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A theoretical approach to a practical challenge –community ecology of dune vegetation and its relation with coastal dynamics

José António Medeiros Macedo

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Tese de Doutoramento apresentada à
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Biodiversidade, Genética e Evolução

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Abstract

Coastal zones host peculiar ecosystem and habitat types of high value for biodiversity, natural resources and other ecosystem services. They are among the most susceptible ecological systems to natural hazards, and their resilience is affected by human pressures and by their vulnerability to extreme environmental events. Coastal sand dunes are a particular type of coastal ecosystem that result from the interaction of aeolian, fluvial and marine processes, such as those related with wave and wind energies, sediment supply and granulometry, salt spray, ground water level, and vegetation cover.

In coastal dune systems, disturbance, stress and biotic interactions are filters determining vegetation. Various abiotic factors affect plant survival in coastal dunes, such as sand burial, high temperatures, water deficiency, nitrogen availability, wind exposure, salt spray, and soil salinity, inducing mechanical damage, restrictions to biomass formation, and dryness of plant tissues. Grime's CSR life strategy scheme postulates the grouping of plant species responding similarly to the environment, capturing fundamental evolutionary strategies for the analysis of functional diversity and community assembly. In a more specific approach, dune plant functional types reveal various extents of adaptation to the local environment, grouping species with common sets of traits and revealing a strong spatial patterning of functional groups along gradients of stress, disturbance and habitat heterogeneity.

Along gradients of environmental severity, distinct levels of plant competition and facilitation have been reported and related to variations in biomass, species diversity and dominance. Recent studies have called for integration between predictions from functional ecology and from species coexistence theory in order to improve our understanding of community patterns and dynamics along severity gradients. In this context, here we aimed to evaluate the interactions between environmental severity, plant strategies and species coexistence as drivers of plant community assembly in dune vegetation, and to assess the influence of prevailing coastal dynamics on community structure along key regional and local environmental gradients. The ultimate goal was to provide scientific bases for adaptive management and monitoring of dune ecosystems.

With the aim of developing a model of community assembly and dynamics in coastal dune vegetation, we developed a detailed study of five dune habitat types organized in vegetation complexes from the beach landward. The research workflow focused on the nature and relative importance of functional filters, biotic interactions and environmental heterogeneity in shaping plant communities that colonize and stabilize coastal dunes. A set of sequential research questions were addressed based on the application of various statistical tools to a test dataset of dune vegetation collected along a regional climatic gradient and across a biogeographic transition in Northern Portugal.

Plant diversity shows a humped-back pattern along the local gradient, with the highest values recorded at the middle of the gradient, in agreement with ecological theory. Along the local gradient there is a clear vegetation zonation, with spatial segregation of species, strategies and functional types typical of seaward habitats from those of landward habitats, mainly determined by environmental sorting of species with specific resource needs and ecological preferences. Segregation is the predominant pattern of co-occurrence within and between habitat types, suggesting an overall prevailing role of species sorting and competition over facilitation in the assembly and dynamics of dune plant communities. Species of functional Type III (the ones with strongest adaptations to the dune environment) and of strategies with an S-component (i.e. stress tolerance) prevail in the seaward, mobile dune habitats, confirming the adaptation and ability of those species to thrive under high environmental severity. A gradual landward replacement of strategies with an S-component by those with an R-component occurs, highlighting the role of environmental stress and resource availability in locally sorting species and thereby structuring plant communities. Type III species were also gradually replaced by Type I and II species in a landward direction, confirming that the harsh conditions in the dune system are effective filters for species with no or moderate adaptations to the combined effect of stress factors and disturbances.

In mobile dunes, plant diversity does not seem to suffer significant changes following a shift to transgressive coastal dynamics, suggesting that this component of community structure may not be an effective indicator of ecological change. Plant strategies and functional profiles exhibited distinct co-occurrence patterns for the two types of coastal dynamics, highlighting that interactions between abiotic filters, species

traits and biotic factors drive vegetation responses to shifts in coastal dynamics. The typical zonation of species, strategies and functional types in mobile dune communities was modified under transgressive coastal dynamics, providing support for new approaches to ecological assessment and monitoring focused on the functional profile of plant communities. No significant regional influence was observed in local scale plant responses but some interactions between local and regional processes were perceived for the whole set of dune habitats. Those interactions should be carefully disentangled before the actual application of our findings in coastal assessment and monitoring.

Resumo

As zonas costeiras albergam ecossistemas e habitats particulares e com elevado valor para a conservação da biodiversidade, recursos naturais e outros serviços dos ecossistemas. Estes ecossistemas estão entre os mais susceptíveis aos eventos naturais, dado o impacte das pressões humanas na sua resiliência bem como a sua vulnerabilidade fenómenos ambientais extremos. Os sistemas dunares costeiros por sua vez resultam da interacção entre de vários processos eólicos, fluviais e marinhos, tais como a energia associada aos ventos e à ondulação, o aporte sedimentar e a granulometria, a salsugem, o nível de água no solo e a cobertura vegetal.

