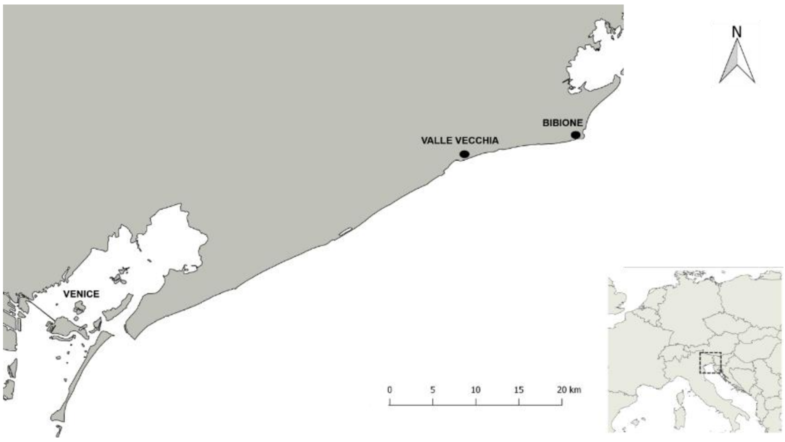

Fig. 1 Location of the two sampling sites in northeast Italy. On the right, an overview of the sites compared to the Italian peninsula

northern Adriatic coastline experimented strong habitat fragmentation, trampling and alteration in geomorphological processes, among others, mainly due to a steady increase in tourist activities and urbanization (Nordstrom et al. 2009), then resulting in few natural remnants along the coastline present today. For these reasons, most of the ecosystems hosted are highly threatened and belong to protected areas such as the Sites of Community Importance (SCIs, Natura 2000 Network), due to the dual presence of both priority habitats and species of Community Importance according to the EU regulations (Habitats Directive 92/43/EEC). The uniqueness of the flora occurring in the Northern Adriatic area is the result of a "crossroad" of species with different origins due to the peculiar biogeographical location. Hence, climatic changes occurred between the third and the first millennium BC, led to important floristic migrations: in fact, species with Alpine, Mediterranean and Eastern native range reached the N-Adriatic coast (Lorenzoni 1983; Gehu et al. 1984; Buffa et al. 2012). Thus, in this biogeographic and bioclimatic context, xero-thermophilous species tend to colonize draining substrates, whereas in the interdune lowlands, it is still possible to find hygrophilous and microthermic entities of montane origin. For this floristic uniqueness compared to the rest of the Mediterranean basin, the conservation value of these plant communities goes far beyond the European environmental conservation policies (Sburlino et al. 2013). For the above-mentioned reasons, there is a need to constantly assess or update the conservation status of coastal dunes ecosystem in order to promote appropriate management strategies to preserve these peculiar environments. At the same time, it is mandatory to determine those biotic/abiotic factors directly or indirectly driving biodiversity patterns in order to propose coastal protection decisions made using rigorous scientific criteria. In this study, through a systematic sampling design based on belt transects, we sampled psammophilous vegetation in two SCIs in northern Adriatic coastline with the following specific aims: i) describe the diversity patterns of sand dune plant communities in two coastal sites for both native and alien species components, ii) assess the conservation status of native plant communities in relation to alien invasion and iii) identify the main drivers of native and alien species diversity and testing for the effect of geomorphological, environmental and human-induced factors related with alien species occurrence.

Materials and methods

Study area

Data on sand dune vegetation were collected in two SCIs named "Valle Vecchia, Zumelle and Valli di Bibione" (IT 3250041) and "Foce Tagliamento" (IT 3250040), both located in northeast Italy (Fig. 1). These areas represent two remnants of the primarily sedimentary northern Adriatic coastline where it is still possible to find wide patch of sand dune vegetation that host a great number of rare species and endemisms. The climate is temperate-subcontinental (Cfa of the Köppen-Geiger classification, Kottek et al. 2006), mean annual temperature is between 10 - 14°C without a dry phase and mean annual precipitation is ca. 828 mm. Both SCIs are fiercely influenced by bora wind, which dramatically decrease thermal limits mainly during the winter. The first study site called Brussa (45.620554°N – 12.942477°E, *datum* WGS84) represents the longest strip of non-urbanized area in the high Adriatic basin (Provincia di Venezia 2010). It consists in a sandy shoreline east-to-west oriented that divide the sea from the lagoon behind (Caorle lagoon); this SCI has a surface of about 20.89 km^2. It is delimited by Porto Falconera on the west side and by Porto Baseleghe on the east side. The sedimentary regime of the littoral is determined by a longshore sediment drift towards the southwest (Fontolan 2004) and the recent trend is stable or slightly in accretion (Fontolan et al. 2014). It hosts several plants and animal species included in the Annexes I and II of the Habitat Directive (Directive 92/43/EEC) and 39.74% of the total SCI surface is covered by habitat of Community Importance. During the reclamation of the lagoon in '60 years, it has been planted an artificial pinewood of *Pinus pinea* L. and *Pinus pinaster* Aiton, which have superseded the native potential vegetation (*Quercetalia ilicis*, Provincia di Venezia 2010). The second sampling site is close to Bibione lighthouse (45.636058°N – 13.097145°E; *datum:* WGS84), it has a surface of 2.8 km^2 of which 43.2% covered by habitat of Community Importance. This site is completely surrounded by a highly urbanized and touristic area. It is delimited on the east side by the mouth of the Tagliamento river and on the west side by Bibione town. The beach is directly influenced by terrigenous deposition; in fact, there is a strong sedimentary input carried by Tagliamento river and in the last years, the sedimentary budget has shown an accretion trend (> 5 m^3/m year, Fontolan et al. 2014).

Sampling Design and Data Collection

The following sampling design was adopted to collect data on plant composition and abundance: first a square grid of 500 m linear dimension was overlaid to each sampling site. In each cell, a random transect was selected following a sea-inland gradient with variable length due to dune width and coast morphology. Transects were partitioned in a set of contiguous squared sub units (plots) of 4 m x 4 m where the occurrence and percentage visual cover estimation of each vascular plant species were assessed. Since this survey is focused on psammophilous vegetation plots, pinewoods and non-sand dune vegetation were not sampled. Fieldworks were carried out during May-August 2016; in total 21 transects and 261 plots were sampled (104 plots in Bibione and 157 in Brussa, respectively). Later on, each plot was assigned to a specific coastal habitat included in the Habitats Directive based on the observed vegetation and on those reported in the SCI map of habitat (source https://www.regione.veneto.it). For the sake of simplification and to make these habitats comparable to other studies, plots were classified in three major recognizable classes based on dune dynamics: i) Foredune including upper-beach, embryo-dunes and mobile dunes (EU habitat code 1210, 2110 and 2120), ii) Fixed dune encompassing those environments dominated by perennial communities of the inland side (EU habitat code 2130 and 6420), iii) Interdune that include distinctive habitats mainly constitute by salt marshes and Mediterranean humid grasslands of tall grasses and rushes (EU habitat code 1403 and 7210). It is worth to note as some of these habitats such as 2130 and 7210, are deemed of priority importance by European Union. All the vascular plants recorded within each plot were identified at the species or subspecies level directly in the field or, most frequently, in the laboratory by using proper identification floras (Pignatti 1982). Nomenclature was standardized according to Conti et al. (2005). Plants were classified as native or alien species, depending on their status given by Celesti- Grapow et al. (2009).

Abiotic variables

Climatic data have been downloaded from the ARPAV website (http://www.arpa.veneto.it). Averages of minimal, mean, maximum values along with their range (maximum-minimum) were calculated for temperature (°C) and relative humidity (RH, %). For precipitations (mm), rainy days, and irradiation (MJm^{-2}) only the average values was computed. In this way, a total of 25 climatic predictors were obtained using baseline climatic data spanning from the period 2008-2015 and encompassing March-October time range. Geomorphological data were derived from the Shape project database (Fontolan et al. 2014); specifically, beach mean width (m), annual deposition rate (m^3/m), shoreline variation (m/year), touristic pressure (number of tourists/m^2) and class of erosion (three levels: accreting, stable and in erosion) were selected. Finally, Elevation (m), slope (°), Northness, Eastness and the standard deviation of slope (as an effective measure of terrain roughness according to Grohmann, et al. 2010) were derived by a LIDAR raster at 1 m resolution using Qgis 2.16.3 with GRASS 7.0.4 (Quantum GIS Development Team 2016).

Statistical Analysis

Analysis of plant diversity patterns

Latent gradients in species composition for both native and alien species were assessed through indirect gradient analysis (Nonmetric MultiDimensional Scaling). Significant differences in community composition were evaluated using multivariate permutational analysis of variance (PERMANOVA, Anderson 2001). Both the analyses were based on a Bray-Curtis similarity matrix on log-transformed species abundances. The following factors were tested in the PERMANOVA design: “Site” (fixed, two levels), “Transect” (random, nested within Site) and “Habitat” (fixed, three levels), along with the interaction “Habitat x Site” and “Habitat x Transect”. A posteriori pairwise comparison was applied to assess the effect of habitat when it resulted significant. All tests were performed with 4999 permutations of residuals under a reduced model using Type I sums of squares. Analysis were performed using PRIMER 6 software (Clarke and Gorley 2006) and the PERMANOVA routine in the add-on package PERMANOVA+ (Anderson et al. 2008). Subsequently, for each group, plot-based rarefaction curves (hereafter SAC, Gotelli and Colwell 2001; Chiarucci et al. 2008) were computed using the exact method in the “vegan” package (Oksanen et al. 2017) to compare patterns as a function of the sampling effort. We calculated also Spatially-Explicit Rarefaction curves (hereafter SER, Chiarucci et al. 2009; Bacaro et al. 2012) to check the consistency of the SAC due to their capability to account for spatial autocorrelation among plots, especially when the extent of the study areas is different (Bacaro et al. 2011; Bacaro et al. 2016). Diversity patterns for native and alien species were also compared using classic partition techniques (Lande 1996; Gering et al. 2003; Crist et al. 2003; Chiarucci et al. 2010) that allows partition of the three components of the diversity (alpha, beta and gamma) across the different spatial scales of investigation (plot scale, transect scale, site scale and the whole study area). This analysis was also performed by splitting native and alien species by habitat. Mean values of each of these components were reported as the proportion of mean species richness. 999 permutations were used to test if there were deviations from randomness in the observed patterns using null model testing.

Exploring relationships of diversities components between native and alien plant communities

The relationship between alien and native richness was tested using simple linear regression. Species complementarity, namely beta diversity, was split in its basic components in both groups: replacement (βrepl, that is a species in one site is substituted by a species in another site) and richness (βrich, the loss or gain of species between sites; for more details about the methodology see Carvalho et al. 2013; Legendre 2014). Beta diversities were further compared using Local Contributors of Beta Diversity (hereafter LCBD, Legendre and De Cáceres 2013) in the R package “adespatial” (Dray et al. 2016).

This analysis is useful to highlight the uniqueness of the sampling units in terms of community composition. 999 permutations were performed to test for randomness in species distribution while preserving the species abundance distributions in the observed data. LCBD values have been visually displayed using the “ggmap” package (Kahle and Wickham 2013). In both the analysis the species sampled in the plots were aggregated by transect.

LCBD values have been derived also according to habitat in each transect, the presence of significant differences was evaluated using Kruskal Wallis rank sum test. When the test resulted significant, using the package “kruskalmc” (Giradoux 2017) an adjusted posteriori pairwise comparisons were performed between pairs of habitat.

Analysis of ecological determinants of native and alien species

The variation partition in the multivariate space of the community matrix for native and alien compartment was computed with respect to the set of available explanatory variables (Peres-Neto et al. 2006; Legendre and Legendre 2012) in order to assess which group of variables (spatial, climatic and geomorphological variables) contributed more in explaining the variability in the dataset; prior to analysis the species matrix was Hellinger-transformed as suggested in Peres-Neto et al. (2006). Since a very high multicollinearity was detected in our predictors, a subset (Tables S1 and S2, Appendix B) was obtained using multivariate forward selection by permutations of residuals (999) under reduced model following the double-stopping criterion proposed in Blanchet et al. (2008). Finally, to highlight which are the main abiotic factors related to alien species spread in sand dune ecosystems, a binomial random intercept model (GLMM) was computed considering the occurrence of alien species in plots, setting the transect factor as the random effect nested in Site. However, the random effect of the transect was not significant according to likelihood ratio test ($\chi^2(2) = 0, p > 0.05$), and a classical Generalized Linear Model (GLM) was then considered. Before building the GLM, all predictors were z-standardized in order to obtain quantitatively comparable regression coefficients. To reduce multicollinearity in the set of climatic variables, a Principal Component Analysis was performed (Table S3, Appendix B). All axes that cumulatively contained greater than or equal to 75% of the variation were considered, this resulted in just the first axis added (91% of the variation explained). Minimum Adequate Model (MAM) was obtained through model averaging according to AIC reduction using package “glmulti” (Calcagno 2013). Variable importance was assessed by weighting standardized regression coefficients by AIC-weights and adding them up for all models in which a variable was included (Burnham and Anderson 2002).

All the analyses were performed using R 3.3.3 (R Core Team 2017).

Results

The pooled species richness of the 261 sampled plots is 127 (Table 1). Among these, 116 have been classified as native (91.4% of the whole sample) and 11 as alien (8.6%). The most frequent families in the total species pool are represented by Poaceae (17.3% of the sampled species), Asteraceae (16.5%), Cyperaceae (5.5%) and Chenopodiaceae (4.7%). The most frequent species are *Elymus farctus* (Viv.) Runemark ex Melderis (occurring in 36.2% of the sampled plots), *Spartina versicolor* Fabre (30.7%) and *Vulpia fasciculata* (Forssk.) Fritsch (30.4%). Among alien species, the most abundant families are Asteraceae (36.4%) and Fabaceae (18.2%) with *Oenothera stucchii* Soldano (61.8%), *Ambrosia coronopifolia* Torr. & A. Gray (57.6%) and *Xanthium orientale* subsp. *italicum* (Moretti) Greuter (44.7%) as the most frequent species.

Species group	**Habitat**		
	Foredune	Interdune	Fixed dune
	n = 126	n = 42	n = 93
Native	4.66 ± 2.81	5.57 ± 2.80	9.31 ± 3.19
Alien	1.75 ± 1.22	1.02 ± 1.33	2.49 ± 0.80

Table 1 Species richness (Mean ± SD) along with number of plots in each habitat for native and alien group

NMDS analysis for native species provides a fairly good representation of the sampled community (Fig. 2a, stress = 0.17): it can be noted as on average plots tend to aggregate according to habitat and sampling site. Conversely, the same unconstrained ordination computed only on alien species (Fig. 2b, stress = 0.18) clearly shows the absence of specific patterns, highlighting the non-specificity with which these species colonize sand dune environments. PERMANOVA outcomes for native and alien species (Table 2) highlight that significant sources of variability in species composition is determined by the spatial scales and habitat: while for native species these differences occurred for each of the considered factors (except for the Habitat x Site interaction), it is interesting to note as for alien species, the main effect of Habitat was not significant, along with the Site x Habitat interaction, confirming the observed NMDS pattern. Post-hoc test reveals a significant difference among all the habitat levels for native species (Foredune *vs* Interdune t = 1.8576, P = 0.0004; Foredune *vs* Fixed dune t = 2.0262, P = 0.0002; Interdune *vs* Fixed dune t = 2.2347, P = 0.0002). The estimated components of variance (expressed as %) are mainly driven by Site and Habitat component for what concern native group, whereas for aliens the factors Site and Transect have to be accounted for most of the variance explained (Fig. S1 in Appendix B). Rarefaction curves (both SAC and SER, Fig. S2 Appendix B) result almost asymptotic considering both species groups, suggesting that most of the species pool have been sampled. Once SER and SAC have been calculated separately by habitat type (Fig. 3), Fixed dune tend on average to host higher number of species as expected compared to Foredune or Interdune habitats in both groups displaying however a greater steepness.

Source of variation	Native species				Alien species			
	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
Habitat	2	61324	3.9843	0.0002	2	11342	1.1213	0.1332
Site	1	26739	2.0687	0.0214	1	37333	3.5279	0.0098
Transect(Site)	19	12190	4.5035	0.0002	19	10615	4.6929	0.0002
Habitat x Site	2	8301.7	1.7481	0.0830	1	3474.6	0.9003	0.4580
Habitat x Transect(Site)	14	6011.4	2.2208	0.0002	12	4368.8	1.9314	0.0002
Residual	218	2706.9	-	-	181	2262	-	-
Total	256	-	-	-	216	-	-	-

Table 2 PERMANOVA output based on Bray-Curtis similarity calculated for native and alien species

Coefficient	LR Chisq	Pr(>Chisq)	Coefficient sign
Class of erosion	16.08	<0.001	
Elevation	27.31	<0.001	+
Beach mean width	13.19	<0.001	+
Beach annual deposition rate	13.55	<0.001	+
Northness	9.79	<0.01	+
Touristic pressure	3.44	0.063	-

Table 3 Analysis of deviance table (Type III Likelihood-Ratio Test) of the GLM model on alien species occurrence

These results suggest that plant communities closer to the sea are characterized by a lower number of species and that are more homogeneous in terms of species pool. It is worth to note how for native species, the SER in Interdune displays different behavior compared to the SAC (Fig. 3a). Proportions of the diversity components (namely α and β), exhibit different patterns according to the investigated species group (Fig. 4). Specifically, alien species present lower levels of beta diversity across plots, transects and sites compared to native ones. Hence, species complementarity decreases substantially moving from native to alien group, specifically at plot scale is higher than that expected from the null models. Thus, significant compositional differences exist among plots in each transect, evidently resembling the effect of the sea-inland gradient. Both alien and native show not significant differences from null expectations across transects, hence highlighting that both these groups essentially share the same species composition within group.

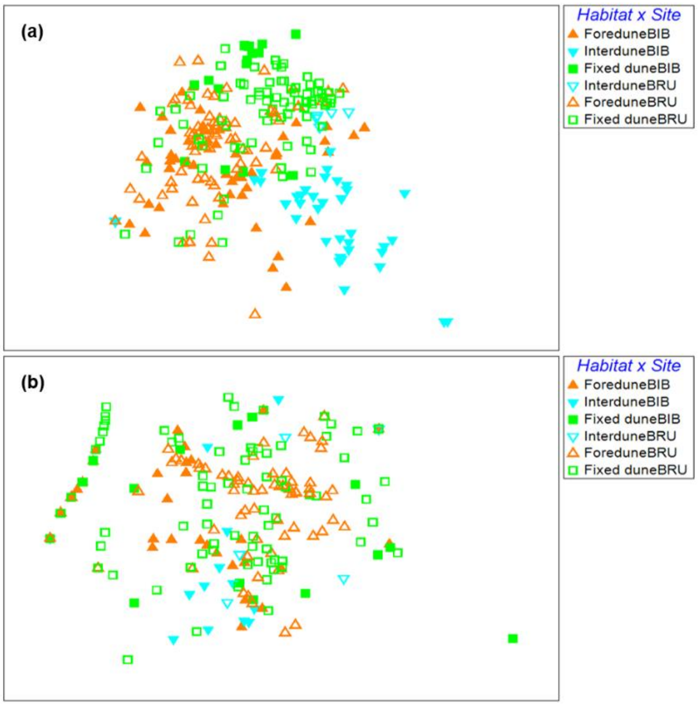

Fig.2 NMDS output based on Bray-Curtis similarity matrix (log-transformed abundance data) for each habitat and sampling site. a) Native species b) Alien species

A similar pattern has been observed for alien species at site level, conversely native species show significant difference between the two sites confirming a difference in the species pools. It is interesting to note how alien species complementarity in Foredune show very few differences across sites. A significant positive linear model (F (2, 259) = 55.77, $p < 0.001$, $R^2 = 0.17$) was found between native and alien species richness (B = 1.26, $p < 0.001$). Decomposition of β diversity in its two components (βrepl and βrich, Fig. S3 Appendix B) highlights that β diversity in this study area is dominated by differences in species gain or loss among transects for both groups (excluding few transects for native species in which the replacement component dominates). A significant multiple linear regression (F (2,17) = 3.652, $p < 0.05$, $R^2 = 0.21$) was calculated between alien βrich and native βrepl and the ratio of native βrepl /βrich. Model output show a notable decreasing trend between alien βrich and native βrepl (B = -0.68, $p < 0.05$, Fig. 6) and a positive relationship with the ratio βrepl /βrich (B = 0.07, $p < 0.05$). The analysis of LCBD shows that these values ranged between 0.0337 and 0.0666 for native species with five transects having significant values; whereas for alien species LCBD varied from 0.0118 to 0.1662 with just one significant value (Fig. 5). Kruskal-Wallis test confirms significant differences in LCBD according to habitat both in native (χ^2 (2) = 25.15, $p < 0.001$) and alien (χ^2 (2) = 13.24, $p < 0.01$). Post-hoc tests show significant values between Foredune *vs* Fixed dune and Foredune *vs* Interdune in native species, whilst alien species display significant differences just between Foredune *vs* Interdune. The variation partitioning approach on species composition data highlights that abiotic variables explain the 36% of the total variation for native species and 40% for the aliens (Fig. 7).