Nos sistemas dunares costeiros, os factores de perturbação ou de stresse e as interacções bióticas actuam como filtros que determinam a composição da vegetação. Vários factores abióticos afectam a sobrevivência das plantas em dunas costeiras, tais como o soterramento pela areia, as altas temperaturas, a deficiência de água, a disponibilidade de azoto ou a exposição ao vento, à salsugem e salinidade do solo, conduzindo a danos mecânicos, restrições na formação de biomassa, e desidratação dos tecidos vegetais. O sistema de classificação funcional CSR proposto por Grime postula o agrupamento de espécies de plantas com respostas semelhantes ao ambiente e exibindo estratégias evolutivas fundamentais para a análise da diversidade funcional e dos padrões de organização das comunidades vegetais. Numa abordagem mais específica, os tipos funcionais de plantas propostos para estes ecossistemas revelam vários níveis de adaptação ao ambiente local, agrupando as espécies em conjuntos com características comuns, revelando uma acentuada padronização espacial dos grupos funcionais ao longo de gradientes de stresse, perturbação e heterogeneidade dos habitats.

Ao longo dos gradientes ambientais dunares, foram identificados diferentes níveis de competição e de facilitação por parte das espécies vegetais e identificados por variações na biomassa, diversidade de espécies e dominância. Estudos recentes têm chamado a atenção para a integração entre os modelos preditivos de ecologia funcional e da teorias ecológicas relativas à coexistência das espécies pro forma a aumentar o conhecimento acerca dos padrões e da dinâmica de comunidades ao longo dos gradientes de severidade ambiental. Neste contexto, procedemos à avaliação das interacções entre as condições ambientais, as estratégias funcionais

das plantas e a coexistência das espécies como base para a organização das comunidade vegetais em dunas costeiras e avaliamos a influência da dinâmica costeira dominante na estruturação das comunidades ao longo de gradientes ambientais regionais e locais. O objectivo final desta investigação residiu no estabelecimento de bases científicas para a gestão e monitorização dos ecossistemas dunares sob uma perspectiva adaptativa.

Tendo por objectivo o desenvolvimento de um modelo de organização e de dinâmica das comunidades vegetais dunares, foi efectuado um estudo detalhado em cinco tipos de habitats dunares dispostos em complexos de vegetação no sentido praia-duna. O trabalho de investigação concentrou-se na natureza e importância relativa dos filtros funcionais, interacções bióticas e heterogeneidade ambiental como factores centrais na formação de comunidades de plantas que colonizam e estabilizam as dunas costeiras. Foram avaliadas aplicação de várias questões de investigação sequenciais através da aplicação de ferramentas estatísticas a um conjunto de dados teste de vegetação dunar recolhidos ao longo de um gradiente climático regional e de uma transição biogeográfica no Norte de Portugal.

A diversidade de plantas exibe um padrão do tipo “humped-back” ao longo do gradiente local, com os maiores valores registados na zona central desse mesmo gradiente, e de acordo com a teoria ecológica. Ao longo deste gradiente observa-se ainda um claro zoneamento da vegetação com a segregação espacial de espécies, estratégias e tipos funcionais típicas de habitats costeiros face aos elementos florísticos de habitats mais interiores. Este zonamento é determinado essencialmente pela seriação ambiental de espécies com necessidades específicas de recursos e preferências ecológicas. A segregação é o padrão predominante de co-ocorrência dentro e entre os diferentes tipos de habitats, sugerindo um papel global dominante da seriação de espécies e da competição sobre a facilitação na estruturação e dinâmica das comunidades das plantas dunares. As espécies pertencentes ao tipo funcional III (as mais adaptadas ao ambiente dunar) bem como as possuidoras de estratégias ecológicas com uma componente S (i.e. tolerantes ao stress) tendem a prevalecer nos habitats das dunas móveis, confirmando a adaptação e a capacidade dessas espécies para prosperar sob condições de elevada severidade ambiental. A sua substituição gradual por elementos com uma componente R em direcção aos ecossistemas terrestres confirma o papel do stresse ambiental e da disponibilidade de recursos na

seriação das espécies e na estruturação das comunidades vegetais. As espécies do tipo funcional III foram igualmente substituídas, de forma gradual, por espécies dos tipos I e II em direcção aos habitats mais interiores confirmando deste modo o papel da severidade ambiental costeira como filtro eficaz para as espécies com adaptações nulas ou moderadas ao efeito combinado de stresse e perturbação.

Nos habitats das dunas móveis, a diversidade de plantas não parece sofrer alterações significativas na sequência de uma alteração para uma dinâmica costeira transgressiva, sugerindo que este componente da estrutura da comunidade pode não constituir um indicador efectivo das alterações ecológicas. Por seu turno, as estratégias e perfis funcionais das plantas dunares exibiram padrões de co-ocorrência distintos sob os dois tipos de dinâmica costeira, assinalando a importância das interacções entre os filtros abióticos, as características das próprias espécies e os factores bióticos na estruturação das respostas da vegetação às mudanças na dinâmica costeira. O zonamento típico das espécies, estratégias e tipos funcionais nas comunidades de dunas móveis foi modificado sob uma dinâmica costeira de carácter transgressivo, fornecendo uma base de investigação para novas abordagens nos domínios da avaliação e da monitorização ecológicas, focadas no perfil funcional destas comunidades vegetais. Não foi observada uma influência regional significativa na resposta das plantas à escala local. No entanto, a ocorrência de algumas interacções entre os processos locais e regionais para todo o conjunto de habitats dunares sugere que essas mesmas interacções deverão ser cuidadosamente estudadas antes da aplicação efectiva destesindicadores na avaliação e monitorização costeiras.

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1. Introduction

1.1. Functional ecology of coastal dune plants

1.1.1. The coastal dune environment

Coastal zones are interfaces between land and sea, hosting peculiar species, ecosystems and habitat types with high value for biodiversity conservation, natural resources and other ecosystem services (Martínez *et al.,* 2006; UNEP**,** 2006; Liquete *et al.,* 2013; IPCC, 2014). The coastal zone can be defined as «the geomorphological area either side of the seashore in which the interaction between the marine and land parts occurs in the form of complex ecological and resource systems made up of biotic and abiotic components coexisting and interacting with human communities and relevant socio-economic activities» (EC, 2009). Accordingly, the coastal zone is characterised by a high dynamism and rapid changes due to various factors, from substrate mobility, sea-water flooding and wind storms, to human settlement and sea level rise (Page & Thorp, 2010).

Coastal dune ecosystems are «ubiquitous elements of the dune-beach system that exist along the shores of many water bodies in the world where waves and currents interact with available sediment and local vegetation to create combinations of form and habitat at the water-land interface» (Psuty, 2008). These ecosystems correspond to about 20% of the world coastline and provide significant social and economic benefits (e.g. protection against flooding, mineral resources, recreation; Carter *et al.,* 1990; Zhang & Baas, 2012). Coastal sand dunes result from the interaction of aeolian, fluvial and marine processes, such as those related with wave and wind energies, sediment supply and granulometry, ground water level, and vegetation cover (Hesp, 2002; Barbosa & Domínguez, 2004; Arteaga *et al.,* 2008). These are usually considered the main drivers of dune formation (da Silva *et al.,* 2008; Houser *et al.,* 2008; Masetti *et al.,* 2008; Miller *et al.,* 2009). Additionally, dune-beach interactions (Fig. 1.1) are crucial for dune development in coastal zones, namely due to aeolian sand transportation from the beach (Sherman & Hotta, 1990; Maun, 2009; Delgado-Fernández, 2011). Those interactions are further influenced by many factors, such as sediment availability, wind speed and direction, beach topography, moisture

content, salt spray, groundwater, as well as living and dead organic material (Brown & McLachlan, 2010; Anthony *et al.,* 2009).

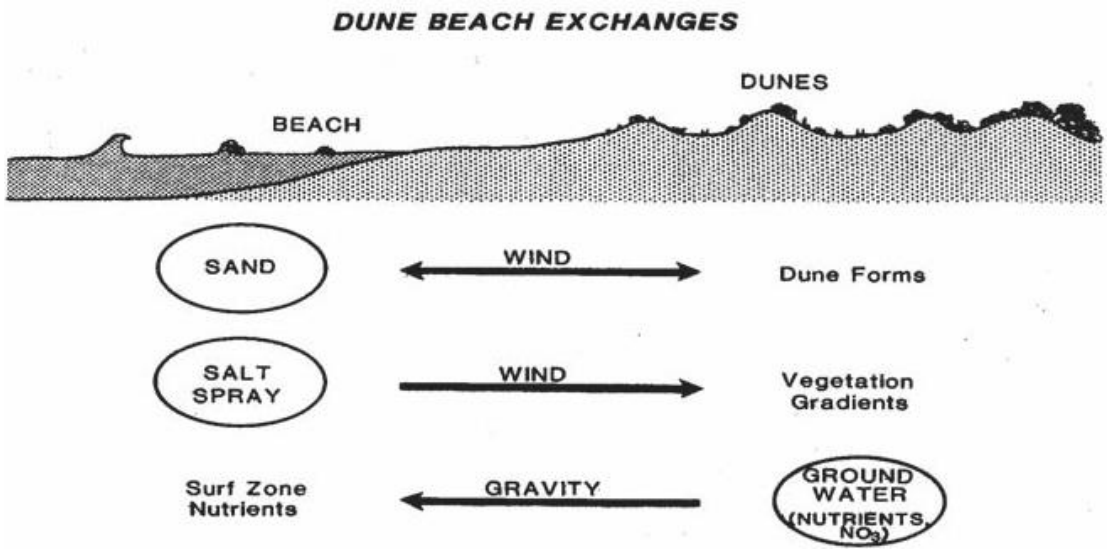

Fig. 1.1 – Exchanges of materials in the dune-beach system. Sand, groundwater, salt (spray) and nutrients are exchanged across the beach-dune interface, shaping landward gradients and plant communities (source: McLachlan & Brown, 2010).

The morphology and development of these coastal sand dunes depends on synergistic interactions between aeolian transportation and **vegetation**, expressed e.g. by the effect of vegetation as an obstacle to wind-blown sand transport (Hesp, 1989, 1991; Zhang & Baas, 2012; Yan & Baas, 2015). Plants act as roughness agents, altering wind fields (Luna *et al.,* 2011), and also as stabilisers, promoting favourable environmental conditions (Baas & Nield, 2010; Miller *et al.,* 2010) while creating spatial patterning of disturbance, stress, and resource availability (Acosta *et al.,* 2003; Biondi, 2007; Miller *et al.,* 2010; Feola *et al.,* 2011; Prisco *et al.*, 2012).

In **Portuguese** coastal sand dune ecosystems, three major types of dune habitats may be distinguished regarding their typical geomorphology, vegetation, and position along the sea-inland gradient: embryonic foredunes, foredunes (also primary or white dunes), and interior (secondary or grey) dunes, with the first two comprising the mobile dunes (Fig. 1.2; Lomba *et al.,* 2008). Embryonic foredunes are the seaward-most dune habitats, linking to the upper beach zone and frequently in contact with the sea (Prisco *et al.,* 2012). Foredunes, located in an inland position from embryonic foredunes (Tsoar, 2000; Psuty, 2008; Ryu & Sherman, 2014) correspond to «shore-

parallel dune ridges formed on the top of the backshore by aeolian sand deposition within vegetation» (Hesp, 2002). Interior dunes occupy the more interior positions, inland from foredunes, and are usually less affected by the sea and by dune-beach interactions (Psuty, 2008; Ciccarelli, 2014). These dunes are usually colonised by a mosaic of several vegetation types, from annual and perennial grasslands, to scrub and wet dune slacks, with these occurring landwards (Fig. 1.2).