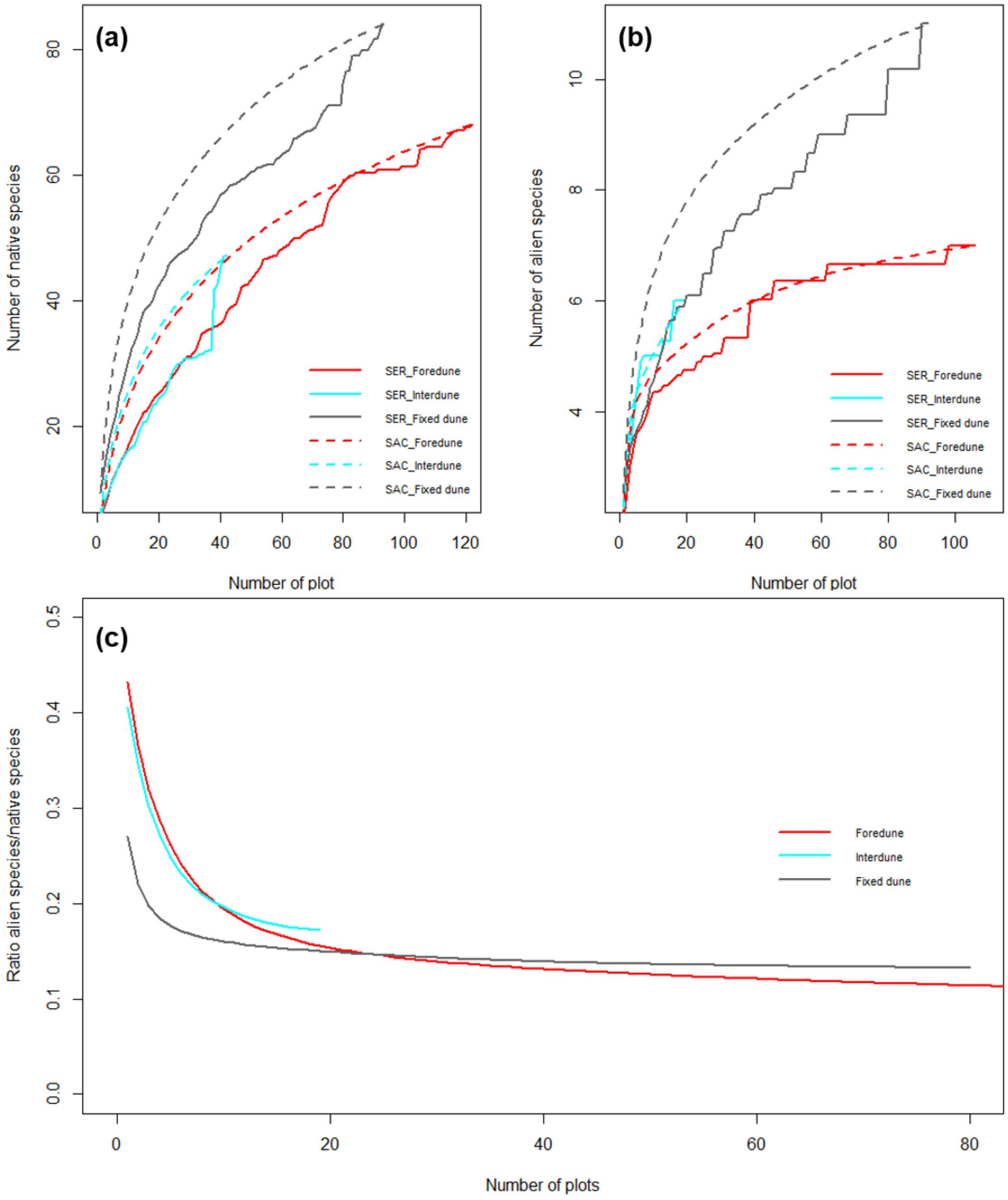

Fig. 3 Rarefaction curve (SAC) and Spatially-explicit rarefaction (SER) for (a) native species and (b) alien species. c) Ratio between alien and native SAC for each habitat, note that only the first part of the x-axis is reported and that the Foredune curve would continue until 106 plots

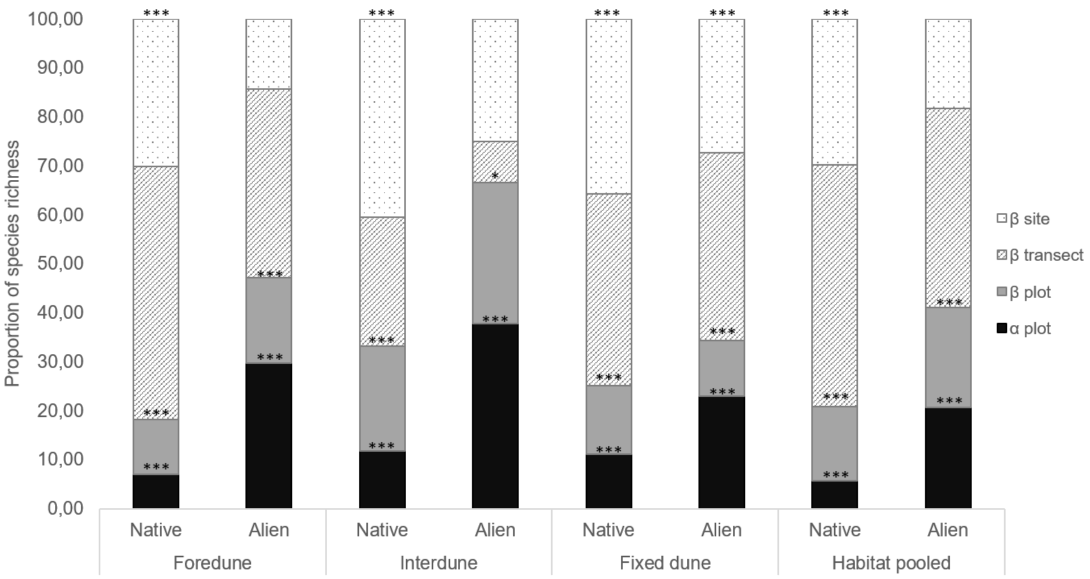

Fig. 4 Diversity components (% of the total) for native and alien species for each habitat and for all habitat pooled. The contributions to the total richness for each scale were determined by the additive partitioning of diversity method (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$)

Notably, climatic and geomorphological predictors in combination encompass most of the variation present in the dataset (32% for native and 34% for aliens), whereas the influence of spatial structure in the dataset is almost completely negligible, probably due to the small extent considered in this study (5% for native and 6% for aliens). Despite climatic and geomorphological predictors account for a similar percentage of explained variation in both groups, PERMANOVA analysis points out that observed differences for alien species occur at a finer spatial scale, namely within habitat along each transect. Furthermore, when only the occurrence of alien species is explored, the GLM output shows that the major determinants of alien presence are represented chiefly by the geomorphological dynamics of the beach (Table 3) and, in a lesser extent, by human-induced factors such as touristic pressure. In particular, elevation, class of erosion, beach mean width and deposition rate are the most significant predictors in explaining alien species presence (with a higher likelihood to find alien species according to an increase in these values). Additionally, Northness and Touristic pressure influence alien occurrences with positive and negative slopes, respectively.

Discussion

Community structure along the environmental gradient

The present work aims at describing diversity patterns of plant communities in northern Adriatic sand dune ecosystems, exploring the relationships and the interactions among native and alien species groups and ecological factors shaping their distribution. The number of alien species we found is in line with other studies in the same area or ecosystem (Campos et al. 2004; Vilà et al. 2007; Chytrý et al. 2008; Del Vecchio et al. 2015). However, despite their apparent low percentage compared to the Italian one (9.4%; the Italian average is 13.4% and that of Veneto region 11.8%, Celesti-Grapow et al. 2010) it should be taken into account that these habitats own a great conservation values because of the elevated proportion of endangered and exclusive plant taxa they host (Van der Maarel 2003; Acosta et al. 2009). Diversity patterns in native and alien species show very different behaviors according to habitat and to the spatial scale investigated.

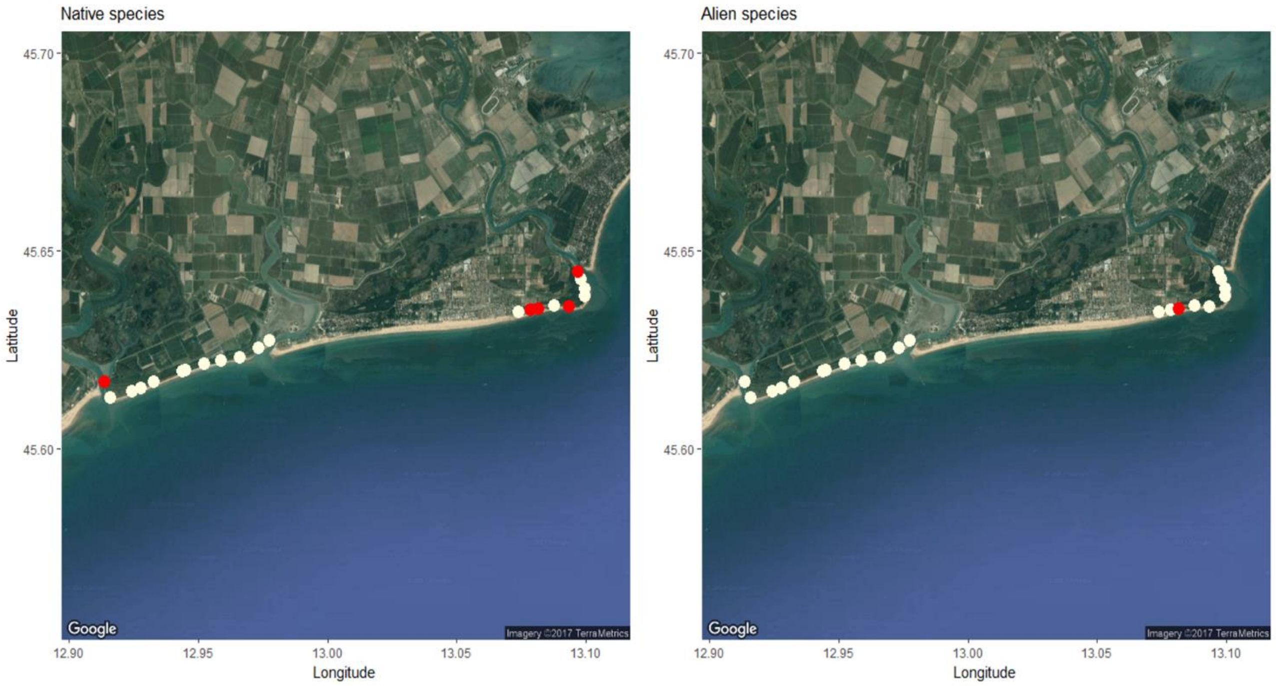

Fig. 5 Map of Local Contributor of Beta Diversity values. In red, the significant transects ($p < 0.05$)

The concept of scale-dependence between native and alien species richness has been already widely debated (Levine and D’Antonio 1999; Fridley et al. 2007) and, in agreement with this statement, our findings support the idea that it is not possible to directly compare the proportion of aliens across areas without taking into account the effects of the spatial scale or the size of the flora (Gotelli and Colwell 2001; Palmer et al. 2006), as the ratios of SAC of our study also confirm. The observed mean difference between SAC and SER is 3.9 species that can be seen as the outcome of spatial dependence among individuals in the space, acting in the same way in both groups (except for interdune habitat). In general, rarefaction curves allow us to be satisfied about the goodness of the sampling effort that is crucial to estimate the correct number of species (Acosta et al. 2009; Chiarucci et al. 2012). In case of sampling bias, some rare or endangered species may not have been recognized or underestimated, resulting in relevant implications for conservation programs. Results of NMDS clearly suggest that the gradient in species composition of native species were only marginally related to that of alien species. natives pattern could be seen as the outcome of the harsh conditions naturally present in these habitats that shape plant communities. It is interesting to note how the apparent absence of such structure in the alien species pool may be seen as an evidence to potential shift towards randomness in the community assembly rules (Santoro et al. 2012). However, it is worth to remind that this analysis may be quite sensitive to the input parameters and few changes may lead to quite different patterns Differences in distributional patterns between native and alien species at local scales have been also reported by some studies on roadside communities (Arévalo et al. 2005) or cultivated systems (Lososová and Cimalová 2009). The presence of strong limiting factors acting in these environments are deemed the main drivers on plant species composition in these ecosystems. Both native and alien species pool in our dataset share the same ecological drivers even though with slightly different proportions and effects, as pointed out in variation partitioning analysis. Foredune habitat confirmed to be extremely species poor and selective for plant species compared to Fixed dune. This can be seen as the result of the harsh conditions that are present closer to the sea such as marine aerosol, lower levels of nutrients and moisture, salt spray (see Perumal and Maun 2006; Carboni et al. 2010; Ciccarelli et al. 2012). On the other hand, Fixed dune tend to be permanent due to the lower exposure to the limiting factors cited above and to the evolution of some adaptations that allow them to survive and reproduce (Wiedemann and Pickart 2004; Acosta et al. 2006). Here, higher level of species richness was observed in both groups as reported also in Vaz et al. (2015) and Marcantonio et al. (2014), among others. The higher number of alien species in the Fixed dune may be seen as a sign that native species assembly have lost their capability to compete with alien species probably due to an effect of human-induced disturbances (e.g. trampling, Del Vecchio et al. 2015) that create gaps in the niche where these species, that are pre-adapted to cope with stresses (e.g. for urban environment Knapp et al. 2008), can easily be integrated and propagate in the surroundings area. One of the more hazardous consequence may be the biotic homogenization of these ecosystems, with the resulting loss of endemism or rare species of which these environments are naturally rich. The model output shows as geomorphological features rather than climate influence alien species occurrence, probably due also as an indirect effect of the small extent of the study area. The importance of geomorphological predictors in the sand dune plant communities has been outlined also in Prisco et al. (2013), where the beach length was the most important factor influencing their habitat distribution models. Similar results were described also in Fenu et al. (2012), where for the total species pool soil properties more than wind-related variables drive distribution of plant communities along the sea-inland gradient. Conversely, in Carboni et al. (2010), climatic variables played a key role in shaping alien species richness. The effect of erosive coastal processes on plant community composition and the potential synergic effect between sand dune erosion and invasiveness still remain unclear and would need longer term investigations (e.g. Hill et al. 2010). Ciccarelli et al. (2012) observed that where the instability of the coast was greater there is a disequilibrium in the community and a highly heterogeneous species composition. Moreover, human-related factors such as trampling and coastal erosion are closely related with habitat degradation and loss (Ciccarelli 2014). This confirm the need to preserve costal habitats in order to ensure effective conservation actions of these endangered habitats.

Beta diversity patterns

In general, analyses of beta diversity may provide useful insights into drivers and assembly rules of plant communities and of the potential mechanisms of invasion considering different spatial scales (Leprieur et al. 2009; Marini et al. 2009). Partition of diversity highlights how most of the diversity can be observed at transect and site scale for native species and at a smaller scale (plot) for aliens.

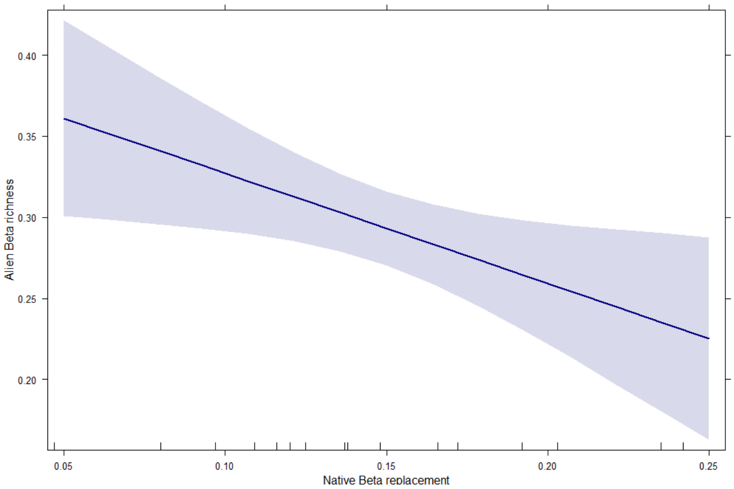

Fig. 6 Relationship between beta replacement of native species and beta richness on alien species. Blue line represents the calculated regression trend

This means that alien species tend to share species composition increasing the scale of analyses. A similar pattern has been described also in Tordoni et al. (2017) for a coastal urban context. Although richness values of native and alien species were correlated at the plot scale, we clearly pointed out that is probably the beta diversity of both species group to regulate equilibrium in the plant community. Decomposition of beta diversity provide a suitable tool to elucidate the mechanisms of assembly of plant sand dune communities along the sea-inland gradient. Our results show how is the richness difference component more than replacement that dominate in our sampling sites. Practically speaking, this means that community change was primarily determined by the loss of species on both groups (originating richness differences among transects) from more dynamics to more stable habitats. Considering alien species, this could be explained as the outcome of the spatial arrangement of the pathways of introduction (e.g. roads and paths, see for instance Marini et al. 2013 for mountain environment, Bacaro et al. 2016 for an oceanic island) thanks to which alien species reflect similar species pool present in the surrounding areas. On the contrary, the larger proportions of beta replacement observed in native species may be easily interpreted as larger adaptions to the harsh conditions present in these habitats, due to their longer residence time.

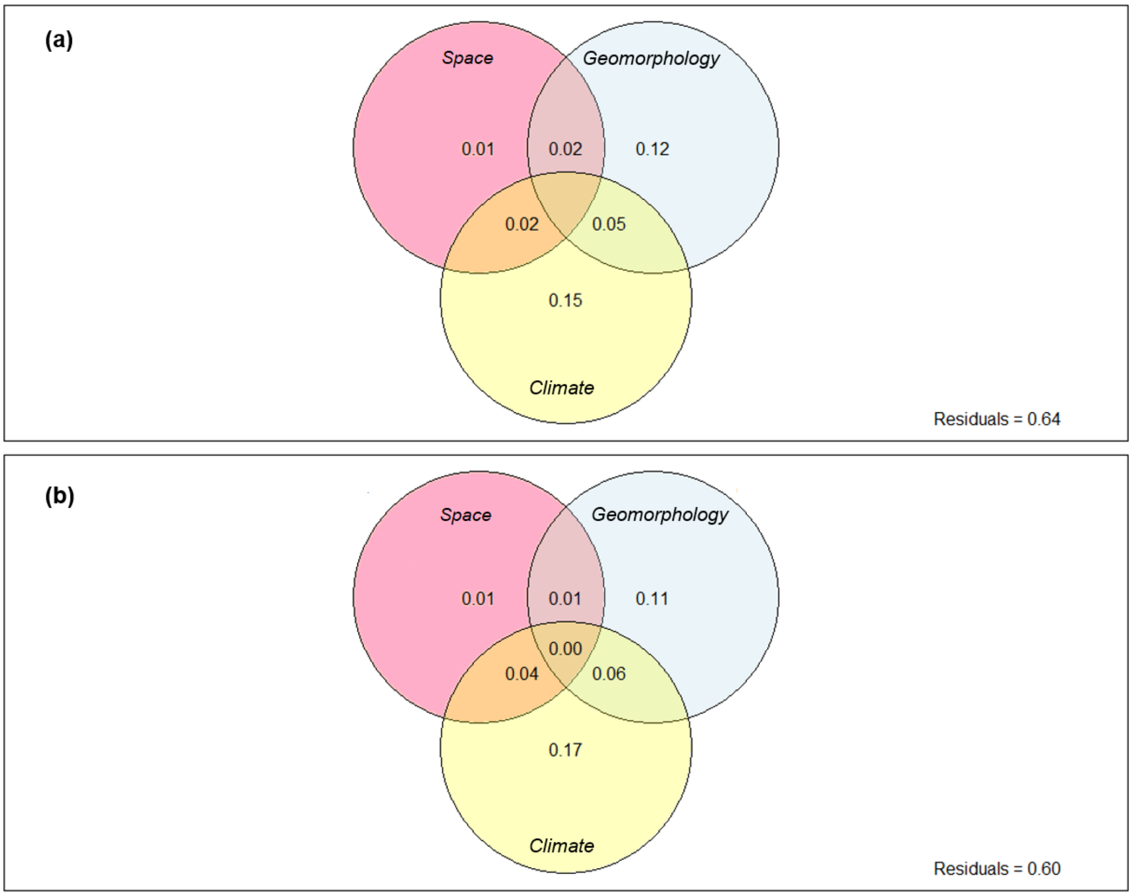

Fig. 7 Partition of the variation of the community matrix according to the three explanatory variable groups. a) Native species b) Alien species

The relationships between beta components clearly highlight how an increase in native beta replacement significantly reduce alien beta richness. This is in agreement with biotic resistance theory (Levine 2000; Levine et al. 2004). which state that resident species in a community reduce the success of exotic invasion through biotic filters such as competition, pathogens and herbivores. For what concerns the significance of LCBD values in native species, this could be manly explained by the presence of Interdune habitat that host a peculiar community which share few species with the other habitats.

Conclusion

Sand dune ecosystems represent fragile environments endowed of peculiar characteristics that make them unique both in terms of species vegetating than habitat features. Nowadays, there is an increasing need for monitoring and active manage these environments through concrete preservation and restoration actions of these habitats, where needed. Thus, coastal ecosystems are currently constrained between human-related threats from one side and shoreline erosion from the other, the so called "coastal squeeze" (Defeo et al. 2009). The present study analyzes through quantitative methods species diversity and their relationships in different coastal plant communities along a sea-inland gradient. A well-structured plant community may cope better with alien invasion that allow indirectly the protection of endemism or rare species. For instance, it would be advisable to preclude or fence some parts of the beach that host priority habitat, rare species or endemisms. Furthermore, we demonstrated that an increase in the beta diversity of native species can cope better with alien species spread ensuring ecosystem integrity and functioning. Eradication programs may be planned where higher levels of alien beta diversity are observed optimizing time and resources. Lastly, it is worth to remind also the several ecosystem services that coastal habitats provide for. Specifically, in a climate change scenario, these ecosystems may have a chief role in coastal protection against storms, in water purification and other sociocultural aspects (Martinez et al. 2004; Van der Meulen et al. 2004; Worm et al. 2006; Everard et al. 2010).

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Chapter 3

Make it simpler: alien species decrease functional diversity of coastal plant communities

Tordoni E, Petruzzellis F, Nardini A, Savi T, Bacaro G Make it simpler: alien species decrease functional diversity of coastal plant communities

(Journal of Vegetation Science – *Under Review*)

Abstract

Sand dune ecosystems are peculiar environments rich in rare species and endemism. Over the last decades, these habitats that naturally suffer harsh abiotic conditions have been heavily threatened by human-induced alterations and biological invasions. However, mechanisms of plant invasion in these habitats are not fully understood, especially in relation to the role of functional diversity of native communities in filtering alien species. In this study, we sampled psammophilous vegetation along belt transects in two sampling sites in northern Adriatic coastline. Our aims were: 1) to assess eventual differences in functional traits between native and alien species; 2) to highlight traits favouring the invasion process; 3) to explore functional diversity patterns in sand dune habitats and detect eventual signals of small-scale functional homogenization induced by the occurrence of alien species. Plant species richness and abundance have been assessed in 128 plots along with a suite of plant functional traits. Differences in trait values between species group within habitat were tested through Wilcoxon rank sum test, and a multiple linear regression was computed to assess traits related to invasiveness. Multivariate statistics (β functional diversity and functional rarefaction curves) were used to explore functional diversity patterns. Our results showed that alien species display different ecological strategies than natives, owing higher values of performance-related traits such as Specific Leaf Area, and displaying lower functional diversity. Moreover, we were able to distinguish a suite of functional traits possibly favoring the invasion process. Our data confirm also that alien species invasion drives the community towards small-scale functional homogenization, with deleterious effects for ecosystem functioning and potential loss of species or reduction in the functional space.

Keywords: Community ecology, Functional homogenization, Functional traits, Functional rarefaction, Quantitative methods.