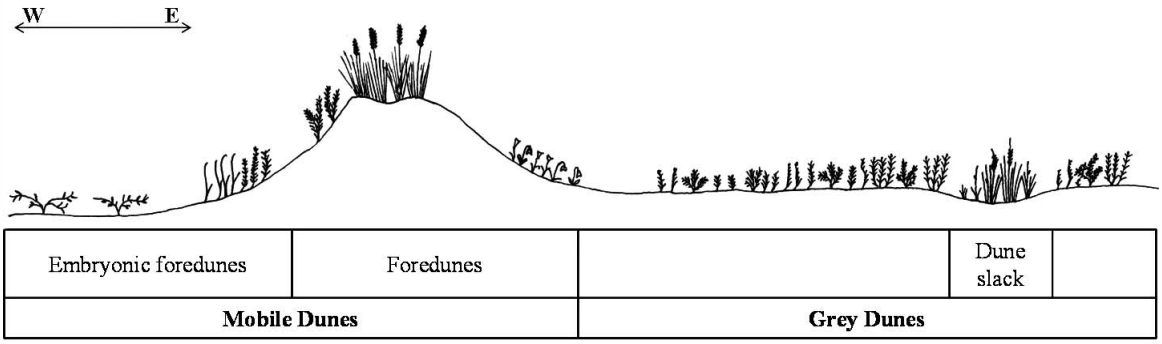

Fig. 1.2 – Typical habitat sequence in the active dune-beach system of Portuguese dunes: mobile dunes include embryonic foredunes and foredune tops, while grey (interior or secondary) dunes usually include a mosaic of annual and perennial grasslands and scrub (landward), with dune slacks occurring at some locations (source: Lomba *et al.,* 2008).

1.1.2. Stress, disturbance, and the coastal dune flora

Ecological systems suffer different types and intensities of environmental stress as well as distinct intensities and frequencies of disturbance (He & Bertness, 2014; Yan & Baas, 2015). From a vegetation ecology perspective, **environmental stress** includes those processes that limit or reduce plant metabolism and biomass production (e.g. shortage of light, water, or nutrients), whereas **disturbance** (Rykiel, 1985; Borics *et al.,* 2013) usually expresses on the partial or total direct destruction of plant biomass (e.g. through rapid desiccation, fire, stormy winds, extreme floods, or human actions; Grime, 1977, 2001; Dornelas, 2010).

In **coastal sand dunes**, disturbance events (e.g. severe storms, extreme sand burial, trampling) and stress (e.g. water deficit, nutrient scarcity, salt spray) are filters determining dune vegetation (Álvarez-Molina *et al.,* 2012; Brunbjerg *et al.,* 2012a,b). Various abiotic factors affect plant performance in coastal dunes, e.g. sand burial, high temperatures, water deficiency, nitrogen availability, wind exposure, salt spray, and soil

salinity (e.g. Rozema *et al.,* 1985; Hesp, 1991; Maun, 1997; Ripley, 2001; Ciccarelli *et al.,* 2009). Sand burial and wind affect the spatial distribution of dune plants (Costa, 1991, 2001; Maun, 2009; Feagin *et al.,* 2015), inducing mechanical damage and dryness of plant tissues (Maun, 2009; Frosini *et al.,* 2012; Alvarez-Molina *et al.,* 2013). Interactions between sand burial and wind may also affect the availability of soil water, nutrients, salinity and air for dune plants (Costa, 1991; Zhibao *et al.*, 2000; Liu *et al.,* 2013, 2014; Fig. 1.3). Due to the complexity of factors and interactions, a general model of plant responses to the combination of these abiotic factors has not been achieved yet (Forey *et al.,* 2009, 2010; Balestri & Lardicci, 2013).

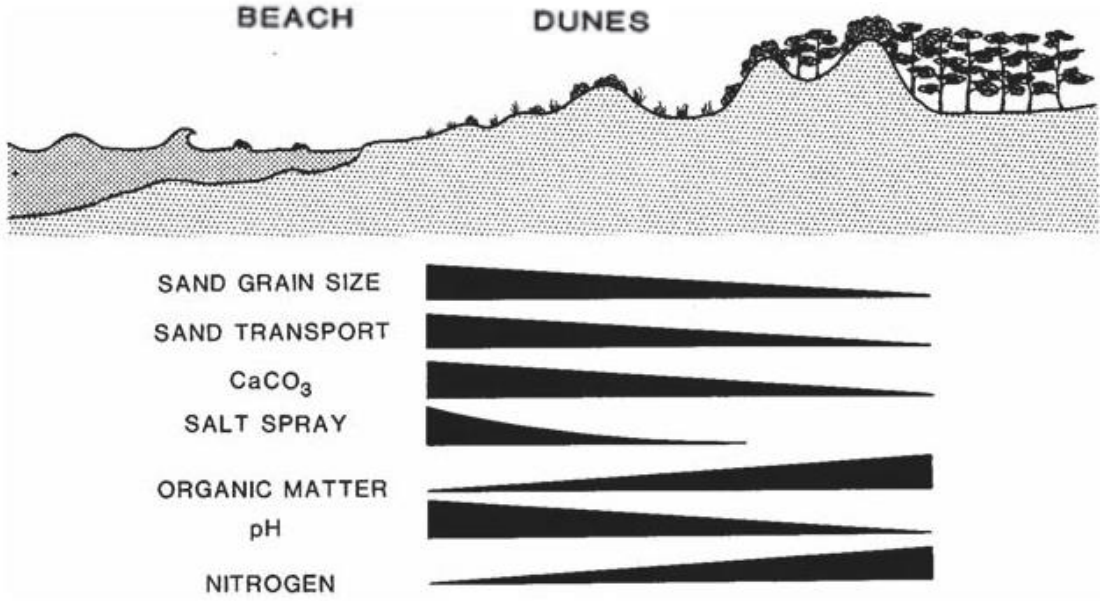

Fig. 1.3 – Variations of the main abiotic factors along a sea-inland direction (left to right) in a dune system. In general, sand grain size, transport and pH decrease landward, whereas organic matter and nutrient availability increase in that same direction (source: McLachlan & Brown, 2010).

Dune plants display **specific adaptations** in order to evade excessive radiation, to survive under water and nutrient stress, and to compete for scarce resources (Ripley, 2001; Ievinsh, 2006; Spanò *et al.,* 2013a,b; Fidalgo *et al.,* 2014). Besides other specific adaptations, dune plants often exhibit: small leaves to decrease evapotranspiration rates; prostrate or cushion shaped habits to face strong winds; deep roots to enable fixation to a mobile substrate and to facilitate water uptake; internodes or rhizomes stimulated by sand deposition and mobility; succulent stems and leaves for water

reserve; CAM and C4 metabolisms as a water economy strategy; and/or root mycorrhizae to assist seedling development and colonization (Ciccarelli *et al.,* 2009; Maun, 2009; Bérmudez & Retuerto, 2014; Li *et al.,* 2015; Medina *et al.,* 2015).

Sand burial influences plant succession and development (Kent *et al.,* 2001), by changing plant growth. Several dune plants show adaptions to burial through aeolian "cushion" growth forms, leaf sclerophylly for mechanical resistance (Costa, 1991; Hesp, 1991), and/or reproductive traits/strategies such as clonality, larger seed mass protecting germination and seedling establishment, elongation of seedlings, and seed dormancy induced by burial or salt spray (Ren *et al.,* 2002; Maun, 2009; Balestri & Lardicci 2013; Sanyal & Decocq 2015). These vary with burial incidence, depth, time of the year and life history (Maun, 1998; Frosini *et al.,* 2012; Fig. 1.4). As an example, foredune tops are usually dominated by perennial tussock grasses due to their tolerance to wind (Kim & Yu, 2009; Vick & Young, 2011) and burial severity, e.g. *Ammophila arenaria*, that uses rhizome elongation to respond to burial (Hesp, 1991).

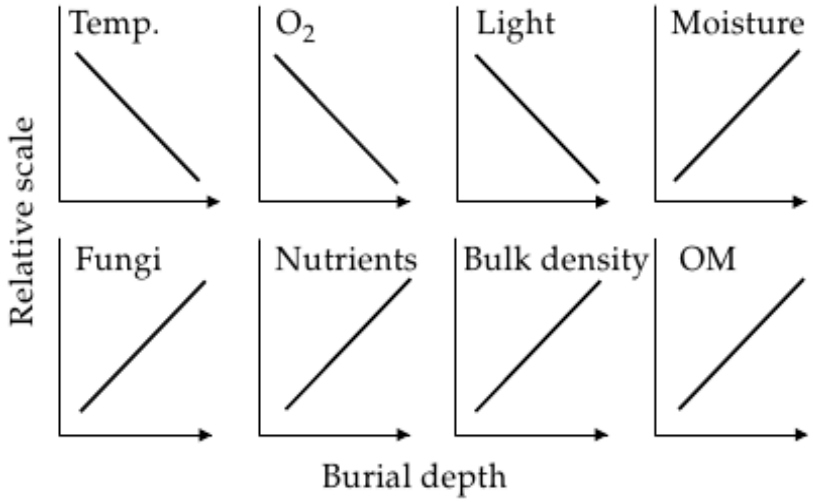

Fig. 1.4 – Variations of soil abiotic factors within the environment (vertical axis) of a plant buried in sand (horizontal axis; source: Maun, 2009).

Coastal dune soils exhibit low water retention capacity and rapid flow of nutrients, despite the high concentration of salt spray micronutrients (Maun, 2009; Joesting, 2011; Gwenzi *et al.,* 2012). **Nutrient limitation** constrains nitrogen economy (Gilbert *et al.,* 2008; Kim *et al.,* 2014), with nutrient availability influencing biomass formation and resource allocation trade-offs (Maun, 1998; Frosini *et al.,* 2012; Balestri & Lardicci,

2013). Salt and water stress also influence dune plants, despite their adaptive responses (Bartels & Sunkar, 2005; Spanò *et al.,* 2013a; Kim *et al.,* 2014b). **Water economy** is vital and, besides the CAM and C4 photosynthetic pathway and succulence, other aspects may promote water use efficiency e.g. leaf rolling and leaf orientation (Ciccarelli *et al.,* 2009; Maun, 2009; Perrone *et al.,* 2015), protective hairiness against sunlight, tissues for wet air storage, and root modifications for water storage (Barbour *et al.,* 1985; Ripley *et al.,* 1999; Ripley & Pammenter, 2008; Bérmudez & Retuerto, 2014). Moreover, dune plants display biochemical mechanisms e.g. antioxidant neutralization of reactive oxygen (Spanò *et al.,* 2013a; Fidalgo *et al.,* 2014).