Introduction

Coastal sand dune ecosystems represent one of the most fragile habitats in the Mediterranean basin (Kutiel et al. 2000). These environments are usually characterized by marked vegetation zonation, associated with strong environmental gradients (Acosta et al. 2009). These habitats often host rare species and endemism, despite the harsh abiotic conditions and stress factors (e.g. sand burial, salinity, drought). As a consequence, sand dune species often exhibit peculiar adaptations to these stress factors (Maun 2009). Dune ecosystems are suffering several threats mostly human-related such as tourism, urbanization, and shoreline erosion (e.g. O'Shea and Kirkpatrick 2000); along with climate changes and biological invasions (Feagin et al. 2005; Prisco et al. 2013). Specifically, biological invasions are deemed one of the most important drivers of biodiversity loss and modification of ecosystem services worldwide (Millennium Ecosystem Assessment 2005). Thus, Invasive Alien Species (hereafter IAS) have strong negative effects on natural ecosystems (Vilà et al. 2011), by modifying species composition (Hejda et al. 2009; Powell et al. 2011) and altering nutrient cycle (Ehrenfeld 2010). However, mechanisms responsible for the IAS spread in sand dune communities are still poorly understood. Disturbances in residence communities often enhance alien species spread due to changes in resource availability and reduced competition (Hobbs 1989; Eschtruth and Battles 2009). However, a deeper understanding of invasion processes from a functional diversity perspective is still lacking (Funk et al. 2008). Functional diversity has gained a pivotal role in ecological research in the last decades, with increasing numbers of published studies and species investigated (Petchey and Gaston 2006). This facet of biodiversity is directly represented through species traits (McGill et al. 2006) that indirectly define species' ecological niches (Lavorel et al. 1997). Functional traits can be classified on the basis of efforts required to measure them, i.e. "soft traits" (more readily quantifiable, e.g. Specific Leaf Area - SLA) versus "hard traits" (difficult to measure or based on time-consuming experimental procedures). More recently, Brodribb (2017) suggested to distinguish functional traits from "mechanistic traits", where the latter are traits whose function can be clearly physiologically defined (e.g. xylem vulnerability to embolism, turgor loss point), whereas general functional traits such as SLA or wood density rather represent 'syndromes' that can be associated to different physiological functions and associated trade-offs.

Plant traits have been successfully used to improve our understanding of ecosystem functioning (Helsen et al. 2012), and for predicting climate-induced changes in vegetation (Lavorel and Garnier 2002). In a meta-analysis on performance-related traits, Van Kleunen et al. (2010) demonstrated that IAS tend to outcompete non-invasive species due to higher values of functional traits related to growth rate and resource acquisition, such as photosynthetic rate. Recent studies (Tecco et al. 2010;

Funk et al. 2016) suggest that there is not a unique suite of traits responsible for plant species invasiveness, but rather highlight the context dependence between traits of invaders and the characteristics of the invaded environment (e.g. Pyšek and Richardson 2008; Funk 2013). The limiting similarity hypothesis proposes that the successful establishment of invasive species would be unlikely if the native species of the recipient community hold similar functional traits and thereby similar resource acquisition strategies as the invader (MacArthur and Levins 1967; Strayer et al. 2006), resulting in increased competition for resources (Funk et al. 2008). Additionally, mechanisms underlying invasiveness markedly change between high and low-resource ecosystems, such as sand dune habitats, with a larger amount of species displaying traits related to resource conservation rather than resource acquisition (Craine 2009; Funk 2013). Generally, in sand dune habitats, it has been observed that species diversity is not correlated with functional diversity, so that taxonomically different species exhibit the same suite of functional traits (Garcia-Mora et al. 1999), especially in communities closer to the drift line. In this study, through a systematic sampling design based on belt transects, we sampled psammophilous vegetation and measured leaf traits (both functional and mechanistic traits) in two sampling sites in northern Adriatic coastline with the following specific aims: i) to test differences in functional traits between native and alien species between habitats, ii) to assess which suite of traits may likely promote invasiveness, iii) to disentangle the effect of IAS on functional diversity patterns of the communities under investigation along with a potential small-scale functional homogenization effect on the resident native species.

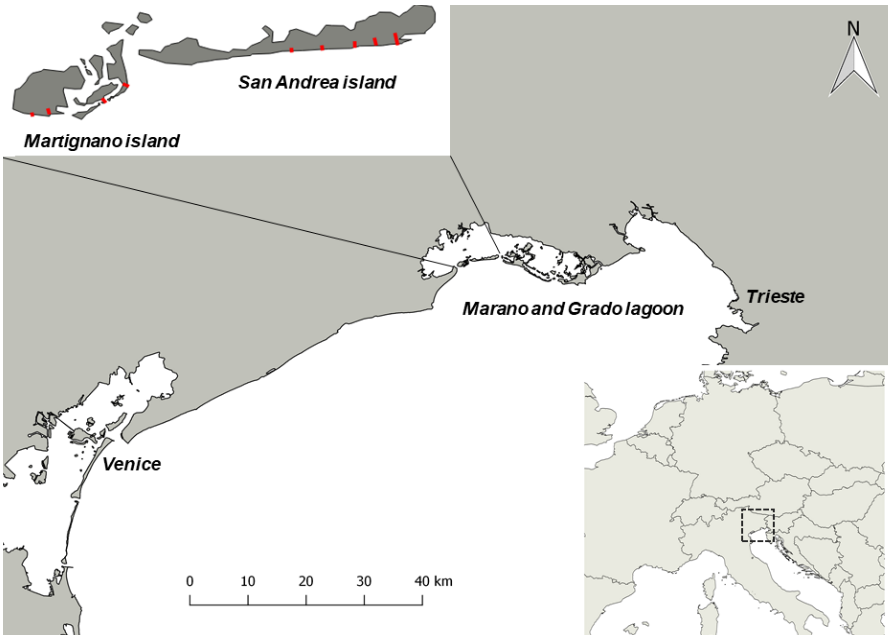

Fig. 1 Map of the study area, on the bottom right the geographical position respect to the Italian peninsula; on top left a particular of the two sampling sites. Red lines represent the transects

Materials and methods

Study area

The study area encompasses some of the few remnants of natural sand dune vegetation in northern Adriatic coastline, namely Martignano island and San Andrea island (Fig. 1). Since 1950s, these ecosystems have suffered strong alterations mainly due to an increase in tourism and urbanization (Nordstrom et al. 2009), resulting in few natural remnants along the coastline. In addition, the actual flora can be considered as the outcome of a "crossroad" of species with different origins (Alpine, Mediterranean and Eastern native range) due to the particular biogeographical location of the study area (Buffa et al. 2012). Both sampling sites belong to a network of European natural protected areas (Natura 2000 Network) called Marano and Grado lagoon (centroid coordinates 45.72216°N – 13.24836°E, *datum* WGS84). Climate in the area is influenced by Bora winds, which decrease thermal limits mainly during the winter. Mean annual temperature is about 12°C and mean annual precipitation averages 1000 mm (source https://www.meteo.fvg.it, reference period 1991-2010 accessed on December 5th 2017). A portion of the study site is characterized by semidiurnal tides and seasonal tidal inundation, emerging from the sea level during the spring–summer period.

Sampling design

To collect vegetation data, a square grid 500 x 500 m in size was overlaid to the two sampling sites. In each cell, a random transect of variable length, according to dune extension and coast morphology (from 16 to 168 m), was identified following a sea-inland gradient. Transects were partitioned in a set of contiguous squared sub units (plots) 16 m^2 each, where the occurrence and the abundance (expressed as cover percentage based on visual estimation) of each vascular plant species were assessed. A total of 9 transects and 128 plots were sampled (41 plots in Martignano island and 87 in San Andrea island, respectively). Once sampled, each plot was assigned to a specific coastal habitat following the European Habitats Directive (92/43/EEC). For sake of comparison, plots were further classified in two major categories: i) foredunes including upper-beach, embryo-dunes and mobile dunes, ii) saltmarshes encompassing habitats associated with tidal flats, salt pans or salt lakes that may be permanently or temporarily wet. All the vascular plants occurring within each plot were identified following Pignatti (1982), and nomenclature was standardized according to Conti et al. (2005). Plants were classified as native or alien species according to Celesti-Grapow et al. (2009). Samples for measurements of functional traits were collected following a slightly different procedure. First, the transects containing the highest number of species in each island were selected. When two or more transects owned a redundant species pool, we discarded the one with the lowest species richness. In total, samples were collected from 6 transects out of 9. At least one individual was sampled for each species within each habitat in each transect. In total, functional traits were measured on 50 out of 75 species, accounting for about 96% of the total plant coverage. For the other species, it was not possible to measure functional traits for several reasons (e.g. dried individuals) and only traits derived from the literature were included in the analysis. Leaves or entire individuals were sampled, wrapped in cling film, put in humid sealed plastic bags, and stored in cool bags until processing in the laboratory. All fieldworks were carried out during June-August 2017. The whole list of functional traits included in this study is summarized in Table 1.

Functional traits measurements

The following leaf functional and/or mechanistic traits were measured: specific leaf area (SLA, mm^2 mg^{-1}), major and minor vein length per unit area (VLA_{major} VLA_{minor}, mm mm^{-2}), osmotic potential at full turgor (π_0, -MPa), water potential at turgor loss point (Ψ_{tlp}, -MPa), N and C content (N % and C %), C to N ratio (C:N), and C and N stable isotope composition ($\delta^{13}C$ ‰, and $\delta^{15}N$ ‰).

SLA was calculated as:

SLA = (Leaf Area) / (Leaf Dry Weight) [mm^2 mg^{-1}] [1]

SLA is generally considered a “soft” structural trait, which correlates with relative growth rate, photosynthetic rate, and nutrient concentration (Cornelissen et al. 2003). Plants adapted to arid and low-nutrient habitats usually have thicker and smaller leaves with increased lifespan and lower SLA (Pérez-Harguindeguy et al. 2013). Fresh leaves were scanned and leaf area was measured using the software ImageJ (Schneider et al. 2012). Leaves were then oven-dried for 48 h at 70°C and leaf dry weight was measured using an analytical balance.

Leaf venation architecture comprehends several structural features influencing plant performance (Sack & Scoffoni, 2013). We specifically measured the length per unit area of major and minor veins (VLA_{major} and VLA_{minor}) as:

VLA = Vein Length/Leaf sample area [mm mm^{-2}] [2]

For VLA_{major}, fresh leaves were scanned using a desktop scanner and the ratio between vein length and sample area was measured using PhenoVein software (Lobet et al. 2013). To measure VLA_{minor}, fresh leaves were cleared in NaOH 1M solution for 48-72 h at room temperature, carefully replacing solution when it turned from transparent to dark coloured. After initial clearance, small portion of leaves of about 1 cm^2 were cut and bleached in NaClO 5% for 1-2 min. Then, samples were treated in a sequence of ethanol solutions at increasing concentration (25%, 50%, 75%, 100%) and maintained in an alcoholic solution of toluidine blue (3%) overnight. Finally, samples were processed in a series of ethanol solutions at decreasing concentration and microscopic slides were finally prepared. Images of small portions (~5 mm^2) of leaves were captured with an optical microscope at 4x magnification equipped with a digital camera (model Syrio-2, Pbinternational) and VLA_{minor} was measured using PhenoVein software.

π_0 and Ψ_{tlp} are considered mechanistic traits, as they are clearly associated with drought resistance (Bartlett et al., 2012b). Measurements were done following the method proposed by Bartlett et al. (2012a) with some modifications. Fresh leaves were first rehydrated for 3h and were then roughly crumbled without the petiole and sealed in cling film. After that, they were immersed in liquid nitrogen (LN_2) for 2 min. Leaves (still sealed in cling film) were then carefully ground and stored in sealed plastic bottles at -20°C until measurements. Samples were thawed at room temperature for 5 min while still sealed in cling film and in plastic bottles, just before measuring π_0 with a dew point potentiameter (Model WP4, Decagon Devices Inc., Pullman, Washington, USA). Ψ_{tlp} was then calculated according to Bartlett et al. (2012b).

Plant Functional Trait	Data type	Attribute
Life form	Nominal	Phanerophyte, Chamephyte, Hemicryptophyte, Geophyte, Therophyte, Helophyte
Photosynthetic pathway	Nominal	C3, C4, CAM
Sprouting	Nominal	-
Vegetative propagation (clonality)	Binary	Clonal, Non-clonal
Flowering length	Quantitative	[Months]
Specific Leaf Area	Quantitative	[mm^2mg^{-1}]
Vein density (minor)	Quantitative	[mm mm^{-2}]
Vein density (major)	Quantitative	[mm mm^{-2}]
Ψ_{tlp}	Quantitative	[-MPa]
π_0	Quantitative	[-MPa]
C:N	Quantitative	-
C	Quantitative	%
N	Quantitative	%
$\delta^{13}C$	Quantitative	‰
$\delta^{15}N$	Quantitative	‰

Table 1 Description of plant functional traits used in this study

Leaf traits related to elemental composition, namely N %, C %, C:N, $\delta^{13}C$ and $\delta^{15}N$, were measured on dried pulverized leaves. Leaves were oven dried (70 °C for 48h) and then pulverized in a mortar. Dry and ground samples were analyzed for carbon and nitrogen contents (% dry weight) and carbon and nitrogen stable isotope ratios was assessed via elemental analyzer/continuous flow isotope ratio mass spectrometry using a CHNOS Elemental Analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) coupled with an IsoPrime 100 mass spectrometer (Isoprime Ltd, Cheadle, UK). All isotope analyses were conducted at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley. Long-term external precision based on reference material “NIST SMR 1577b” (bovine liver) is 0.10‰ and 0.15‰, respectively for C and N isotope analyses.

Statistical Analysis

Community-level Weighted Means (CWMs) and Rao’s quadratic entropy (hereafter Rao Q) per plot (as a measure of functional diversity) were calculated through package FD (Laliberté et al. 2014) for native and alien species group and for the whole community. Differences in quantitative functional traits values between native and alien species within habitat were tested trough Wilcoxon rank sum test. A multiple linear regression analyses was computed between the normalized cover of alien species as the response variable (obtained for each plot dividing the total alien cover by the total plant cover in order to exclude empty spaces and make it independent from the local plant community coverage). As explanatory variables, CWMs per plot plus the habitat factor (2 levels: Foredunes and Saltmarshes) were used to assess which functional traits may be related with invasiveness. Prior to analysis, quantitative CWMs were standardized (zero mean, unit variance) to obtain comparable regression coefficients. A Minimum Adequate Model (MAM) was obtained using package “glmulti” (Calcagno 2013) through AIC minimization criteria plus a backward procedure to avoid multicollinearity among selected explanatory variables.

CWMs were also used to calculate pairwise functional distances among plots through the package “adiv” (Pavoine 2017): a generalization of the Gower distance allowing the treatment of various statistical types of variables was applied (for more details about methodology see Pavoine et al. 2009). The obtained distance matrix was used to detect shifts in functional composition between habitats in each species group (alien and native). To this aim, a functional β diversity metric was calculated using the framework proposed by Baiser & Lockwood (2011). The average pairwise dissimilarities were tested for location differences between group centroids in the multivariate space though permutations (999) using *betadisper* function in the “vegan” package (Anderson et al. 2006; Oksanen et al. 2017). Since permutation test performed on group centroids had the wrong type I errors, spatial medians were selected as group centroids as suggested by Oksanen et al. (2017).

Functional rarefaction curves (Ricotta et al. 2012) based on the analytical computation of Rao quadratic diversity index have been also calculated separately for native and alien species group. However, considering the large difference in the number of species within each group, comparing functional rarefactions derived by such a different assemblage, may provide trivial results. For this reason, we set up a null model to test the potential bias in patterns of functional rarefaction due to the imbalance in species number in natives and aliens. In more detail, a restricted randomization procedure was adopted: first, a functional distance matrix was calculated considering functional traits belonging to 9 randomly selected native species by the whole native assemblages. Then, the Rao Q statistics were calculated multiplying the functional distances obtained in this way for the abundances of the alien composition matrix. This procedure was repeated 999 times and the "average" functional rarefaction curve was calculated. This curve expresses the expected functional diversity of an assemblage of native species that resemble the diversity (in terms of distribution and abundance) of the observed alien community. Furthermore, the relationship between the Rao quadratic diversity (as response variable) and the normalized cover of alien species was evaluated by a simple linear regression model. Two separate models were fitted in each habitat to detect alien cover effect on functional diversity splitting the dataset according to an arbitrary threshold of normalized alien cover (≤ and > 50 % of normalized alien cover, respectively). Finally, functional uniqueness was calculated in each species pool within habitat according to the framework proposed by Ricotta et al. (2016). This index measures the diversity decrease obtained by including interspecies dissimilarities in the calculation of functional diversity, and its complement may represent a valuable measure of community-level functional redundancy (Ricotta et al. 2016). Both functional rarefaction curves and functional uniqueness index have been computed using "adiv" package (Pavoine 2017).

All statistical analyses were performed using R 3.4.1 (R Core Team 2017).

Results

A total of 75 species was detected (9 aliens and 66 natives). The rate of invasion (12%) resulted lower than reported for the total Italian vascular flora (13.4%) but higher than the average of the Friuli Venezia Giulia Region (9.9%; Celesti-Grapow et al. 2010). Among alien species, the most abundant were *Oenothera stucchii* Soldano (54.7 % of the sampled plots), *Xanthium orientale* subsp. *italicum* (Moretti) Greuter (46.9 %) and *Ambrosia psilostachya* DC. (45.3 %). All the alien species found in the survey are deemed invasive according to the Italian alien checklist except one (*Yucca gloriosa* L., now considered naturalized); most of them (78 %) originated from North America. Averaged plot species richness for each habitat is reported in Table 2. Wilcoxon test showed significant differences for most functional traits in each group (Fig. 2). On average, alien species accounted for higher SLA and VLA_{minor} in both habitats being less drought resistant (higher π_0 and Ψ_{tlp}). These species also displayed higher N % and lower $\delta^{13}C$ and C:N, especially in saltmarshes. A significant regression model (F (4, 101) = 16.17, $p < 0.001$, $R^2_{adj} = 0.37$) was obtained using 3 traits out of the 15 available. Specifically, the MAM minimizing the AIC value (best fit 1012.4) showed an increase of the standardized alien cover moving from saltmarshes to the foredunes habitat, with a general negative linear relationship of alien cover with respect to the C:N ratio and a positive relationship with Ψ_{tlp} and SLA (Table 3).

Species group	Habitat	
	Foredunes	Saltmarshes
	n = 97	n = 31
Total	5.84 ± 2.85	7.42 ± 2.13
Native	3.54 ± 2.22	6.35 ± 1.87
Alien	2.03 ± 1.15	1.06 ± 1.26

Table 2 Species richness (Mean ± SD) between habitats in each species group

Variable	**Estimate**	**SE**	**Pr(>|t|)**
(Intercept)	55.35	2.95	***
Habitat (Saltmarshes)	-37.27	7.93	***
SLA	30.22	5.61	***
Ψ_{tlp}	7.19	3.24	*
C:N	-22.20	5.24	***

Table 3 Minimum Adequate Model of the GLM computed using normalized alien cover as response variable (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant)

Wilcoxon test showed significant differences for most functional traits in each group (Fig. 2). On average, alien species accounted for higher SLA and VLA_{minor} in both habitats being less drought resistant (higher π_0 and Ψ_{tlp}). These species also displayed higher N % and lower $\delta^{13}C$ and C:N, especially in saltmarshes. A significant regression model (F (4, 101) = 16.17, $p < 0.001$, $R^2_{adj} = 0.37$) was obtained using 3 traits out of the 15 available. Specifically, the MAM minimizing the AIC value (best fit 1012.4) showed an increase of the standardized alien cover moving from saltmarshes to the foredunes habitat, with a general negative linear relationship of alien cover with respect to the C:N ratio and a positive relationship with Ψ_{tlp} and SLA (Table 3).

Permutations of functional distances according to habitat revealed a significant difference in functional complementarity (β diversity) for native species (F (1, 125) = 22.04, $p = 0.001$) with average distances to median of 0.37 in foredunes and 0.23 in saltmarshes. On the other hand, alien species showed a not significant outcome (F (1, 104) = 0.5, $p = 0.461$) with average distances of 0.27 and 0.25 in foredunes and saltmarshes, respectively. Functional rarefactions (Fig. 3) displayed a very clear pattern, as all the curves reached the asymptote meaning that our sampling effort optimally captured total functional diversity in sand dune communities. Native species saturated at higher level of Rao Q index accounting for a higher functional diversity compared to alien species pool.

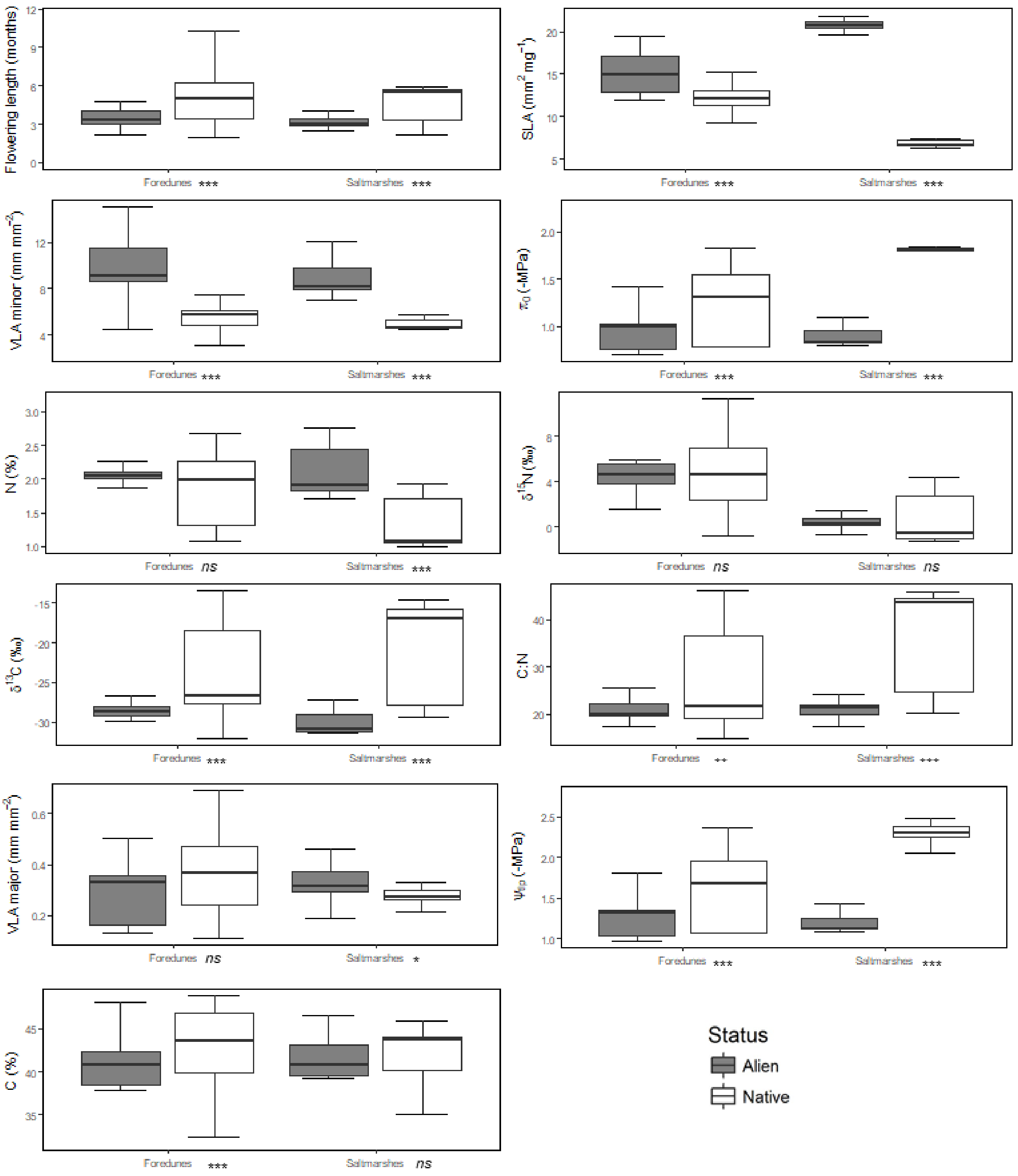

Fig. 2 Summary showing CWMs of quantitative functional traits in native and alien species between habitats. Significance of Wilcoxon test are reported (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = Not Significant)

The null model further supports this outcome. Indeed, despite replacing the functional traits in the alien species with those of nine native species randomly selected and keeping fixed the spatial structure of the alien community, the functional diversity of natives still remained higher than that of the aliens. Fig. 4 represents the trend of Rao Q index according to alien cover in each transect. On average, a decrease in functional diversity (lower Rao Q) is associated to a peak in alien species coverage (e.g. T6 and T9). This trend is further corroborated by a significant simple linear regression between Rao Q and alien cover analyzing separately the dataset according to alien cover threshold (≤ and > 50 %, respectively; Fig. 5). In addition, larger range of community-level functional uniqueness (ΔU) are observed in native species indicating higher plot-to-plot variability in the dispersion of trait values. On the other hand, alien species traits are more redundant (lower ΔU, Table 4).