1.1.3. Adaptive strategies and functional groups in the dune flora

According to Grime (2001), **plant strategies** may be defined as «groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology». Plant strategy schemes highlight the dissimilarities in ecological performance among plants and try to organize species in categories or along spectra according to their ecological features (Westoby, 1998; Reich *et al.,* 2003; Laughlin & Laughlin, 2013). Some of the more widely used general classifications of plants according to their responses to the environment are: (1) Grime's (1974, 1977, 2001) CSR plant strategy scheme, based on three crucial factors for plant development (competition, stress, and disturbance); (2) the functional types of Garcia-Mora (García-Mora *et al.,* 1999), also based on three major vegetation responses to environmental changes; (3) the life-form system of Raunkiaer (Raunkiaer, 1934; Marini *et al.,* 2012), recently expanded by Bunce *et al.,* (2008, 2010, 2013) and applied by other works (e.g. Mücher *et al.*, 2009; Metzger *et al.*, 2013; Ortega *et al.*, 2013; Kosmidou *et al.*, 2014; Lang *et al.*, 2015); and (4) Westoby's (1998) LHS scheme based on three key functional traits (specific leaf area, canopy height, and seed weight).

According to Grime (2001), plant evolution may be tied to the expression of three primary strategies (Fig. 1.5), which define the CSR system. Each one of those strategies can be recognized through several plant traits comprising morphological features, allocation of resources, and responses to stress and disturbance conditions (Grime, 1977; Fig. 1.5). **Grime's CSR system** has contributed to the integration of

evolutionary constrains with plant/environment interactions, and to the understanding of important characteristics of species, communities, and ecological processes (Wilson & Lee, 2000; Schmidtlein *et al.,* 2012). According to the relationship between productivity and stress/disturbance, it is possible to define three extreme strategies: (1) Competitors (C), able to exploit conditions of low stress and low disturbance; (2) Stress-tolerators (S), associated to conditions of high stress and low disturbance; and (3) Ruderals (R), related to conditions of low stress and high disturbance (Grime, 1977, 2001). Although habitats exploited by each of the main CSR strategies represent extreme combinations of environmental conditions, under moderate conditions and combinations of environmental stress and disturbance, secondary intermediate strategies tend to dominate (Grime, 2001).

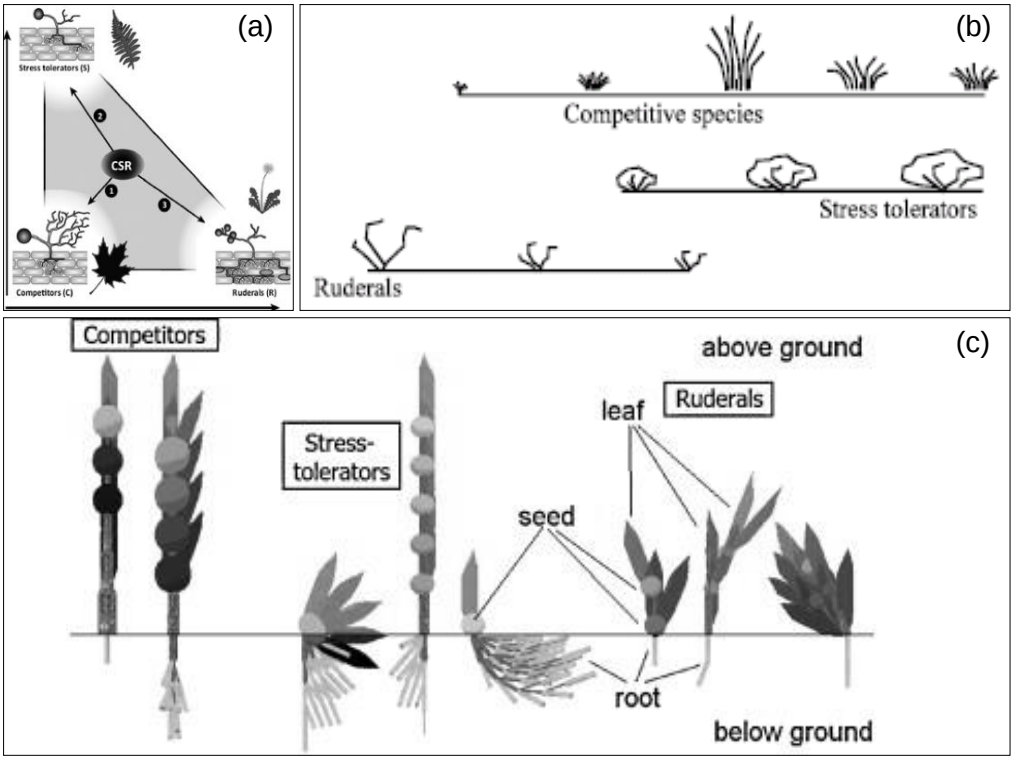

Fig. 1.5 – Central aspects of the CSR plant strategies theory: (a) Grime's CSR triangle (adapted from Mulder *et al.,* 2013); (b) dominance gradient regarding stress (towards right) and disturbance (towards left) responses (adapted from Tarhouni *et al.,* 2007); (c) Examples of morphologies for the main C, S and R strategies (adapted from Bornhofen *et al.,* 2011).