	Alien species		**Native species**	
	Foredunes	Saltmarshes	Foredunes	Saltmarshes
min	0.30	0.31	0.28	0.34
mean	0.40	0.48	0.59	0.57
max	0.66	0.73	0.84	0.88
ΔU (max - min)	0.36	0.42	0.56	0.54

Table 4 Summary statistics of community-level functional uniqueness by habitat for each species group

Discussion

Functional traits in sand dune communities

Our results highlight that IAS tend to outcompete native species due to higher SLA, π_0 and Ψ_{tlp} and thus minimizing leaf construction and maintenance costs (Fig. 2). In a low-resource system like sand dune environments (Maun et al. 2009), native species are expected to have a competitive advantage over invasive species (Daehler 2003). According to the biotic acceptance theory (Stohlgren et al. 2006), environments richer in resources can potentially host more alien plants. However, it is well known that many alien species do occur even in stress-prone ecosystems (e.g. Funk and Vitousek 2007). According to the leaf economics spectrum (LES, Wright et al. 2004), invasive species are generally characterized by a “fast-return” strategy (Funk 2013) or “acquisitive” strategy (Díaz et al. 2016) and our results are in agreement with this pattern. Native species apparently invested more biomass to develop “conservative” leaves (lower SLA) more resistant to drought stress (more negative values of π_0 and Ψ_{tlp}), which may promote longer leaf lifespan and higher survival chances in the face of abiotic and biotic stress factors (Wright et al. 2004). Despite the higher SLA, IAS also had higher VLA_{minor}, which has been often correlated to a reduced resistance to water transport within leaves and, thus, higher photosynthetic rates (Sack and Frole 2006; Funk and Vitousek 2007). This is particularly true in phylogenetically distant species (Brodribb et al. 2010), whilst the trend is not always consistent when closely related species, or species occurring in the same habitat are compared (Roth-Nebelsick et al. 2001; Nardini et al. 2014). In the present study, $\delta^{13}C$ was significantly lower in IAS, indicating that these species might have higher gas exchange rates than native ones, supporting the hypothesis that alien plants also reach higher photosynthetic rates (Van Kleunen et al. 2010).

Several studies have showed that invasive species tend to be more performant than non-invasive species (e.g. Van Kleunen et al. 2010; Godoy et al. 2011), irrespective of biogeographical location or biological factors. In addition, IAS frequently show more successful dispersal strategies, based on the production of larger amount of seeds with higher germination rates compared to natives (Lloret et al. 2004; Dauer et al. 2007). These patterns are supported by the output of our model, whereby IAS coverage was mainly related to resource use and acquisition traits, namely SLA, C:N and Ψ_{tlp}. In particular, by minimizing leaf construction costs (higher SLA) and drought resistance (higher Ψ_{tlp}), while maximizing resource acquisition (lower C:N), made IAS very abundant in the study area (Table 3). The decrease in alien cover moving from foredunes to saltmarshes is the likely outcome of strong limiting factors in this habitat (e.g. higher soil salinity), much more selective for IAS than for native species that are better adapted to withstand water and salt stress (Casolo et al. 2014). Consequently, stronger differences in functional trait patterns between native and alien species are observed in saltmarshes. It is also possible that here the IAS do not directly compete with native species, as they mostly grow in summer or they possibly access different nutrient pools (as indicated by the higher N %), highlighting their potential niche distinctiveness (Pérez-Ramos et al. 2012). Clearly, measuring below ground traits may help disentangling this conundrum of functional ecology (Dawson 2015).

Functional diversity in sand dune communities

Patterns of functional diversity in coastal sand dune communities tend to follow the well-known sea-inland gradient (Acosta et al. 2006). Particularly, our results show that functional diversity increases moving from the drift line to the inner part of the beach (Fig. 4), that is less exposed to harsh abiotic conditions (Ricotta et al. 2012). Accordingly, species growing closer to the sea are more specialized and share the same suite of functional traits, unlike species growing inland less exposed to the strong limiting factors (Garcia-Mora et al. 1999; Acosta et al. 2006).

Carboni et al. (2013) suggested that differences in species composition alone (and then in phylogeny) should be interpreted with caution as a proxy for functional structure, as this approach may fail to capture the major functional aspects of the community under investigation. Likewise, a simulation study performed by Baiser and Lockwood (2011) revealed that the relationship between taxonomic and functional diversity strongly depend on trait redundancy and overlap, that is the more a species pool exhibits unique trait composition, the greater is the risk of functional homogenization.

Our findings suggest a potential risk of invasion-induced small-scale functional homogenization of the native communities, as shown by the observed lower values of Rao Q index for alien species (see Fig. 3).

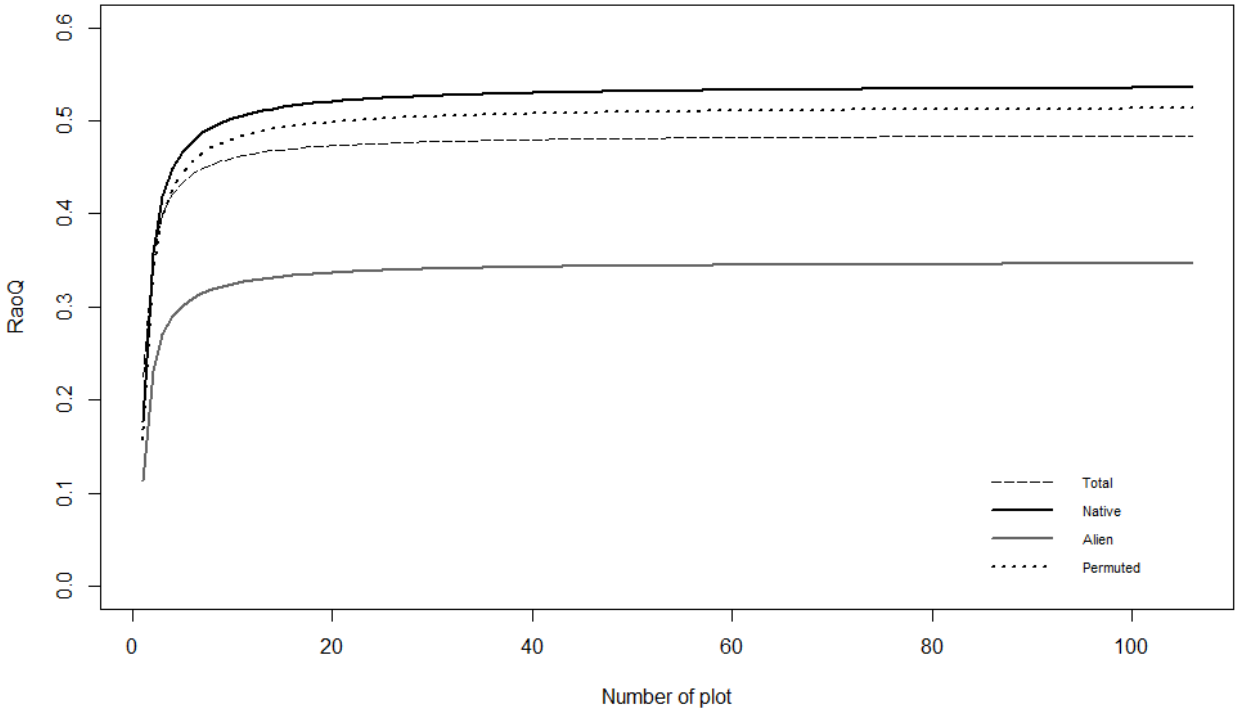

Fig. 3 Functional rarefaction curves of expected functional diversity (RaoQ) and cumulative number of plots considering all species pooled (total), native species, alien species and the curve averaged from permutations (permuted). Please note that x axis was cut to 106 plots

To the best of our knowledge, whereas several studies investigated the role of IAS in biotic homogenization (e.g. McKinney and La Sorte 2007; Qian and Guo 2010), only few of them assessed the role of IAS from a functional point of view (Abadie et al. 2011; Tobias and Monika 2012; Brice et al. 2017). Functional homogenization has been already detected in other ecosystems (Brice et al. 2017) and organisms (Villéger et al. 2014), and it is generally associated with several triggering causes (e.g. landscape disturbance in Abadie et al. 2011, flooding in Brice et al. 2017). Under an invasion scenario, as the one proposed in Quian and Ricklefs (2006), we expect to observe a growing number of IAS or of their abundances to detriment of native species in the next future. Albeit a taxonomic homogenization is not always associated to a functional homogenization (Sonnier et al. 2014), we hypothesize that changes in community composition caused by human-induced ecosystem alterations along with alien species spread may reduce the functional diversity of native communities leading to small-scale functional homogenization, as reported also in Lambdon et al. (2008). In support to this hypothesis, a decrease in functional diversity was associated with increased IAS cover

(Fig. 5). Indeed, when IAS cover exceeds 50% of the total plot vegetation cover, a significant decrease of functional diversity (Rao Q) is observed. This may be due to the role of rare species that owe specific functions such as maintaining ecosystem functioning through periods of environmental changes (Lyons et al. 2005). Moreover, it has been experimentally demonstrated that the removal of rare species can increase the susceptibility of communities to invasions (Lyons and Schwartz 2001). Additionally, the larger range of uniqueness (ΔU) observed in native species, could be the legacy of greater residence time that allowed native species better adapted to environmental niches (Pyšek et al. 2009).

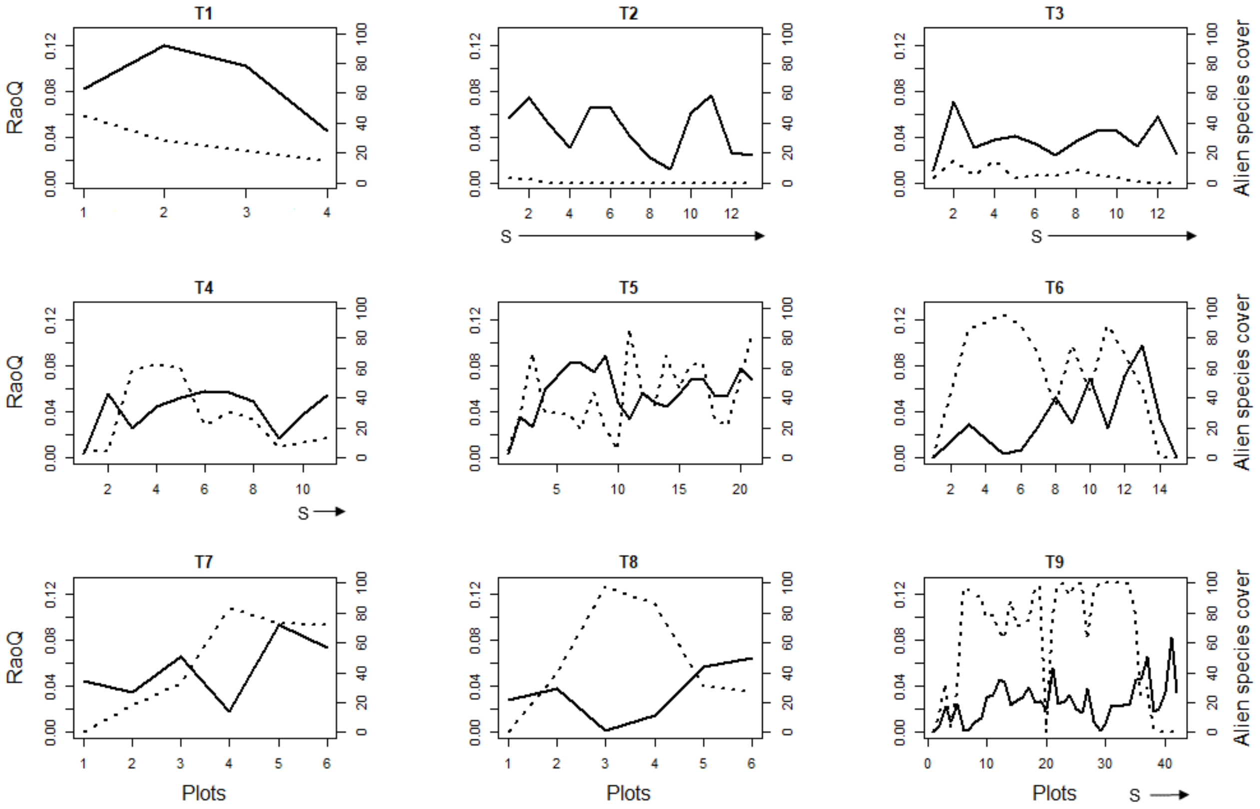

Fig. 4 Pattern of functional diversity (RaoQ, solid lines) and normalized alien species cover (dotted lines) along each transect. The S below x axis denotes the starting plot of the saltmarshes

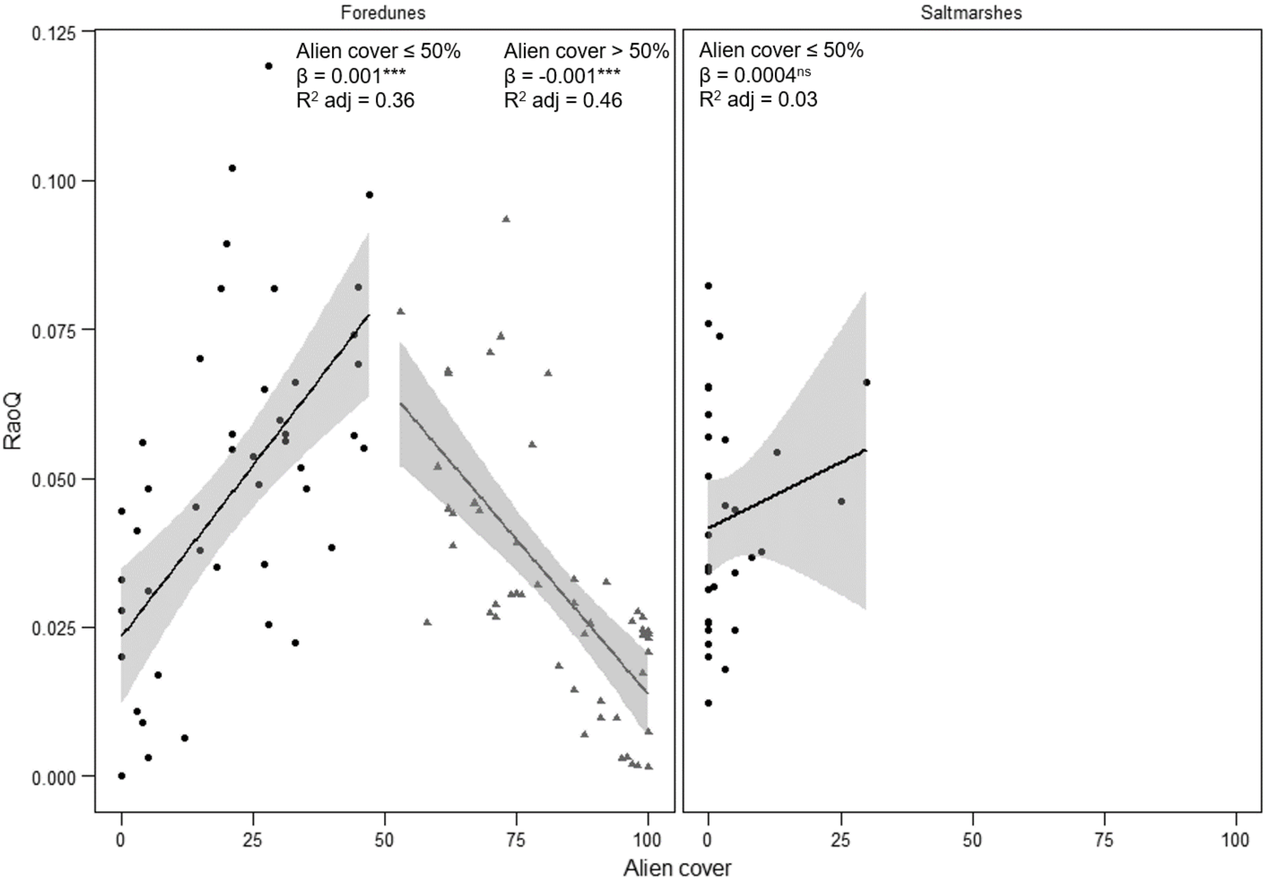

Fig. 5 Relationship between RaoQ and normalized alien cover in each habitat, shaded area represents 95% confidence intervals (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = Not Significant)

Our study also introduces some methodological novelty in the analysis of the invasion patterns and processes. In fact, our analysis proposed the use of functional rarefaction techniques to evaluate the expected functional simplification of plant community due to the IAS presence along with their potential functional homogenization effect. Accordingly, the developed null model described above shows the expected functional diversity reduction assuming a reference plant community corresponding to the sampled alien species assemblage (in terms of abundances and spatial distribution). As can be easily deduced, the functional diversity of the randomized communities was decreased with respect to the observed native community, mainly due to the underestimation of rare species typical of sand dune environments. To conclude, we pointed out how alien species may affect native species pool beyond the simple taxa reduction, namely through reducing the local functional diversity of the communities under investigations.

Conclusion

This is one of the first studies including a large number of functional traits measured in different species in sand dune environments. Our results suggest that native species display functional traits more associated to stress resistance whereas alien species are characterized by traits linked to acquisitive strategy coupled with a better resource use. Nevertheless, it is worth stressing the concept that the invasion process is strongly context-dependent and IAS can have distinct impacts in recipient native community in different ecosystems both at taxonomic and functional levels (e.g. Hulme et al. 2013; Funk et al. 2016). Furthermore, a signal of potential functional homogenization in sand dune ecosystems has been detected due to the lower functional diversity and community-level functional uniqueness expressed by alien species. Nonetheless, as pointed out by Tobias and Monika (2012), functional homogenization should be explicitly studied as an independent phenomenon. Future outlooks foresee to increase the extent of the study area to assess if the signal of functional β diversity remains constant at larger spatial scales. Secondly, it will be crucial to integrate root and seed functional traits considering also intraspecific variability (Petruzzellis et al. 2017) to depict a more comprehensive framework of the invasion strategy.

Acknowledgments

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Chapter 4

Disentangling plant diversity in sand dune ecosystems: a global perspective from patterns to processes

Tordoni E, Bacaro G, Weigelt P, Cameletti M, Janssen J, Acosta ATR, Bagella S, Bergmeier E, Buckley HL, Ciccarelli D, Forey E, Hennekens SM, Lubke RA, Mahdavi P, Peet RK, Peinado M, Sciandrello S, Kreft H Disentangling plant diversity in sand dune ecosystems: a global perspective from patterns to processes

(*In preparation*)

Abstract

Coastal sand dune ecosystems represent fragile environments rich in endemism and key stone species that occur from the polar regions to the tropics. These habitats experience harsh abiotic conditions and high natural levels of disturbance but are nowadays increasingly threatened by human-induced encroachment and biological invasions. Here, we collated a global dataset of 14,841 plots and phytosociological relevès from coastal sand dune ecosystems around the world to discern global patterns of native and alien plant diversity across habitats and floristic kingdoms and at understanding the main determinants of species richness in native and alien species. Generalized Linear Models were performed to explore patterns of species richness; Bayesian Generalized Linear Mixed Models have been applied to assess the main ecological determinants underlying native and alien species richness, thanks to their capability to cope with zero inflation and complex model structures. Models' results highlighted how native and alien species showed different patterns according to habitat and floristic kingdom; specifically, native species richness tended to increase according to the sea-inland gradient showing higher values in Cape and Paleotropical kingdoms. Conversely, alien species richness was more homogeneous across habitats and kingdoms. Bayesian GLMMs suggested strong differences among the drivers influencing native and alien species richness. In more detail, anthropogenic factors such as Gross Domestic Product may be considered the main drivers of alien species richness whilst native species richness seems to be more influenced by a combination of climate and habitat features. In conclusion, we demonstrated how native and alien species in coastal sand dune environments behave differently across habitats and floristic kingdoms and how they are differentially influenced by various ecological factors. Gaining a more detailed and more mechanistic understanding of the causes of invasion worldwide would allow more focused control and management measures, which would more effectively mitigate new invasions before they cause major impacts and become too costly to control and eradicate.

Keywords: Alien species, Bayesian modelling, Biogeography, Generalized Linear Mixed Model, Invasion paradox, Species richness.

Introduction

The coastlines of our planet extend to approximately 1.5 million km of which about 16 % are sandy beaches (Martínez et al. 2013). Along these coastlines, sand dune ecosystems are widely distributed and occur from the polar regions to the tropics, encompassing a wide range of climates, biomes and habitats (Snead 1972; van der Maarel 1993a, b; Maun 2009). Sand dune ecosystems provide key ecosystem services such as protection from erosion and storms as well as water purification and storage (Van der Meulen 2004; Everard et al. 2010; Garcia-Lozano and Pintò 2017). Vegetation plays a primary role both in sand dune formation and consolidation thanks to its ability to stabilize the substrate and to enhance sand deposition (Maun 2009). Additionally, the great diversity observed in these ecosystems in terms of plant community composition, species rarity and endemism has been already well acknowledged in literature (e.g. Martínez et al. 2008; Acosta et al. 2007, 2009). Regardless of their differences in species composition, these environments are characterized by strong azonal features (Acosta et al. 2009; Mahdavi and Bergmeier 2016). Thus, sand dune habitats can be framed in a peculiar sea-inland gradient (’zonation’) that is generally constant across sites and biomes and originates from the harsh ecological conditions to which these habitats are exposed. Specifically, sand burial, sand blasting, marine aerosol and lack of nutrients represent the strongest limiting factors acting on sand dune species and habitats. An estimated 41% of the human population lives within 100 km of the shoreline (World Resource Institute 2005), and the number and proportion of people living in coastal areas is steadily increasing in the last decades (Curr et al. 2000; Reidesma et al. 2006; Brown et al. 2013). This has led to the fact that many sand dune environments have recently suffered high levels of habitat simplification and heavy loss of biodiversity (Dolan and Walker 2006). Human encroachment including tourism and urbanization on the one hand along with an increased shoreline erosion have led to the so called “coastal squeeze” (Defeo et al. 2009), leaving these ecosystems ‘trapped’ between erosion on the coastline and human settlements inlands. Another source of concern derives from biological invasions that are deemed a severe threat to worldwide biodiversity (second only to habitat loss and fragmentation, DAISE 2009; EEA 2012). Several ecological studies already demonstrated the negative effects of alien species on natural ecosystems including modification of species composition, perturbation of trophic networks, and habitat homogenization (see Vilà et al. 2011 for a meta-analysis). It has been calculated that the social cost of biological invasion has been accounted for approximately 5% of global Gross Domestic Product (Pimentel 2002), only in Europe this cost has been estimated in about EUR 12 billion €/year (Kettunen et al. 2008). Others negative impacts of alien species have been detected on ecosystem services and socio-economic sectors such as agriculture, fisheries and forestry (Vilà et al. 2010).