Grime's CSR life strategy scheme underlines the grouping of nuclear plant traits responding similarly to the environment (García Novo *et al.,* 2008; Timmermann *et al.,* 2014), thus capturing fundamental evolutionary strategies as an important comparative

approach for the analysis of functional diversity and community assembly (García Novo *et al.,* 2008; Lewis *et al.,* 2014a,b). Disturbance and stress, core processes in Grime's theory, are known to play a major role in the assembly and dynamics of **coastal plant communities**, as described above. This is an important argument for the application of this functional scheme to explore community assembly and dynamics in coastal dune systems (Macedo *et al.,* 2010; Ciccarelli, 2015).

Plant functional types include species with common life strategies, usually sharing some assortment of functional traits (García Novo *et al.,* 2008; Brooker, 2010). Those functional types are commonly employed to analyse community patterns (Dyer *et al.,* 2001; Schellberg & Pontes, 2012). Dune species reveal various extents of adaptation to their local environment, hence enhancing the difficulty to establish a common set of traits to describe dune plant functional types (García Novo *et al.,* 2008; Pintó *et al.,* 2014). Still, as example, Feagin & Ben Wu (2007) found a strong patterning in the spatial distribution of functional groups along the dune elevation gradient. Moreover, local habitat heterogeneity, a foremost driver of diversity patterns, may also affect the distributional abundance of plant functional types in coastal dune systems (Stallins, 2003).

Feagin & Ben Wu (2007) obtained three plant functional groups for **coastal dune systems** in Galveston Island (Texas, USA), which were named colonizers, soil binders and competitors. These functional types are adapted to segments of the environmental gradient: (1) colonizer plants occur in low sand elevations with scarce organic matter and moderate to high intensities of disturbance and stress; (2) soil-binders occur on moderate elevations in embryonic dunes with sediment transport buffered by organic matter; and (3) competitors occur on developed dune ridges whit high density of vegetation (Feagin & Ben Wu, 2007). Specifically for foredune habitats, Gallego-Fernández & Martínez (2011) considered five plant functional types: species with strong tolerance to sand burial and salinity, more common along accreting dune systems; species with strong tolerance to sand burial and occurring in all conditions of coastal dynamics; and three groups encompassing those plants without specific adaptations and responses to sand burial and salinity. Page & Thorp (2010) considered three types of dune plants regarding sand instability and burial, based on previous work by Kirkpatrick & Harris (1999) for dune vegetation of Tasmania Island, Australia, and aimed primarily for supporting restoration processes: (1) primary species

(sand-biding grasses, succulent creepers), contributing to support unstable sand substrates through fast development; (2) secondary species (grasses, sedges, herbs, low shrubs) located close to the sea, but only copping with moderate sand burial; and (3) tertiary species (taller shrubs, trees), occurring inland of frontal dunes and developing especially at larger distances from the sea.

In the **Iberian Peninsula**, García-Mora *et al.* (1999) proposed a classification with three functional types related to the extent of adaptation to the dune ecology, in order to describe vegetation responses to changes in dune dynamics and to the major environmental factors controlling community assembly. Based on data from foredune vegetation in the Gulf of Cadiz, southern Spain, those three functional types were described based on a set of functional traits and morphological characters of plant species (Fig. 1.6): Type I, corresponding mainly to winter annuals of moderate size, presenting soft leaves and no specific adaptations to the dune environment, usually related to more stable soils; Type II, comprising mostly perennial plants characterized by the presence of a "below-ground spreading root network" and other assumed adaptations to environmental stress; and Type III, consisting mainly of plants with some ability of dispersal by sea-water and capability to resist sand burial (García-Mora *et al.,* 1999, 2000; Williams *et al.,* 2001). Silva *et al.* (2004) studied disturbance and conservation of coastal dune systems based on the three functional types proposed by García-Mora *et al.* (1999), in Costa da Caparica, Southern Portugal, providing evidence of the importance of this classification for dune plant-environment interactions, and thus ecosystem state assessment.

1.2. Community ecology of coastal dune vegetation

Dune plant community structure and dynamics also result from the interaction of species and individuals with environmental stress gradient and disturbance events (Reice, 1994; Ciccarelli *et al.,* 2012; Cavieres *et al.,* 2014; Amici *et al.,* 2015). Those communities can be analysed based on distinct diversity components, namely species richness, evenness, and composition (Cavieres & Badano, 2010; Leps, 2013). Patterns of plant diversity in the dune environment relate with dune topography (Honrado *et al.,* 2010) and to environmental gradients acting at several spatial scales (regional or local) (Forey *et al.,* 2008; Fidalgo *et al.,* 2014; Chozas *et al.,* 2015). These gradients influence the responses of individual plants to environmental conditions, and affect species co-occurrence as well as community assembly and dynamics (Fidalgo *et al.,* 2014; Laliberté *et al.,* 2014; Vaz *et al.,* 2015).