Coastal dune habitats are often reported to host many alien species, especially neophytes (introduced after 1500 AD; Von Holle and Motzkin 2007; Carboni et al. 2010) and are considered one of the most invaded ecosystems in Europe (Chytrý et al. 2008). Here alien species are exerting the strongest ecological impacts (see for instance Santoro et al. 2011) that may lead recipient communities even towards the extinction of native taxa of great conservation value, like endemic and keystone species, which are naturally abundant in sand dune ecosystems (Acosta et al. 2009). The effects of invasion are strongly scale-dependent and this topic has been already widely debated in literature (Levine and D'Antonio 1999; Fridley et al. 2007), even though a strong debate persists among scientists chiefly on the scale of the changes caused by alien species (Powell et al. 2011; Kumschick et al. 2015). Although one of the most prevalent impacts of alien species is represented by a reduction in the species richness of the invaded community (Vilà et al. 2015), the relationship between native and alien species across different spatial scales still remain a matter of discussion in plant ecology, producing different interpretations of the phenomenon for the different spatial scales considered. In more details, negative relationships are described at a finer scale (e.g., experimental or small-scale studies) while the opposite trend is observed increasing the observation scale (from landscape scale up to biome). At this regard, scientists coined the term 'invasion paradox' to describe the dynamic behavior of the interaction of scale and native–alien richness patterns (Fridley et al. 2007). Several studies (e.g. Forey et al. 2008; Brunbjerg et al. 2012) have shown that a suite of stressors and disturbance factors interact in shaping plant communities at different spatial scales; specifically, at a finer scale, biotic interactions predominate (Lortie et al. 2004) whereas environmental and biogeographical factors such as summer droughts and shoreline alterations become predominant increasing the spatial extent (Jiménez-Alfaro et al. 2015). Recently, great efforts have been made to disentangle broad-scale patterns of species richness across different taxa (e.g. Kreft and Jetz 2007 for vascular plants; Dyer et al. 2017 for birds; Song et al. 2017 for terrestrial nematodes). Several theories have been proposed to elucidate mechanisms responsible of species richness worldwide; most of them rely on the so called "water-energy dynamics" (Currie et al. 2004; Kreft and Jetz 2007) where species richness is controlled mainly by resources availability and climate constraints (Francis and Currie 2003). Other hypotheses act synergistically with the latter; in fact, outside wet regions, patterns of species richness may be driven by the sensitivity of most plants to frosts or droughts (Wiens and Donoghue 2004). Environmental heterogeneity has been claimed as a potential cause of species richness gradients through increased available niche space and enhanced species adaptations and coexistence (Stein et al. 2014). At last, historical and evolutionary processes (e.g. past climatic and geological events, Kerkhoff et al. 2014) have been considered to have a pivotal role in the formation of these gradients. More recently, König et al. (2017) pointed out as a complex interplay of ecological and environmental filters act to shape global species turnover in vascular plants.

To our knowledge, a comprehensive study shedding light on the relationships between patterns of native and alien species diversity in sand dune ecosystems and on their main drivers among habitats, across floristic kingdoms and considering different spatial scales, is still lacking. Here, we present for the first time a global analysis of vascular plant diversity using a large dataset of vegetation plots from five continents (Fig. 1). We focused on native and alien species richness, exploring their patterns and assessing the main processes underlying their distribution at a global scale. The following specific aims were addressed: i) to disentangle the global patterns of native and alien plant diversity on coastal sand dune ecosystems across habitats and floristic kingdoms, ii) to confirm the existence of an interaction between the spatial scale and the native-alien richness pattern, as foreseen by the invasion paradox theory and iii) to understand which are the main determinants of variation in species richness in native and alien species in these endangered ecosystems.

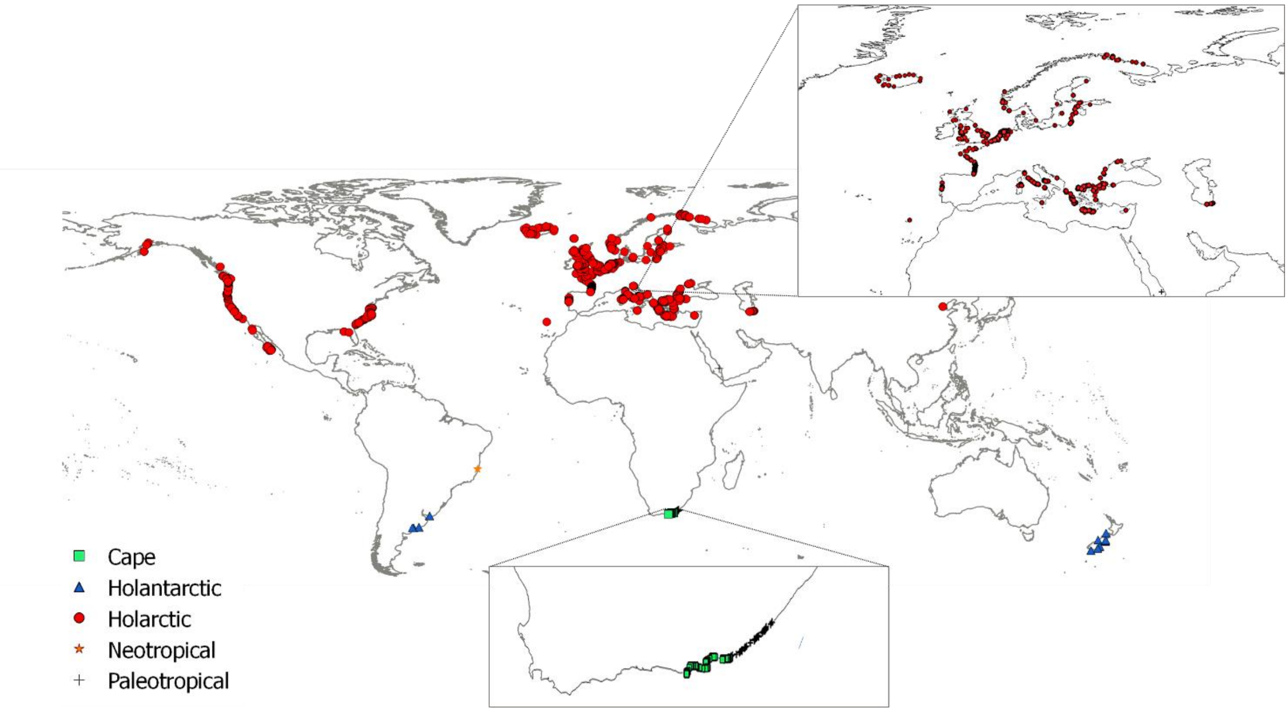

Fig. 1 Global map showing the distribution of the vegetation plots according to Takhtajan’s floristic kingdoms

Materials and methods

Study sites and species data

We collated a database consisting of 14,841 vegetation plots sampled in coastal sand dune communities distributed across Europe, North America, South America, Africa and Oceania. Species richness per sampling unit was obtained by plots and phytosociological relevès derived from literature and plant database (both public than private, see Table S1 in Appendix C). A study/relevé had to comply with the following inclusion criteria: 1) to present a georeferenced location, 2) to own a defined plot dimension, 3) to belong to a defined habitat or vegetation class (see below for the adopted classification). Species names were standardized at species level using taxonomy from Taxonomic Name Resolution Service (Boyle et al. 2013; http://tnrs.iplantcollaborative.org/). Furthermore, doubtful species and records not identified at the species level were omitted. The status of the species (native or alien), if not provided by data supplier, was assigned using online databases or national alien species checklists (see Table S2 in Appendix C). Thus, two response variables were obtained by the full set of plots: a) native species richness and b) alien species richness. Any observation with missing data for any of the variables described below was excluded from the analysis leaving 12,031 plots for analysis.

Environmental variables

We tested the following climatic variables as possible predictors of native and alien species richness: *Mean annual precipitation* (mm/year); *Precipitation seasonality* (a measure of the percentage variation in monthly precipitation totals over the course of the year; the larger the percentage, the greater the variability of precipitation); *Mean annual temperature* (°C) and *Temperature seasonality* (this is a percentage measure of temperature change over the course of the year). Climatic data were obtained from CHELSA database (Karger et al. 2017, accessed 04/05/2017), a high-resolution climatology (30 arc seconds, ~1 km) spanning the years 1973 to 2013. Values were assigned to each plot using Qgis 2.18.12 with GRASS 7.2.1 (Quantum GIS Development Team 2017). Each plot was classified into three main *habitat types*: (1) foredunes including upper beach, embryo dunes and mobile dunes, (2) fixed dunes encompassing communities dominated by perennial plants vegetating in the inner part of the coastline and (3) interdunes that comprehend distinctive habitats mainly constitute by swales and humid depressions. This classification based on dune dynamics was necessary to standardize the habitat due to the great heterogeneity present across the globe and to make this study comparable to the main body of literature on these environments (e.g. Forey et al. 2009; Lucrezi et al. 2014; Ciccarelli 2015). We also included *Insularity* (Mainland *vs* Island) and floristic *Kingdom* according to the floristic division of Takhtajan (1986) to control for the generally lower diversity of island communities and the effect of unquantified historical biogeographical processes.

Anthropogenic variables

We also considered a set of anthropogenic variables as potential predictors driving alien richness, as it has been already acknowledged in literature (e.g. Bellard et al. 2016; Chapmann et al. 2017). These are intended as surrogates of propagule pressure and/or potential introduction pathways. Among these, for instance, human population density has been identified as one of the main predictors of alien species richness at continental scale (Pyšek et al. 2010). *Year* of sampling was included to assess if there is an effect of time in the surveys. *Adjusted human population density* (people / km^2) based on the Gridded Population of the World (GPWv4, resolution 30 arc seconds) which provides gridded human population density estimated for the year 2015, adjusted to match United Nations (UN) estimated national-level population counts. As a proxy for trade volume, we used *Gross Domestic Product per capita*, (http://data.worldbank.org) based on Gross Domestic Product (hereafter GDP) constructed on purchasing-power-parity (PPP) per capita GDP (year 2015). Among human-related variables, proximity of airports, sea ports and cities have been recognized as facilitators of biological invasions for several taxa (e.g. Seebens et al. 2013; Bellard et al. 2016), we thus decided to include in this study the following predictors: *Distance to nearest city* with more than 50000 inhabitants (http://forobs.jrc.ec.europa.eu/products/gam/download.php); *Distance to nearest airport* (Pope and Sietinsone 2017) and *Distance to nearest port* (Ports 2013 - European Commission, Eurostat/GISCO; http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/transport-networks) .

All these datasets were accessed on 12/9/2017. Distances were calculated through proximity analyses using QGIS 2.18.12 with GRASS 7.2.1 (Quantum GIS Development Team 2017).

Statistical analyses

Species richness patterns

Differences in species richness across floristic kingdoms and habitats were tested using Generalized Linear Model (GLM). A Poisson GLM was initially fitted for native species richness but, considering the presence of overdispersion in the distribution of this response variable (the ratio between the mean and its variance was much higher than 1), standard errors were corrected applying the “quasipoisson” family errors. Alien species richness was modeled by a negative binomial GLM since the response variable had a high number of zeros (Gelman and Hill 2007). The explanatory power of each predictor was evaluated through Likelihood Ratio Tests in the package *car* (Fox and Weisberg 2011) and effects were displayed using the package *effect* (Fox 2003). As a measure of model fit, the amount of deviance accounted for each GLM (D^2, Guisan and Zimmerman 2000; Barbosa et al. 2014) was also computed. To quantitatively assess the “invasion paradox”, we fitted a negative binomial GLM to describe alien species richness as a function of native species richness, sampling unit size and their first-order interaction.

Ecological drivers

The ecological drivers of native and alien species richness were evaluated by means of a Bayesian Generalized Linear Mixed Models (hereafter BGLMMs) with random intercept to account for the study author. The variable habitat was nested in the floristic kingdom since not all the levels in habitat variable were present in all kingdoms. Due to the presence of an extreme plot size variability (range 0.04 - 10000 m^2), and aware of the well-known species-area relationship (Arrhenius 1921), plot size has been directly added in the models as a covariate to control for its effect on species richness. In order to linearize the relationship with species richness, some predictors were transformed as follow: population density and GDP were $\log_{10}$ (x+1) transformed whereas plot size was $\log_{10}$ transformed. Furthermore, before computing BGLMMs, all quantitative variables were standardized (zero mean, unit variance) in order to obtain quantitatively comparable coefficients.

BGLMMs were computed using package *rstanarm* (Stan Development Team 2016) since it allows to perform a full Bayesian inference using Hamiltonian Monte Carlo (HMC, see Betancourt et al. 2017 for more details about methodology) through its variant called No-U-Turn sampler (NUTS). It has been recently demonstrated that this algorithm tends to outcompete other Bayesian algorithms, being more efficient in drawing from the posterior distribution of the parameter and therefore saving computing time (Betancourt et al. 2017). Priors were specified having normal distribution (mean 0, standard deviation 1). To isolate the effect of each group variable, four models were fitted (two for native and two for alien species) considering environmental and anthropogenic variables separately. The error families were the same as for the GLM (Poisson and negative binomial for native and alien species, respectively). All models were run with four chains of 2000 iterations each, whereby the first 1000 samples of each chain were discarded before further analysis (so called warmup period) with a thin rate of 10. Hence, all reported results were based on 400 posterior samples (100 per chain). Convergence of all chains was assessed by assuring that all the potential scale reduction statistics (Rhat index) were below 1.1, and that the minimum number of effective samples were above 100

(Gelman and Rubin 1992). To control the number of divergent iterations, the following parameter were tuned: target acceptance rate (adapt_delta) of HMC was set to 0.999, the stepsize to 0.001 and max_treedepth to 20 to allow the algorithm to efficiently sample in a highly-curved space. The mean, standard deviation, Rhat values, effective sample size and the 95% credible intervals (uncertainty interval) of the posterior distributions of the parameters of interest were reported. For ease of interpretation, if the Bayesian uncertainty interval did not include zero, it was assumed that the independent variable has an effect on the response variable. Furthermore, the possible occurrence of spatial autocorrelation in each model was assessed by means of spline-correlograms using package *ncf* (Bjornstad and Falck 2001). 95% pointwise bootstrap confidence intervals were calculated from 1000 bootstrap samples of Pearson residuals after accounting for the level of spatial autocorrelation explained by the explanatory variables in each model. To further explore the role of ecological drivers on species richness, a variation partitioning approach through partial linear regressions was used to assess the total variation in native and alien species richness into purely environmental, purely anthropogenic, shared and unexplained fractions (Borcard et al. 1992; Legendre 2008).

All analyses were performed using R 3.3.3 (R Core Team 2017); detailed model formulas and specifications of the R code used were available in Appendix C.

Results

Global pattern of native and alien richness in sand dunes

Overall, values of native and alien species richness strongly varied among habitats and floristic kingdoms (Table 1). For native species, fixed dunes tended to have higher species richness compared to foredunes in all the floristic kingdoms. Interdunes tended to show intermediate values. Surprisingly, in some kingdoms such as the Cape and Holantarctic, alien species displayed an opposite pattern in respect to habitat compared to native species. This was further confirmed by the GLM results showing the trend of species richness across floristic kingdoms (Fig. 2). There was a significant interaction between habitat and floristic kingdom both for native and alien species (Likelihood Ratio Test χ^2 (6) =195.4, $p < 0.001$, $D^2_{adj} = 0.40$; χ^2 (6) =119.54, $p < 0.001$, $D^2_{adj} = 0.19$; respectively). These explanatory variables revealed to be strong predictors of global variation of species richness for natives whereas are relatively weak predictors for alien species (there is a difference of 21% of deviance explained by the two models). For native species (Fig. 2a), fixed dunes had higher species than foredunes within kingdoms. Cape and Paleotropical kingdoms had highest species richness for the three habitats considered. In contrast, Holantarctic resulted to be the significantly poorest ones.

Species group	Floristic kingdom	Foredunes (*n*= 4683)	Interdunes (*n* = 736)	Fixed dunes (*n* = 6612)
Native species	Cape	12.72 ± 7.78	12.12 ± 6.42	20.46 ± 9.74
	Holantarctic	1.02 ± 1.26	8.37 ± 5.16	10.42 ± 6.82
	Holarctic	6.17 ± 4.30	9.75 ± 8.56	16.3 ± 9.34
	Neotropical	-	-	9.27 ± 5.98
	Paleotropical	8.36 ± 4.62	16.40 ± 4.20	23.23 ± 8.00
Alien species	Cape	0.61 ± 0.70	0.12 ± 0.34	0.50 ± 0.51
	Holantarctic	2.42 ± 1.98	0.86 ± 1.40	0.98 ± 1.01
	Holarctic	0.27 ± 0.57	0.44 ± 0.86	0.34 ± 0.62
	Neotropical	-	-	0
	Paleotropical	0.06 ± 0.23	0.20 ± 0.42	0.31 ± 0.58

Table 1 Species richness (Mean ± SD) of Native and Alien species across habitats and floristic kingdoms

Unlike native species, alien species (Fig. 2b) had similar species richness values across all floristic kingdoms except for the Holantarctic that showed the highest level of alien species richness. The pattern showed greater variation respect to native species; specifically, foredunes showed higher level of alien plants respect to fixed dunes in Cape and Holantarctic kingdoms whilst the converse was observed in Holarctic and Paleotropical kingdoms. On average, interdunes tended to have lower levels of invasion. A negative relationship between native and alien species richness was observed without taking into account spatial scale (Fig. 3a). Interestingly, when the grain size is considered as showed in Fig. 3b, the slope of the relationship seems to shift from negative values to positive according to the grain size considered, in agreement with the “invasion paradox” expected pattern. The GLM with alien species richness as response variable showed a significant interaction between native richness and plot size (b = 0.0001, $p < 0.001$; Fig. 3b).

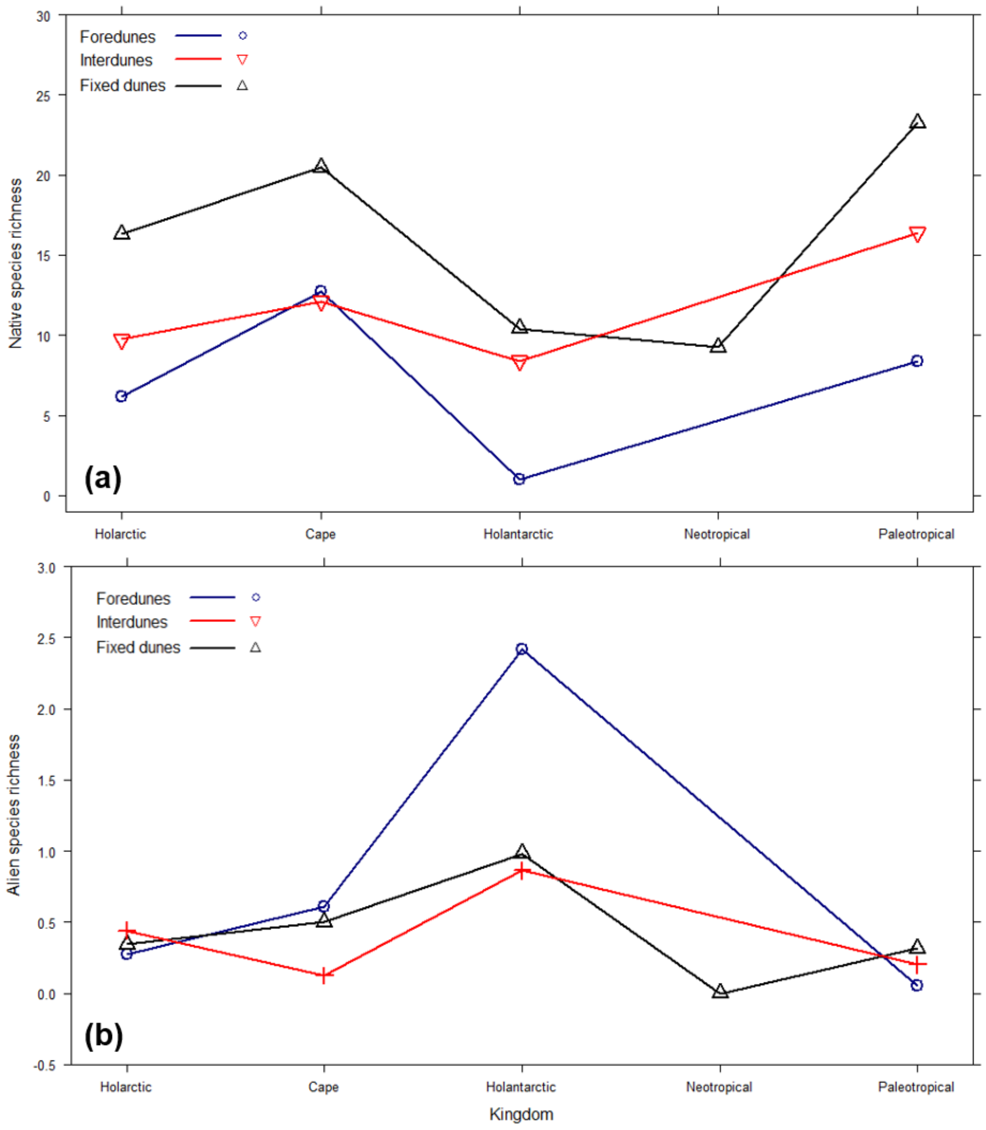

Fig. 2 GLM output showing the trend of species richness according to habitat and floristic kingdoms. a) Native species and b) Alien species

Global ecological determinants of native and alien richness

Bayesian GLMMs revealed large differences between alien and native species richness according to the two groups of variables considered. Native species richness more strongly reflected global environmental gradients and was only marginally related to anthropogenic variables. On the contrary, alien species richness was more strongly associated to human-related variables (Fig. 4). These outcomes are further corroborated by variation partitioning approach where native species are mainly driven by environmental variables whereas for alien species, as expected, anthropogenic variables accounted for greater percentage of variation explained (Fig. 5). Specifically, native species richness significantly differed among habitat and, furthermore, it was positively related to mean annual temperature (posterior mean 0.11 ± 0.01 SD), temperature seasonality (0.06 ± 0.02) and mean annual precipitation (0.05 ± 0.01). A negative posterior mean was observed for precipitation seasonality (-0.08 ± 0.01), meaning that higher seasonality was associated with less species. Insularity, in contrast, seemed to not have a pronounced effect on local coastal dune diversity of native plants. The only anthropogenic variables with a positive effect on native species richness were population density (0.10 ± 0.01) and distance to the closest airport (0.02 ± 0.004). A marginally positive effect was observed for the variable year (0.001 ± 0.002). For alien species, some strikingly different results were obtained. Interestingly, and in contrast to native species, insularity had a clear negative effect on alien species richness (-0.43 ± 0.18). Negative effects were also observed for mean temperature (-0.22 ± 0.06), precipitation amount (-0.11 ± 0.01) and precipitation seasonality (-0.18 ± 0.06). All anthropogenic predictors tested were highly informative (credible intervals do not overlap zero) confirming what already observed in previous studies. Notably, a positive trend was observed with GDP (0.78 ± 0.10), population density (0.05 ± 0.02) and year of sampling (0.01 ± 0.002), as expected. Generally, highly disturbed sites that were close to human activities and/or had been heavily transformed by humans had greater chance to host alien species, regardless of biodiversity present in the area. Accordingly, a negative posterior mean is observed considering the distance to the closest city (-0.20 ± 0.02) whereas a positive effect of the distance to the closest airport was found (0.12 ± 0.02). All the four spline correlograms (Fig. S1 in Appendix C) did not present any evidence of spatial autocorrelation in the residuals allowing us to be quite confident about model parameter estimates.

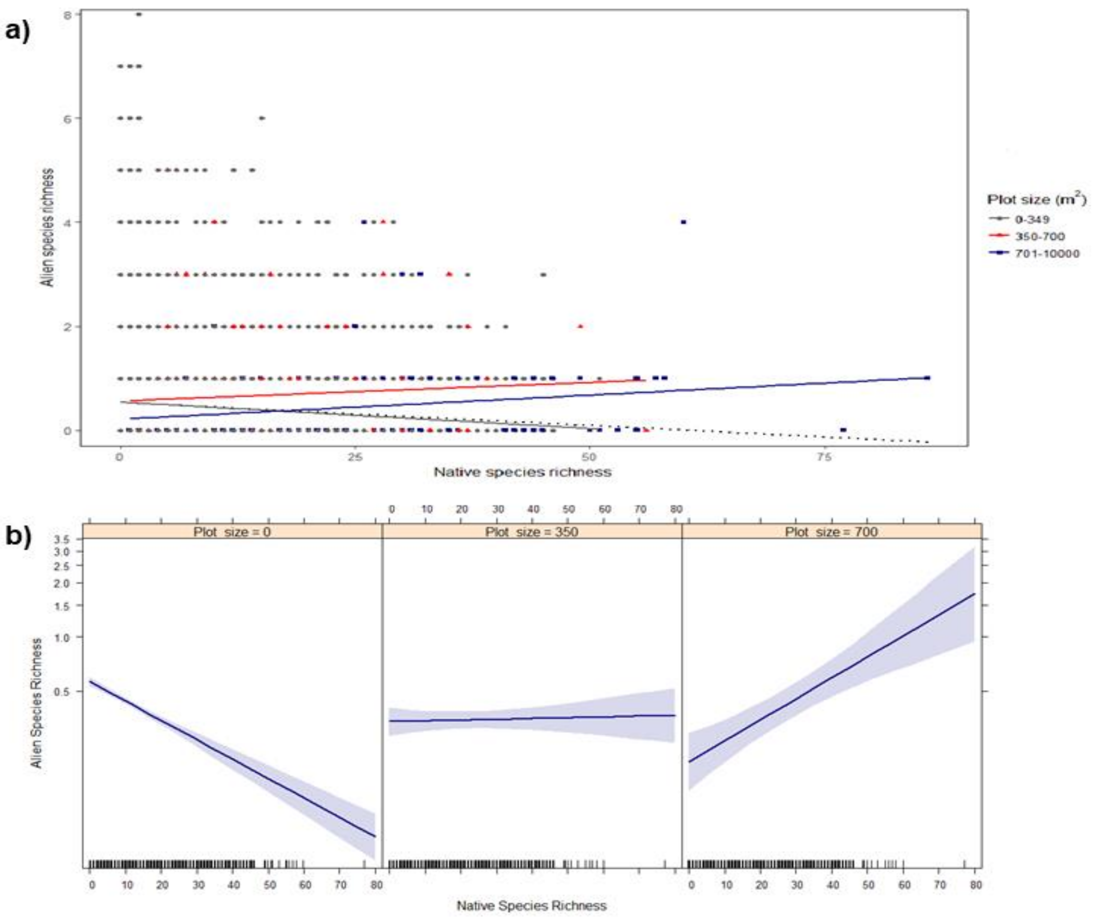

Fig. 3 a) Scatterplot illustrating the relationship between alien and native species richness. Dotted line represents the overall regression trend. b) GLM output displaying the dynamic pattern between alien species richness and the interaction of native species richness and plot size

Discussion

Diversity patterns across floristic kingdoms

To the best of our knowledge, this is the first global study investigating diversity patterns of native and alien plant communities in sand dune ecosystems across different sand dune habitats and floristic kingdoms. We also explored the relationships between native and alien species and the main environmental and anthropogenic factors associated with their global distribution. Overall, some surprisingly contrasting patterns emerged among habitats and floristic kingdoms and species richness. Among floristic kingdoms, higher species richness was detected in Cape and Paleotropical kingdoms while the Holarctic and Holantarctic seemed to be significantly poorer (Fig. 2). This result confirms well known general trends for vascular plants (e.g. Kier et al. 2005).

Native species showed a general increase of species richness along the sea-inland gradient from the usually species poor foredunes to more diverse communities on fixed dunes. This confirms earlier local and regional case studies from around the world (Acosta et al. 2009; Miller et al. 2010; Monserrat et al. 2012; Ciccarelli et al. 2012; Vaz et al. 2015; Jiménez-Alfaro et al. 2015). The increase in species number along the dune gradient is due to the variable effect of limiting factors acting in these environments; hence, poor soil conditions, low levels of nutrients, salt spray, marine aerosol, sand shear and other soil features influence the distribution of species in these habitats (Houle 2008; Acosta et al. 2009; Angiolini et al. 2017). Thus, foredunes confirm to be on average extremely species poor compared to the other habitats and this pattern is constant across the globe even though a strong biogeographical signal is evident across floristic kingdoms. Communities in fixed dunes tend to become more perennial hosting higher species richness thanks to the greater stability of habitats. Furthermore, plant species have developed adaptations to survive and reproduce under relatively harsh conditions (Wiedemann and Pickart 2004; Acosta et al. 2009) being progressively less exposed to the above cited factors. Thus, our analysis pointed out as, irrespective to the floristic kingdom considered, there is a strong gradient of species richness moving from the foredunes to the inner part of the beach. All this highlight the strong azonality of these environments that are mainly driven by species sorting (filtered through local abiotic conditions) and biotic interactions among species such as competition and facilitation (Forey et al. 2008; Brunbjerg et al. 2012; Vaz et al. 2015).

The effect of habitat on alien species richness seems to be much less pronounced as highlighted also by the narrower range in Fig. 2b and by the coefficients in the Bayesian model not overlapping zero; this pattern has been already observed at local scale in other studies (e.g. Tordoni et al. 2017 for a coastal urban environment). This may be explained by the capability of alien plants to spread their propagules across habitats (see Simberloff et al. 2009 for a review on the role of propagule pressure in biological invasions) associated with trampling in touristic beaches and proximity to artificial surfaces (Malavasi et al. 2014) along with the higher capability to take advantage in both favorable and unfavorable environments maintaining their fitness thanks to their phenotypic plasticity (Richards et al. 2006; Davidson et al. 2011; Tordoni et al. 2017). The average number of alien species results to be relatively constant in all the kingdoms except for the Holantarctic ones. Thus, our data show, on average, higher values of alien richness with respect to the other kingdoms in New Zealand sites. In agreement with previous studies (Hilton et al. 2005, 2006), this suggests that New Zealand foredunes are heavily invaded by alien species, especially the Marram Grass (*Ammophila arenaria*), that has been planted to construct or re-establish foredunes or stabilize transgressive dune systems (Johnson 1992).

Several authors have described a scale-dependency between native and alien species richness (see Levine and D’Antonio 1999; Davies et al. 2005, among others). In our large dataset, we found a general negative linear relation between native and alien species; however, the same relationship explored for different sizes of the sampling units, confirmed the occurrence of the invasion paradox proposed by Fridley et al. (2007). Accordingly, even though a very fine spatial grain seems to show a clear negative trend between native and alien richness (e.g. Levine 2000), the opposite happens increasing the sampling unit size (Stohlgren et al. 2003, among others). Fridley et al. (2007) did not provide a single answer to this behavior but rather a suite of possible explanations. At a fine scale, environmental and disturbance-based features predominate and shape community composition. Sampling effects may arise in the sense that communities may include particularly invasion-resistant or competing species; another possible explanation relies on the concept that, in stressful environment such as sand dune ecosystems, facilitative interactions may ease the establishment and colonization of alien species across multiple trophic levels and functional groups (Brooker et al. 2008; Forey et al. 2009; Von Holle 2013). On the other hand, at a larger spatial scale, biotic processes are buffered by well-known biogeographical theories among which spatial heterogeneity plays a crucial role. The same pattern has been found by Altieri et al. (2010), who propose that large-scale relationships can be explained by small-scale positive interactions that commonly occur across multiple trophic levels and functional groups. Furthermore, communities under dispersal or vegetating in highly disturbed ecosystems (e.g. roadside habitats) often exhibit these positive relationships (Brown and Peet 2003). This is the first study providing an important confirmation for the invasion paradox at the global scale in sand dune environments; in our case, the “rich get richer” (Stolghren et al. 2006) hypothesis, dominating at the larger spatial scales, interplay with the strong environmental filtering effect that, in sand dunes, shapes the native plant community to be one of the poorest assemblage.

Ecological drivers of plant species richness

Bayesian BGLMMs and variance partitioning revealed that different sets of predictors (environmental and anthropogenic, Fig. 4 & 5) act differently on native and alien species, respectively. Climatic and ecological variables well describe worldwide patterns of native species richness. The role of climate on plant species richness has been figured out in earlier studies (Francis and Currie 2003; Kreft and Jetz 2007). Hawkins et al. (2003) in a literature review, reported that water-energy interactions represent the strongest constrains to global diversity gradients. Similarly, global models predict that absolute water and energy availability account for > 60% of plant species richness (Cramer and Verboom 2017). At a global scale, the distribution and the strong geographical differences in the floristic composition of plant communities have been classically attributed to climatic differences and regional scale processes such as speciation and extinction (Ricklefs 1987, Brunbjerg et al. 2014), despite these communities share universal sea-inland gradients in local environmental conditions. The positive relationship between native species richness and anthropogenic factors such as population density and distance to the closest airport was not surprising. One possible explanation relies in the so called intermediate disturbance hypothesis (IDH, Connell 1978) where the highest biological diversity in sand dune plant communities is detected along an intermediate level of a disturbance gradient like that of population density and urbanization, as already reported in other studies (e.g. Grunewald 2006; Lucrezi et al. 2014). However, the coastal squeeze may favor the spread of plant species with specific ecological properties, such as generalist species like ruderals and alien species, that could displace most sensitive native species (García-Mora et al. 1999; Isermann et al. 2007; Powell et al. 2011). The year of sampling, despite having a statistical effect on native species richness, could be considered almost negligible. Coastal dune habitats have been often reported to harbor many neophytes, with a general consensus with a stronger propagule pressure considered among the most important causes of greater invasion intensities (Chytrý et al. 2005; Carboni et al. 2010). However, alien species richness is not just explained by human activities but also shows the imprint of natural processes, as observed also in some global studies considering different taxa (Gallardo et al. 2016; Dyer et al. 2017; Pyšek et al. 2017). It is generally accepted that islands are more invaded than mainland since they tend to harbor more alien species both per unit area and as a proportion of total species richness (Lonsdale 1999; van Kleunen et al. 2015; Pyšek et al. 2017), surprisingly we observed a higher alien species richness on mainland respect to islands. This is in agreement on what observed in Vilà et al. (2010) comparing Spanish coastal plant communities. The smaller species pool presents on islands compared to mainland could provide for a possible explanation of this pattern (Vilà et al. 2010); other reasons may rely on the smaller propagule pressure thanks to a lower population density in islands compared to mainland (average density of 201.15 *vs* 515.52, respectively) or in the strong adaptations of native species to the harsh conditions that are present in these environments that may buffer against alien species spread (Diez et al. 2009), since not all the alien species can be able to withstand. In addition, islands may often present a lot of habitats in a relatively restricted space allowing them to spread in more favorable habitats than coastal dunes.

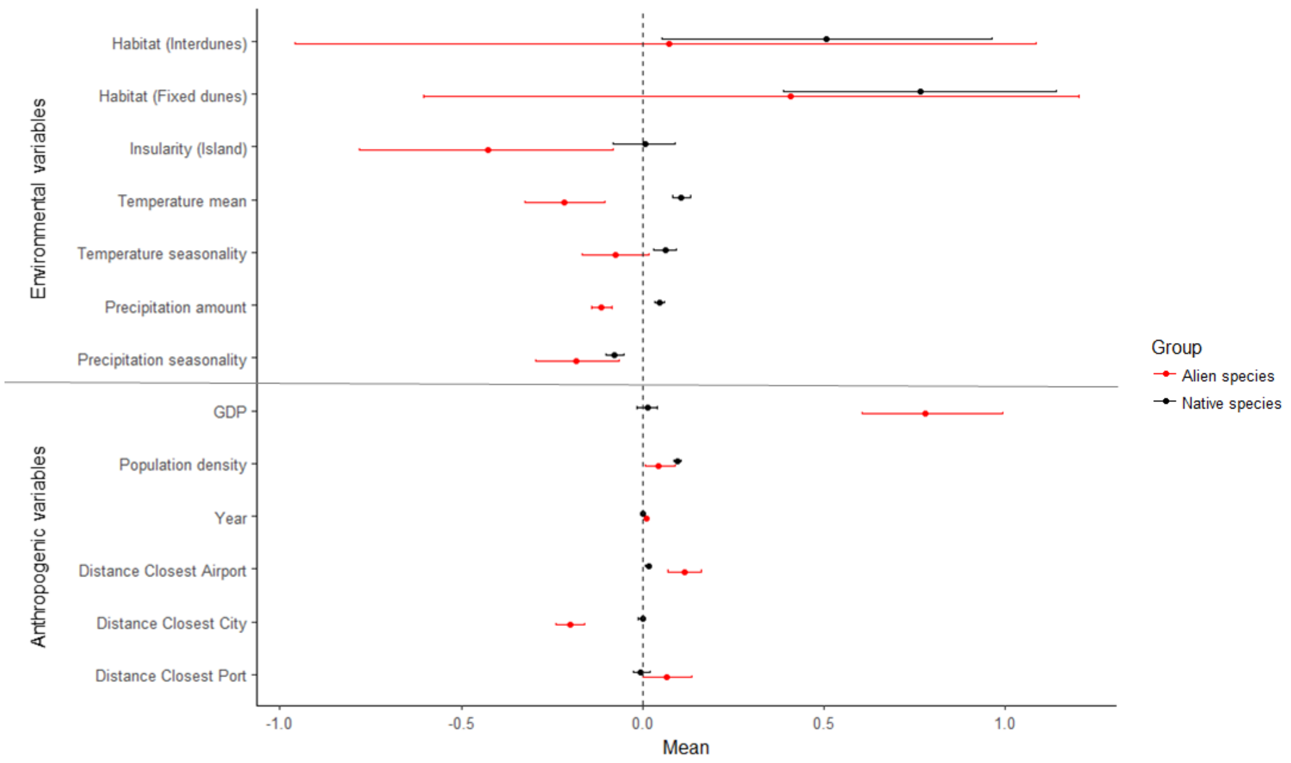

Fig. 4 Summary of Bayesian GLMMs (Posterior mean ± 95% credible intervals)

At last, we cannot exclude that this pattern might arise just as a sampling effect due to plot location (only few of them are in small islands). Among anthropogenic factors, socio-economic factors such as per capita GDP (which is directly related to a country's volume of trade as well as the disposable income of its population) and population density (proxy for urbanization) play a key role in explaining alien species richness as reported also in other studies, even between different taxa (McKinney 2006; Chytrý et al. 2008; Carboni et al. 2010; Pyšek et al. 2010). The positive trend between alien richness and year of the study may be explained from one side by the relatively recent interest in this topic along with changes in research intensity and global trades (Hulme 2009; Hulme et al. 2013) but also from the effect of the so called “residence time” (the time since the introduction of a taxon to a new area occur) intended as another proxy for propagule pressure (Rejmánek et al. 2005). Cities are often the introduction epicenter of alien species (Vitousek et al. 1997; Pyšek 1998; Tordoni et al. 2017), due to synergic effects of human activities and transports that ensure a high dispersion rate of the propagules through road network (Hulme 2003; Chytrý et al. 2008; Bacaro et al. 2015). The distances to the closest city may be easily related to the concept of the pathways of introduction and spread and they can be considered among the major drivers of invasion throughout the world (Bellard et al. 2016). More in general, especially across coastal regions, movement of plant species has occurred by introducing alien species to new areas both unintentionally (through major trade routes, Tatem and Hay 2007; Tatem 2009; Chapman et al. 2016; Bellard et al. 2016) and intentionally (for instance by preventing sand drift or by establishing ornamental plants). In conclusion and once more, our results corroborate the massive impact of human activities on natural and fragile ecosystems such as those represented by sand dune habitats: we confirm that, globally, the increasing trends of alien species richness across landmasses represents a recent phenomenon related to human transport of propagules and introduction of alien species influencing native species patterns.

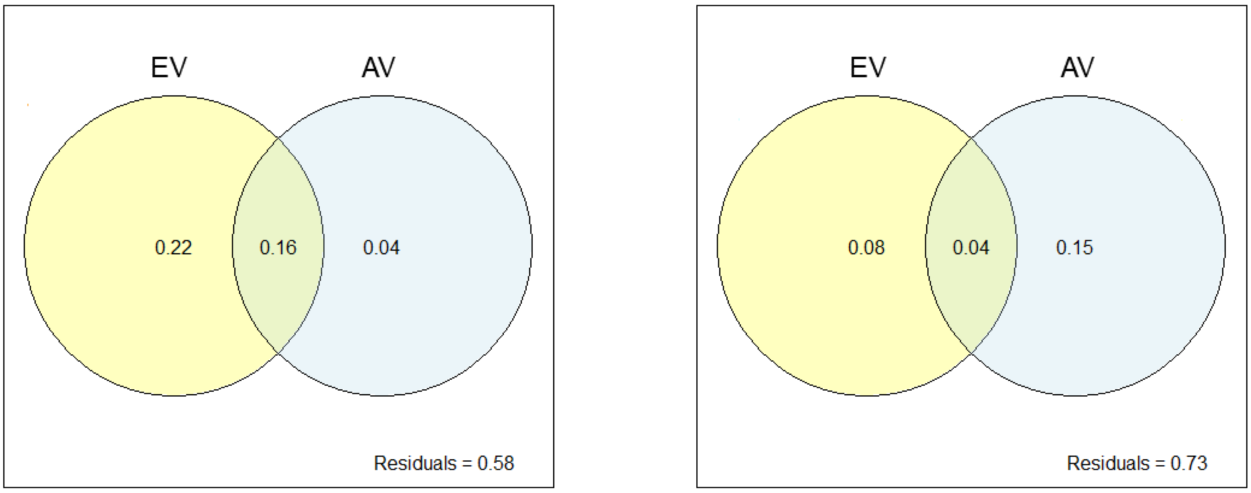

Fig. 5 Variation partitioning of native (left) and alien (right) species richness. EV= Environmental Variables, AV= Anthropogenic variables

Conclusion

This study provides a general picture of the global pattern of native and alien species richness than earlier attempts in sand dune environment. Here, we demonstrated how native and alien species in coastal sand dune environments behave differently across habitats and floristic kingdoms and how they are differentially influenced by various ecological factors. Even though there is a strong imprint of natural processes such as climate variables in both species groups, the effect of anthropogenic impacts is much more pronounced on alien species. Gaining a more detailed and more mechanistic understanding of the causes of invasion would allow more focused control and management measures, which would more effectively mitigate new invasions before they cause major impacts and become too costly to control and eradicate. Our results also represent important evidences for the prediction of future invasion resulting from ongoing globalization and human activities. Future outlooks foresee to integrate the geographical gaps present in the database, to elucidate patterns of beta diversity aiming at understanding species turnover and its ecological drivers. Finally, by integrating functional and phylogenetic information into the modelling framework would allow us to improve the global picture of these fragile ecosystems.

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General conclusions

Key findings and implications

The broad goal of this thesis was to explore diversity patterns in coastal ecosystems due to the current threats to whom these environments are undergoing. The main achieved conclusions rely on the fact that habitat diversity and, consequently, a well-structured community reduce alien species spread mainly acting as biotic filters (competition) and exploiting all the resources available. These mechanisms result in the reduction of alien α and β components (Chapter 1 and 2). For disturbed coastal ecosystems such as urban areas and port areas, where alien species introduction and spread is especially enhanced, these results pose important evidences for future management strategies. On the other hand, in natural coastal sand dunes, it seems that geomorphology more than climatic variables drive the spread of exotics. In both cases, native communities confirm to be strongly habitat and spatially structured whilst alien species exhibit less complementarity at a locale scale and produce a homogeneous composition pattern. These results are reflected also for what concerns the functional diversity; accordingly, native community seems to be more diversified and richer than alien community; as a consequence, the spread of alien species might indirectly lead to the potential functional homogenization of the communities under investigations with the consequent loss of unique traits and species (Chapter 3). At a global scale, the relationship between native and alien species shows a dynamic behavior depending on the size of the sampling unit: at finer scales, it resulted negative and, on the contrary, it was positive at larger spatial scales (Chapter 4). The causes behind this pattern are multiple and span from environmental and disturbance-based features dominating at smaller spatial scale (Forey et al. 2009; Von Holle 2013) to biotic processes and spatial heterogeneity acting on the larger one (e.g. Altieri et al. 2010). In addition, the patterns observed across habitats and floristic kingdoms are not consistent between native and alien groups; indeed, native species richness follows the sea-inland gradient (irrespective of the floristic kingdoms) whereas alien richness values tend, on average, to be similar across habitats but mutable among different realms. Anthropogenic factors may be claimed as the main drivers of alien species richness whilst native seems to be more influenced by a combination of climate and habitat features. Propagule pressure is the key factor driving alien species spread in coastal environments as also claimed in other studies (Carboni et al. 2010; Malavasi et al. 2014, among others). Specifically, in urban area, the constant availability of propagules and the great connectivity characterizing cities ensure the maintenance of established alien populations as already observed in several studies (Kowarik et al. 2013; Aronson et al. 2015; Ricotta et al. 2017). In sand dune ecosystems, the inner part of the beach confirms to be the most invaded portion of the beach both at local and global scale especially for Holarctic and Palaeotropical realms, probably because is subjected to the strongest propagule pressure (Carboni et al. 2010). According to what observed in this thesis, I can confirm that alien species spread is driven both by the mechanisms proposed in the Elton’s theory of invasibility (*biotic resistance*, Elton 1958; Levine and D’Antonio 1999; Fridley et al. 2007) along with that proposed by Davis (Davis et al. 2000). This latter suggests that the contemporary presence of suitable propagule and the larger the difference between gross resource supply and resource uptake, the more susceptible is the community to invasion. Accordingly, intermediate levels of natural disturbances and abiotic stress offer the best scenario where alien species may colonize and spread.

Coastal habitat conservation

Hosting species and habitats of great conservation and ecological values, coastal ecosystems (especially sand dunes) are one of the most protected ecosystems in Europe. Since it has been clearly established in literature that alien species pose a serious threat to these environments having strong negative impacts as already discussed in the introduction section (e.g. Vilà et al. 2011; Socolar et al. 2016), it is mandatory to foresee appropriate management strategies and to constantly update the conservation status of these sites. This thesis offers a suitable tool to elucidate the patterns and mechanisms of invasion along with the main drivers responsible for it. The steady increase of urbanization in coastal areas along with the contemporary need to preserve habitat integrity is probably the major challenge we are currently facing. Accordingly, a coherent urban strategy should be developed both preserving traditional cultural landscape and green patches within the urban matrix along with their integration with residential and tourism interests (Maiorano et al. 2006; Malavasi et al. 2013). As showed in some studies, the ecosystem services provided by coastal zones could be determinant in the near future also in prevision of a sea-level rise with its related effects such as flooding, especially for the so called low-elevation coastal zone (LECZ; e.g. Neumann et al. 2015). According to the above and given the protection provided by coastal areas from flooding events, their loss can cause greater exposition to sea-level rise and coastal hazards (especially in Africa and Asia), causing a possible reversion of the coastward migration trend due to increasing impacts from climate change, subsidence and extreme events (Neumann et al. 2015). For what concerns the alien species issue, it is worth to remind that not all the coastal ecosystems are invaded with comparable intensity, hence the importance of sustainable and effective management practices will be crucial for alien management and their potential eradication. Accordingly, useful suggestions include closely monitoring recreational areas such as campsites and bathing facilities to control the potential settlement and spread of ornamental casual species. Furthermore, national and local policies should promote best practices to avoid and contrast alien species spread. For instance, the development of a horizon scanning and early detection framework (e.g. Sutherland and Woodroof 2009) for risk assessment could help to foresee the arrival of new alien species (e.g. monitoring shipping routes in port areas). Another point is to act with timely containment measures as soon as a new species was detected. In this regard, a citizen science approach may help to speed up and make the process more sustainable and practicable at local and regional scale (e.g. Dickinson et al. 2010; Bois et al. 2011). I have further showed off that effectively management actions may be planned acting where higher levels of alien β diversity are observed so optimizing time and resources; in addition, it would be advisable to preclude or fence some parts of the beach that host priority habitat, rare species or endemism to allow a greater protection of these habitats chiefly from trampling.

Research outlook and future perspectives

Although coastal environments are deemed a model system to study ecological relationships among species, future outlooks can be considered in order to produce a more exhaustive research. For what concerns urban areas, similar research questions as those raised in chapter 1 could be addressed in other coastal cities to confirm the consistency of observed patterns. The integration of plant survey with information on trade network and shipping routes may provide useful insights in the comprehension of invasion mechanisms. At a regional scale, it would be necessary to increase the extent of the study area at least until the mouth of Po river, thus including most of the sand dunes remnants in northern Adriatic coastline. This would result also in analysis of regional scale processes and dynamics in order to better understand invasion mechanism acting at greater extents. Considering the functional diversity approach, it would be interesting to study how the inclusion in the analysis of traits related to the root system could improve our understanding of the invasion processes, since they may have a pivotal role in alien species spread as hypothesized also in Dawson (2015). At a global scale, it would be interesting to fill the gaps in the database including data from Australia and Southeast Asia. Then, it would be interesting to assess both β diversity global patterns in these ecosystems (see for instance König et al. 2017 for global turnover on vascular plants) and their drivers associated with information of functional diversity. Finally, another noteworthy approach is the use of remote sensed data to assess biodiversity (in terms of spectral heterogeneity) in a cost-effective and comprehensive way, these techniques seem very promising both from a taxonomic and a functional point of view (Rocchini et al. 2018; Schneider et al. 2017). To conclude, given the rapid pace with which global changes are occurring, it is mandatory that research make steps forwards quickly associated with effective conservation and mitigation measures.

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Appendix

Appendix A

Supplementary Materials to Chapter 1 - Diversity patterns of alien and native plant species in Trieste port area: exploring the role of urban habitats in biodiversity conservation

Fig. S1 Plot-based rarefaction curves at different spatial scales considering all species pooled

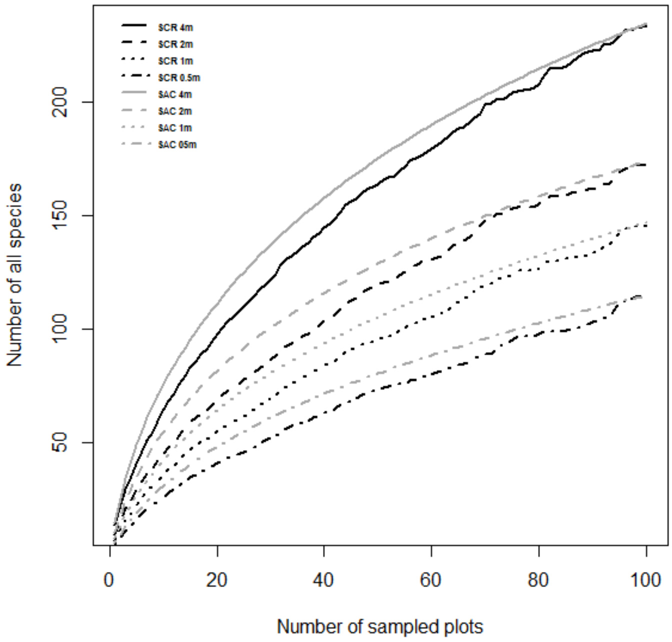


Fig. S2 Spatially-Constrained Rarefaction curves (SCR) and rarefaction curves computed with exact method (SAC) considering all species pooled for each spatial scale investigated

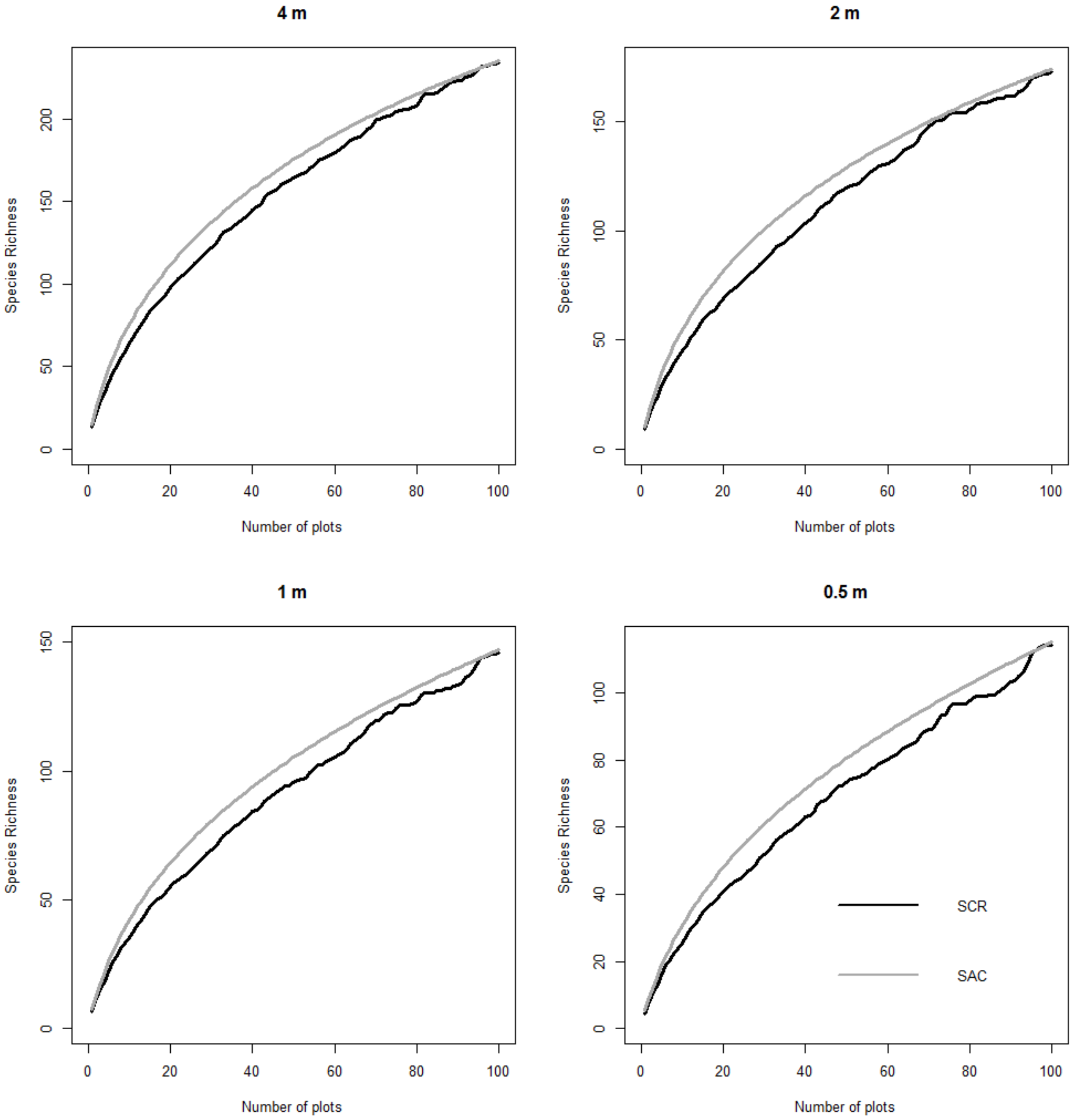
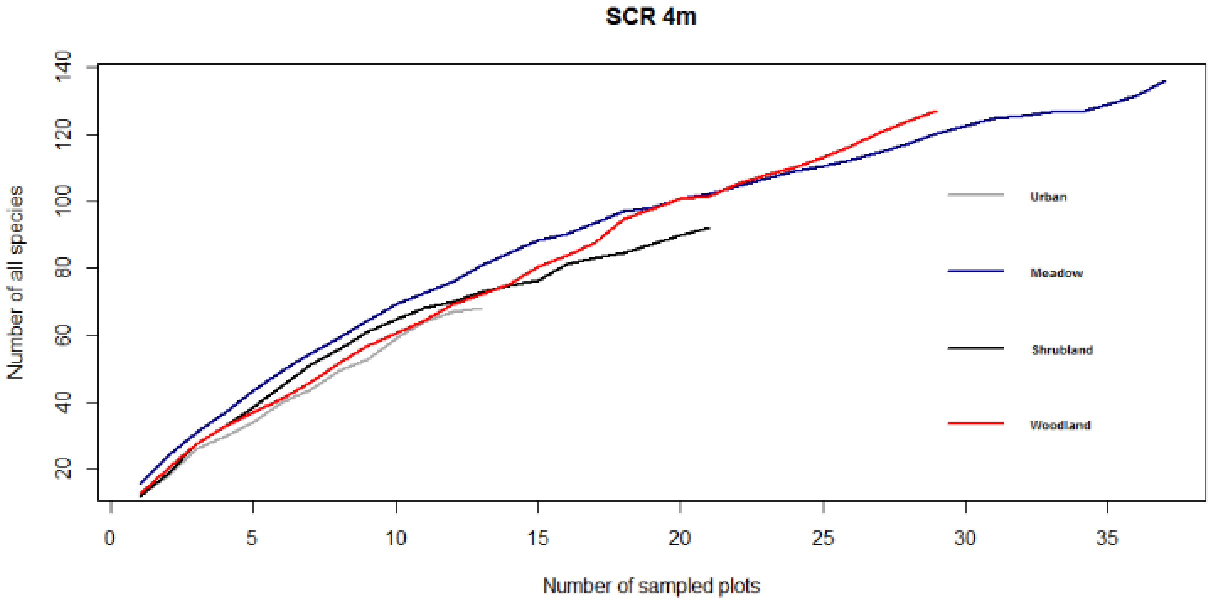


Fig. S3 Comparison between Spatially-Constrained rarefaction curves (SCR) and plot-based rarefaction curves (SAC) calculated with the exact method at largest spatial scale (16 m^2)



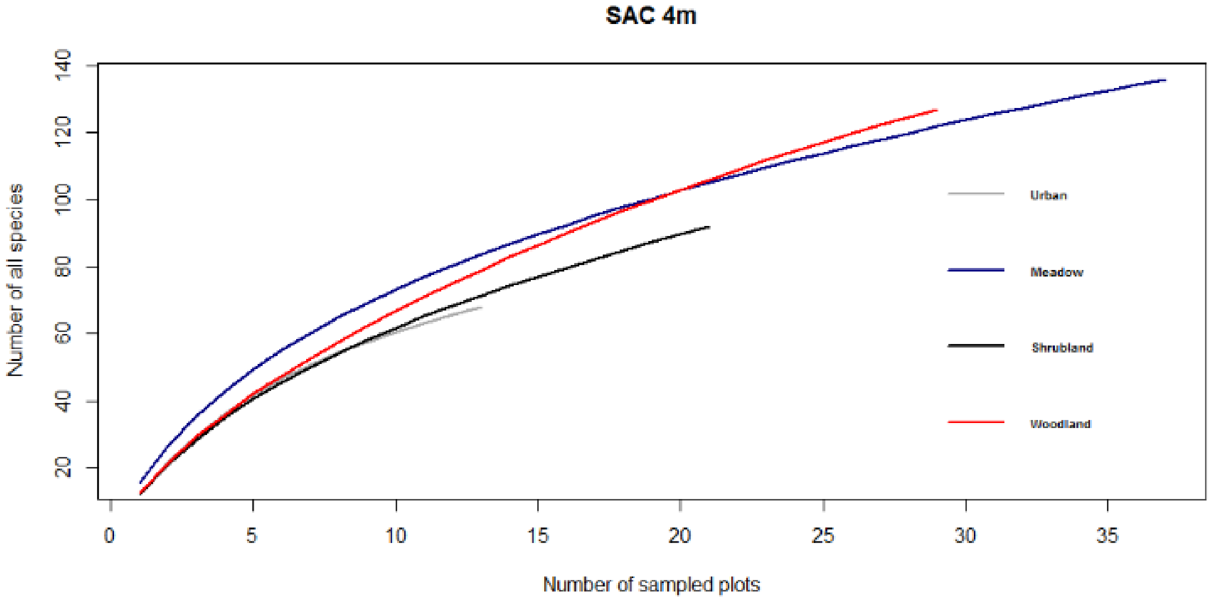


Fig. S4 Percentage of total plant species richness explained by alpha and the beta components of diversity according to spatial scale. The contributions to the total richness for each scale were determined by the additive partitioning of diversity method (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = Not Significant)

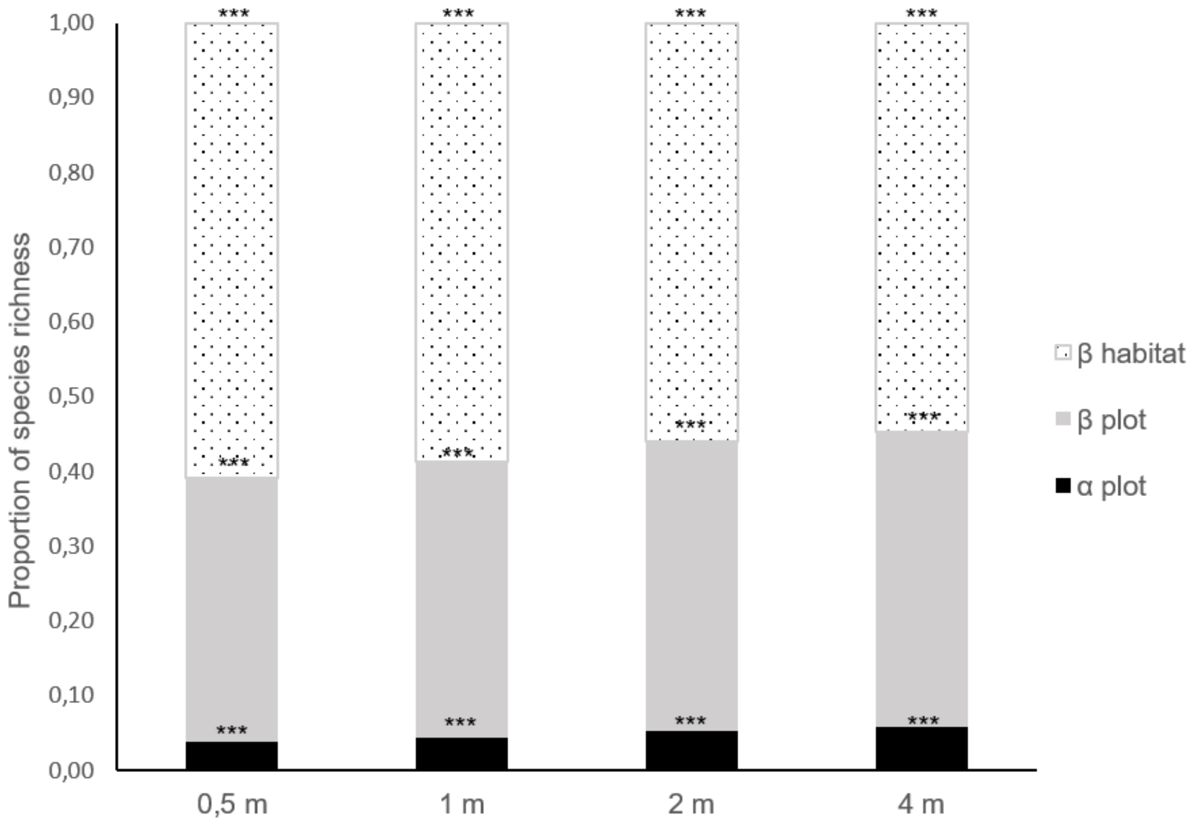
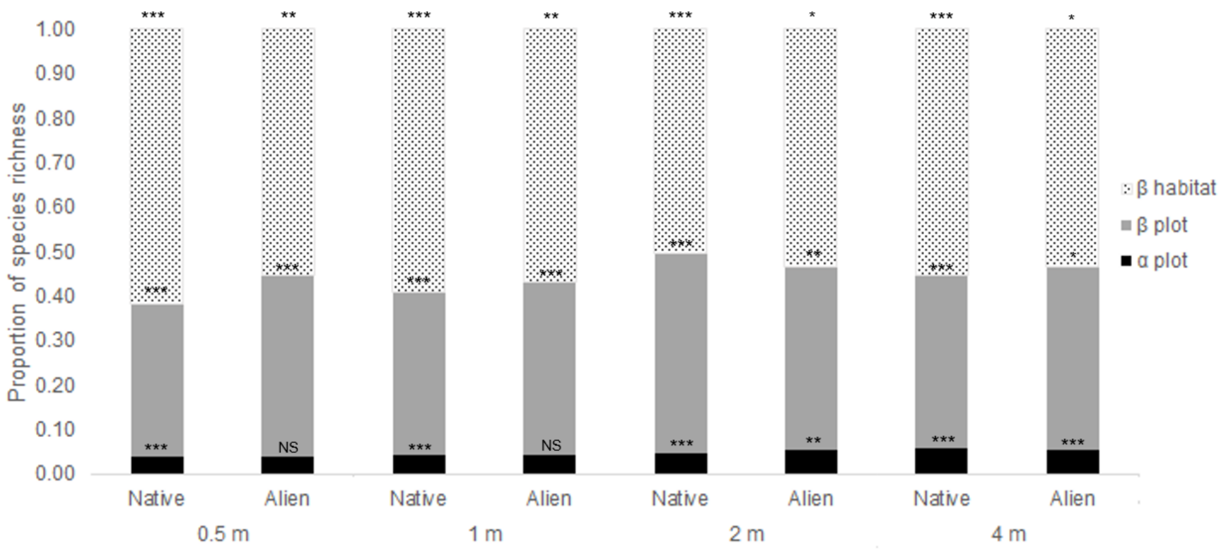


Fig. S5 Percentage of total plant species richness explained by alpha and the beta components of diversity according to spatial scale and habitat class. The contributions to the total richness for each scale were determined by the additive partitioning of diversity (*** = *p* < 0.001; ** = *p* < 0.01; * = *p* < 0.05; NS = Not Significant)



Appendix B

Supplementary Materials to Chapter 2 - Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline

Table S1

Summary statistics (mean, minimum, maximum) of the variables used in variation partition obtained after forward selection on alien species

	Mean (Min-Max)
Spatial variables	
X (EPSG 3003)	1810894 (1805157 - 1819535)
Y (EPSG 3003)	5060145 (5058462 - 5062760)
Geomorphological variables	
Habitat	1 level (Foredune)
Slope	3.83 (0.10 - 18.34)
Elevation	1.83 (0.08 - 3.45)
Eastness	0.05 (-1.00 - 1.00)
Annual deposition rate	18.00 (-12.40 - 31.70)
Climatic variables	
mean (Rainy days)	6.96 (6.78 - 7.08)
max (Tmin)	13.10 (12.58 - 13.90)
range (Tmin)	0.87 (0.85 - 0.90)
min (Tmean)	17.18 (17.01 - 17.44)
mean (Tmean)	17.91 (17.80 - 18.07)
max (Tmean)	18.51 (18.39 - 18.69)
range (Tmean)	1.33 (1.25 - 1.37)
min (Tmax)	21.57 (21.31 - 21.75)
mean (Tmax)	22.57 (22.20 - 22.83)
max (Tmax)	23.30 (22.76 - 23.66)
max (RH_min)	0.56 (0.54 - 0.58)
min (RH_mean)	0.71 (0.70 - 0.72)
max (RH_mean)	0.80 (0.80 -0.81)
min (RH_max)	0.93 (0.92 - 0.94)
mean (Irradiation)	559 (552-570)

Table S2

Summary statistics (mean, minimum, maximum) of the variables used in variation partition obtained after forward selection on native species

	Mean (Min-Max)
Spatial variables	
X (EPSG 3003)	1811930 (1805157 - 1819539)
Y (EPSG 3003)	5060383 (5058462 - 5062762)
Geomorphological variables	
Habitat	2 levels (Foredune, Interdune)
Class of erosion	1 level (Erosion)
Slope SD	1.35 (0.14 - 7.08)
Elevation	1.72 (0.08 - 3.45)
Touristic pressure	0.73 (0.01 - 3.61)
Beach width	119.3 (83 - 193)
Annual deposition rate	15.26 (-12.40 - 31.70)
Climatic variables	
mean (Σ Precipitations)	683.2 (667.9 - 695.4)
mean (Precipitations)	86.47 (85.17 - 87.44)
mean (Σ Rainy days)	55.48 (54.26 - 56.64)
mean (Rainy days)	6.93 (6.78 - 7.08)
min (Tmin)	12.64 (12.31 - 13.00)
mean (Tmin)	13.17 (12.84 - 13.52)
max (Tmin)	13.21 (12.58 - 13.90)
range (Tmin)	0.87 (0.85 - 0.90)
min (Tmean)	17.21 (17.01 - 17.44)
mean (Tmean)	17.93 (17.80 - 18.07)
max (Tmean)	18.53 (18.39 - 18.69)
range (Tmean)	1.32 (1.25 -1.37)
min (Tmax)	21.53 (21.31 - 21.75)
mean (Tmax)	22.52 (22.20 - 22.83)
max (Tmax)	23.22 (22.76 - 23.66)
range (Tmax)	1.69 (1.45 - 1.91)
mean (RH_min)	0.52 (0.50 - 0.53)
max (RH_min)	0.56 (0.54 - 0.58)
min (RH_mean)	0.71 (0.70 - 0.72)
max (RH_mean)	0.80 (0.80 -0.81)
max (RH_max)	0.98 (0.98 - 0.99)
mean (Irradiation)	561 (552-570)
mean (Σ Irradiation)	4343 (4338 - 4349)

Table S3
Spearman correlation coefficient of the climatic variables with the first axis of PCA

Variable	Spearman's ρ
mean (Σ Precipitations)	0.98
mean(Precipitations)	0.91
mean (Σ Rainy days)	1.00
mean (Rainy days)	0.99
minimum (Tmin)	-0.99
mean (Tmin)	-0.99
max (Tmin)	-1.00
range(Tmin)	-0.79
minimum (Tmean)	-0.99
mean (Tmean)	-0.99
max (Tmean)	-0.99
*range(*Tmean*)*	0.96
min (Tmax)	0.99
mean(Tmax)	0.99
max (Tmax)	0.99
range (Tmax)	0.99
min (RH_min)	-0.94
mean (RH_min)	-0.94
max (RH_min)	-0.93
min (RH_mean)	-0.93
max (RH_mean)	-0.85
min (RH_max)	-0.92
max (RH_max)	0.24
mean (Irradiation)	-1.00
mean (ΣIrradiation)	0.31

Figure S1

Estimated components of variance (expressed as percentages) calculated for each factor of the PERMANOVA analysis

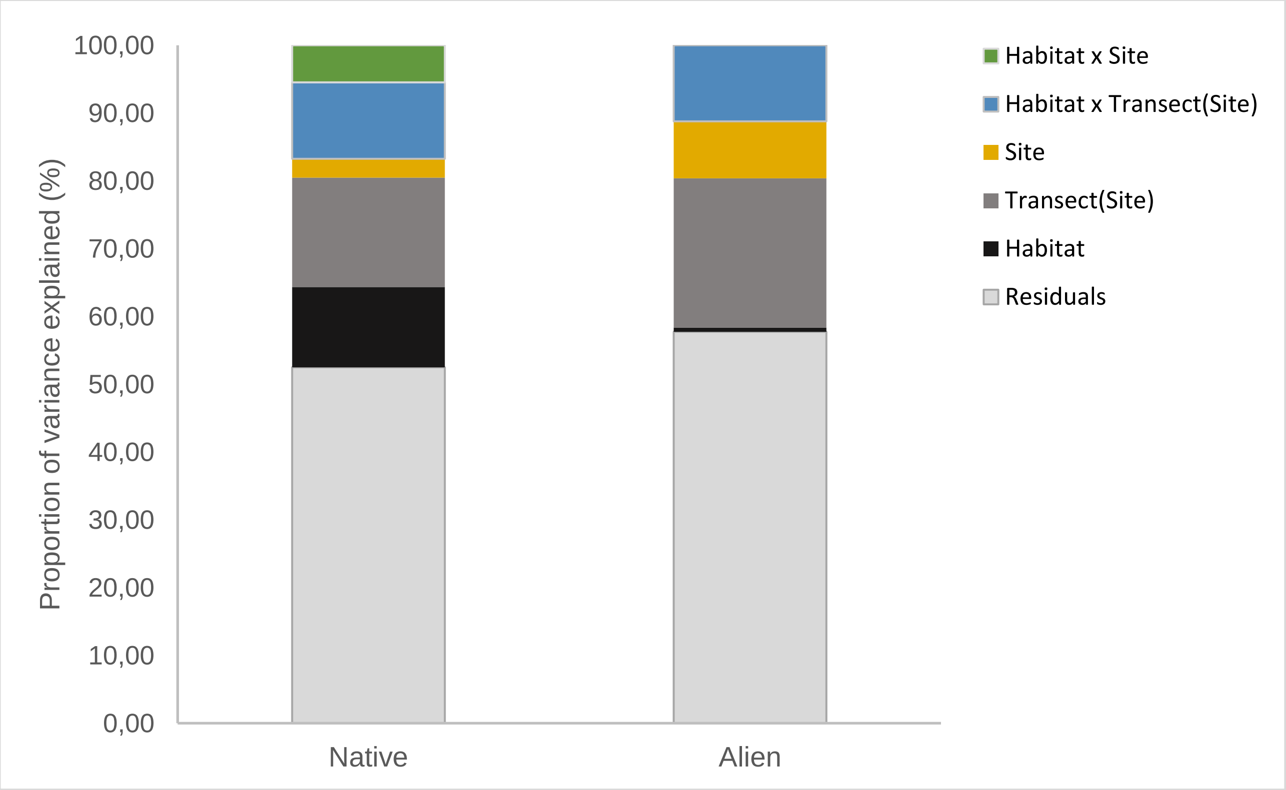


Figure S2

Plot-based rarefaction curves (SAC) and Spatially-explicit rarefaction curves (SER) for native and alien species

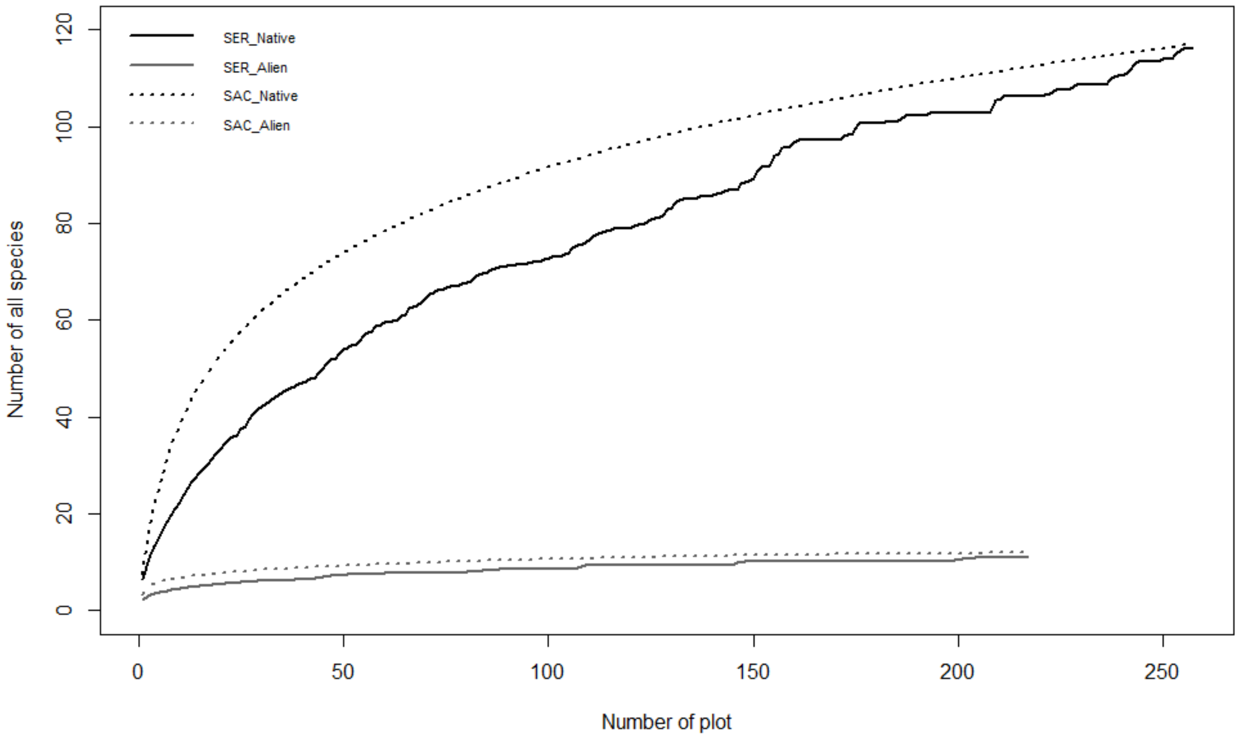
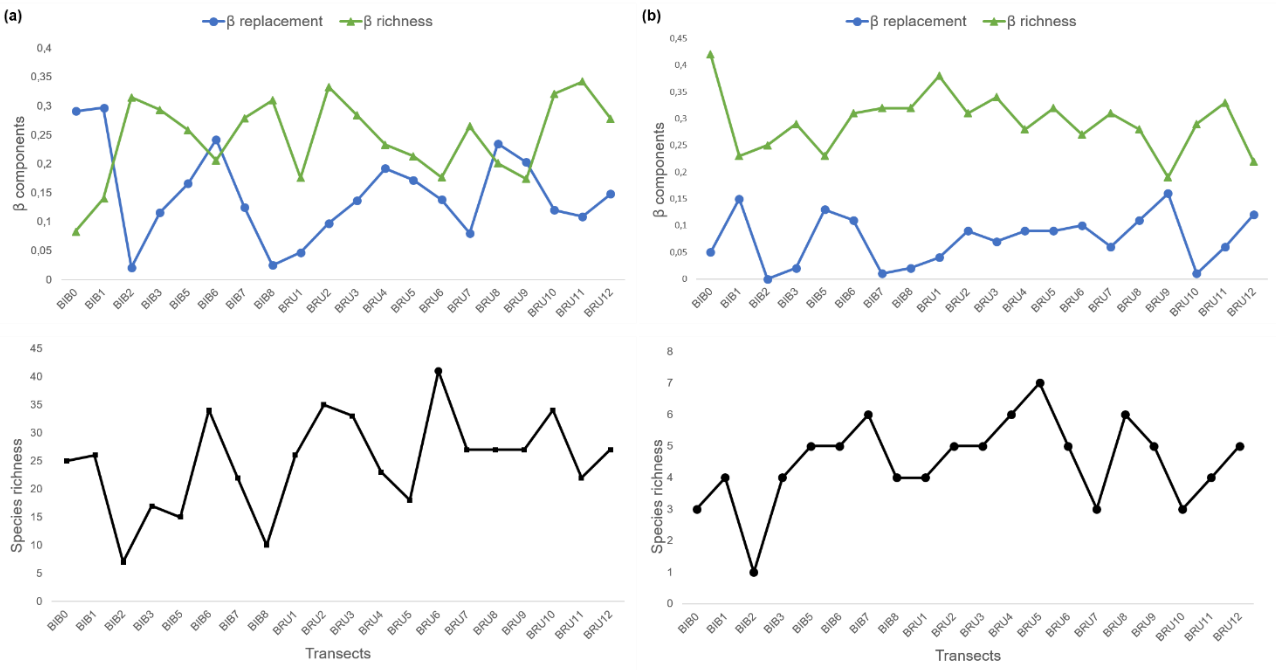


Figure S3

Trend line of beta diversity components (βrepl and βrich) for a) native species and b) alien species in each transect; black line represents the trend line of species richness



Appendix C

Supplementary Materials to Chapter 4 - Disentangling plant diversity in sand dune ecosystems: a global perspective from patterns to processes

Table S1

Data summary showing number of plots, range of plot sizes in the region, year of sampling and name of data supplier for each country/region

Country/Region	N° plots	Plot size range (m^2)	Year of sampling	Data supplier/Reference
Argentina	121	100	2005-2012	Celsi and Monserrat (2008); Fontana (2005); Monserrat et al. (2012)
Brazil	48	100	2013	Giaretta et al. (2013)
Uruguay	22	1	2009	Castineira-Latorre et al. (2013)
Western North America (including Mexico and Alaska)	950	2-1000	1995-2011	Manuel Peinado
Eastern North America (Florida, N-S Carolina, Virginia)	553	25-1000	1988-2014	Robert K. Peet
St. George Island (Florida)	441	1	2015	Thomas E. Miller
Europe (including Madeira and European Russia)	7271	0.04-10000	1930-2016	European Coastal Vegetation Database[1]
Italy	3092	1-16	2002-2016	Alicia T. Acosta, Simonetta Bagella, Daniela Ciccarelli, Saverio Sciandrello, Enrico Tordoni
Crete (Greece)	110	12-100	1989-2016	KRITI database[2]
Iran and Greece	213	25	2011-2012	Parastoo Mahdavi
Belgium	302	9	2007-2014	Sam Provoost
France	773	100	2003	Estelle Forey
Portugal	92	9-25	2015	Vaz et al. (2015)
New Zealand	625	4	2008-2010	Hannah Buckley

Saudi Arabia	10	50	1996	El Demerdash (1996)
South Africa	152	100	1981-1984	Roy Lubke
China	66	25	2015	Zhao et al. (2015)

[1] EU-00-017 - European Coastal Vegetation Database (http://www.givd.info/ID/EU-00-017)

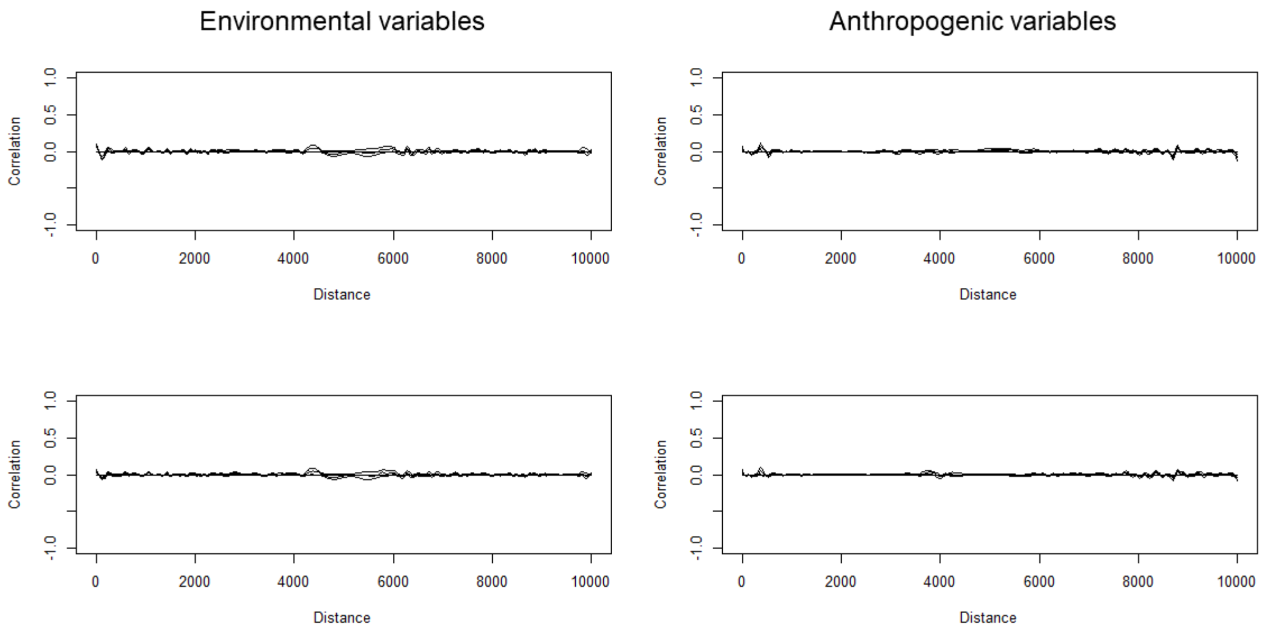
[2] EU-GR-001 – KRITI database (http://www.givd.info/ID/EU-GR-001)

Table S2

References used for assessing the status of a species (native or alien) where not provided by data supplier

Country	Source
Europe	DAISIE; EuroMed Plantbase; NOBANIS
Belgium	Van Landuyt et al. (2012)
Bulgaria	Petrova et al. (2013)
China	Xu et al. (2012); Jiang et al. (2011)
Crete	D'Agata et al. (2009)
Croatia	Boršić et al. (2008)
Cyprus	Hadjikyriakou and Hadjisterkotis (2002)
European Russia	Morozova (2014)
Finland	Niemivuo-Lahti (2012)
France	Fried (2010)
Greece	Arianoutsou et al. (2010)
Iceland	Wasowicz et al. (2013)
Italy	Celesti-Grapow et al. (2009)
Madeira	Borges et al. (2008)
New Zealand	Howell and Sawyer (2006); Wilton et al. (2016)
Norway	Gederaas et al. (2012)
Portugal	de Almeida and Freitas (2006)
Sweden	Tyler et al. (2015)

Figure S1
Spline correlogram with 95% point-wise bootstrap confidence intervals of the Pearson residuals from the four BGLMMs. Native species models in upper panels while alien models in lower panels



Model specification

Patterns species richness

1) GLM native species Fig. 2a. Model R code: glm(SR_nat~Habitat*Kingdom, data=db_stand, family= “quasipoisson”)

$$y_i \sim quasiPoisson, i = 1, \ldots, 12031$$

$$E(y_i) = \mu_i \text{ and } Var(y_i) = \theta\mu_i$$

$$\log(\mu_i) = \beta_0 + \sum_{j=2}^{3} \beta_j^H I_{ji}^H + \sum_{j=2}^{5} \beta_j^K I_{ji}^K + \sum_{j=2}^{9} \beta_j^{HK} I_{ji}^{HK}$$

where I_j^H is the dummy variable for the *j*-th category of the habitat factor variable (reference category = foredunes, *j=2* fixed dunes and *j=3* interdunes) and I_j^K is the dummy variable for the *j*-th category of the Kingdom factor variable (reference category = Holarctic, j=2 Cape, j=3 Holantarctic, j=4 Neotropical and j=5 Paleotropical). Analogously, I_j^{HK} is the dummy variable for the interaction between habitat and kingdom.

2) GLM alien species Fig. 2b. Model R code: glm.nb(SR_ali~Habitat*Kingdom, data=db_stand)

$$y_i \sim NegativeBinomial,\ i = 1, \ldots, 12031$$

$$E(y_i) = \mu_i \text{ and } Var(y_i) = \mu_i + \lambda {\mu_i}^2$$

$$\log(\mu_i) = \beta_0 + \sum_{j=2}^{3} \beta_j^H \, I_{ji}^H + \sum_{j=2}^{5} \beta_j^K \, I_{ji}^K + \sum_{j=2}^{9} \beta_j^{HK} \, I_{ji}^{HK}$$

where I_j^H is the dummy variable for the *j*-th category of the habitat factor variable (reference category = foredunes, *j=2* fixed dunes and *j=3* interdunes) and I_j^K is the dummy variable for the *j*-th category of the Kingdom factor variable (reference category = Holarctic, j=2 Cape, j=3 Holantarctic, j=4 Neotropical and j=5 Paleotropical). Analogously, I_j^{HK} is the dummy variable for the interaction between habitat and kingdom.

3) GLM invasion paradox Fig. 3. Model R code: glm.nb(SR_ali~SR_nat*plot size)

$$y_i \sim NegativeBinomial,\ i = 1, \ldots, 12031$$

$$E(y_i) = \mu_i \text{ and } Var(y_i) = \mu_i + \lambda {\mu_i}^2$$

$$\log(\mu_i) = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{1i} X_{2i}$$

where X_1 is the native species richness and X_2 is the plot size.

Model equations Bayesian GLMM

For native species Fig. 4. Model R code: stan_glmer(SR_nat~ environmental/anthropogenic variables+(1|id_study)+(Habitat|Kingdom), family= “poisson”, prior = p1, chains=4, iter=2000, thin=10,cores=4, data = db_stand, control = list(adapt_delta = 0.999,stepsize=0.001,max_treedepth = 20)))

$$y_{ijk} \sim Poisson$$

with i = id_study (i=1,…,45), j = kingdom (j=1,…,5) and k = habitat (k=1,…,3)

$$E(y_{ijk}) = \mu_{ijk}$$

$$Var(y_{ijk}) = \mu_{ijk}$$

$$\log(\mu_{ijk}) = \beta_0 + \beta_{0i} + \beta_{0j} + \beta_{1j} H_{ijk} + \boldsymbol{\delta X}_{ijk}$$

β_0 is the global intercept

β_{0i} is the study-specific intercept modeled as random effect given by $\beta_{0i} \sim N(0, \sigma_{RIi}^2)$

β_{0j} is the kingdom-specific intercept modeled as random effect given by $\beta_{0j} \sim N(0, \sigma_{RIj}^2)$

β_{1j} is the kingdom-specific slope for the habitat H_{ijk} (reference category is foredunes) modeled as random effect given by $\beta_{1j} \sim N(0, \sigma_{RS}^2)$

$\boldsymbol{X}_{ijk}$ is the vector of environmental/anthropogenic predictors with corresponding vector of coefficients $\boldsymbol{\delta}$

For alien species Fig. 4. Model R code: stan_glmer (SR_ali~ environmental/anthropogenic variables+(1|id_study)+(Habitat|Kingdom), family= “Negative binomial”, prior = p1, chains=4, iter=2000, thin=10,cores=4, data = db_stand, control = list (adapt_delta = 0.999,stepsize=0.001,max_treedepth = 20)))

$$y_i \sim NegativeBinomial$$

$$E(y_i) = \mu_i$$

$$Var(y_i) = \mu_i + \lambda {\mu_i}^2$$

$$\log(\mu_{ijk}) = \beta_0 + \beta_{0i} + \beta_{0j} + \beta_{1j} H_{ijk} + \boldsymbol{\delta X}_{ijk}$$

β_0 is the global intercept

β_{0i} is the study-specific intercept modeled as random effect given by $\beta_{0i} \sim N(0, \sigma^2_{RIi})$

β_{0j} is the kingdom-specific intercept modeled as random effect given by $\beta_{0j} \sim N(0, \sigma^2_{RIj})$

β_{1j} is the kingdom-specific slope for the habitat H_{ijk} (reference category is foredunes) modeled as random effect given by $\beta_{1j} \sim N(0, \sigma^2_{RS})$

$\boldsymbol{X}_{ijk}$ is the vector of environmental/anthropogenic predictors with corresponding vector of coefficients $\boldsymbol{\delta}$

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