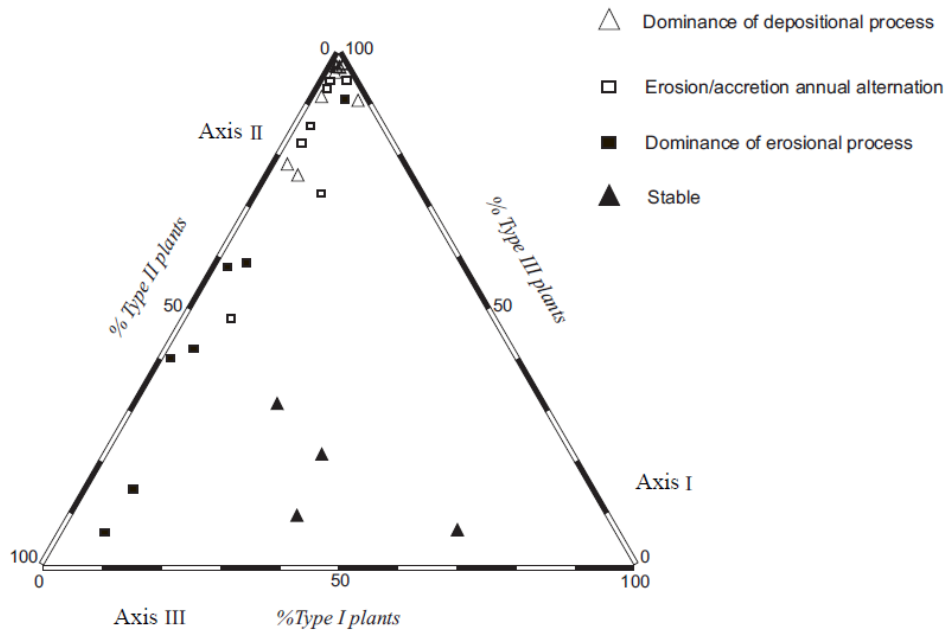

Fig. 1.6 - Foredune characterization through the relative cover of the three functional types. Overall, coastal erosion induces dominance of Type II plants, whereas Type III plants are dominant under meta-stable conditions (source: García-Mora *et al.,* 1999).

1.2.1. Biotic interactions and species coexistence

According to Götzenberger *et al.* (2012), **assembly rules** are «any constraint on species coexistence». Wilson & Sykes (1999) emphasises that these should be «restrictions on the observed patterns», focusing on empirical data rather than on the processes themselves. Modern theoretical formulations emphasize that community assembly may be shaped through filters of species dispersal, abiotic environment, and biotic interactions (Tilman, 1988; Callaway, 2007; Ulrich & Gotelli, 2010; Stokes & Archer, 2010; Luzuriaga *et al.,* 2012).

Biotic interactions among plants are essential to understand community patterns and to predict their dynamics (Michalet *et al.,* 2006; Brooker *et al.,* 2008; Mod *et al.,* 2014). Their role as a community driver is complex and varies along gradients of environmental severity (Bonsall *et al.,* 2003; Jeffers *et al.,* 2011). Plant interactions can be: positive (e.g. facilitation), extending species beyond their expected geographical range; negative (e.g. competition), excluding species from adequate habitats and reducing their distribution; or neutral, with no significant effects on distribution for both species (Damgaard, 2005; Callaway, 2007; Lortie & Turkington, 2008; Armas *et al.,* 2009; Schöb *et al.,* 2013a,b).

Facilitation corresponds to a positive effect of one species (the benefactor) on associated neighbour plants (the beneficiaries), promoting plant development and dispersal (Schöb *et al.,* 2013b). According to the “stress-gradient hypothesis” (SGH; Bertness & Callaway 1994), facilitative interactions are expected to prevail under extreme levels of environmental severity, leading to the aggregation of species or species groups. According to the “Intermediate-Disturbance Hypothesis” (IDH; Wilson & Sykes, 1999; Roxburgh *et al.,* 2004), from intermediate to high levels of environmental stress and/or disturbance, facilitation may adjust plant composition by compensating the effects of competitive exclusion (Bertness & Callaway 1994; Michalet *et al.,* 2006; Le Bagousse-Pinguet *et al.*, 2014). This rationale is often used to explain species diversity maintenance and the high diversity rates at intermediate disturbance levels (Wilson & Sykes, 1999; Roxburgh *et al.,* 2004).

Competition, on the other hand, corresponds to the ability of a given plant or species to decrease the performance and development of another plant or species, promoting their spatial segregation (Grime, 2001; Armas *et al.,* 2009). According to the SGH, competitive interactions are expected to prevail under low levels of environmental severity (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Armas *et al.,* 2009). Still, some studies have reported the prevalence of competition (along with species sorting) over facilitation in harsh environment of coastal dunes, in apparent deviation with the SGH assumptions (e.g. Maltez-Mouro *et al.,* 2010; Vaz *et al.,* 2015). The relation between competition and facilitation along gradients of environmental severity has been thoroughly studied over the last decade (e.g. Franks & Peterson, 2003; Michalet *et al.,* 2006; Maltez-Mouro *et al.,* 2010; see Brooker *et al.,* 2008, and Pugnaire, 2010, as reviews). In coastal sand dunes, distinct patterns of segregation or aggregation (co-occurrence patterns hereafter) have been reported (Damgaard, 2010; Santoro *et al.,* 2012; Vaz *et al.,* 2015). These patterns can be largely determined by, and also contribute to the distinct levels of plant diversity which characterise the variety of dune habitats (Acosta, 2009; Bérmudez, 2013).

1.2.2. Plant community assembly along environmental gradients

The assessment of the **relative importance** of competition and facilitation as drivers of community assembly have focused on testing predictions from the SGH (Bertness & Callaway, 1994; Pugnaire, 2010; Fig. 1.7) and the HBR (Grime, 1973). The SGH states that facilitation should prevail over competition under stressful conditions, with biotic interactions shifting from competition to facilitation along a gradient of increasing environmental severity (e.g. Bertness & Callaway, 1994; see Brooker *et al.,* 2008 for a review; He & Bertness, 2014). Concurrently, the HBR suggests that facilitation should prevail from intermediate to high levels of environmental severity, promoting plant species diversity above otherwise expected values (Grime, 1973; Michalet *et al.,* 2006; Brooker *et al.,* 2008).

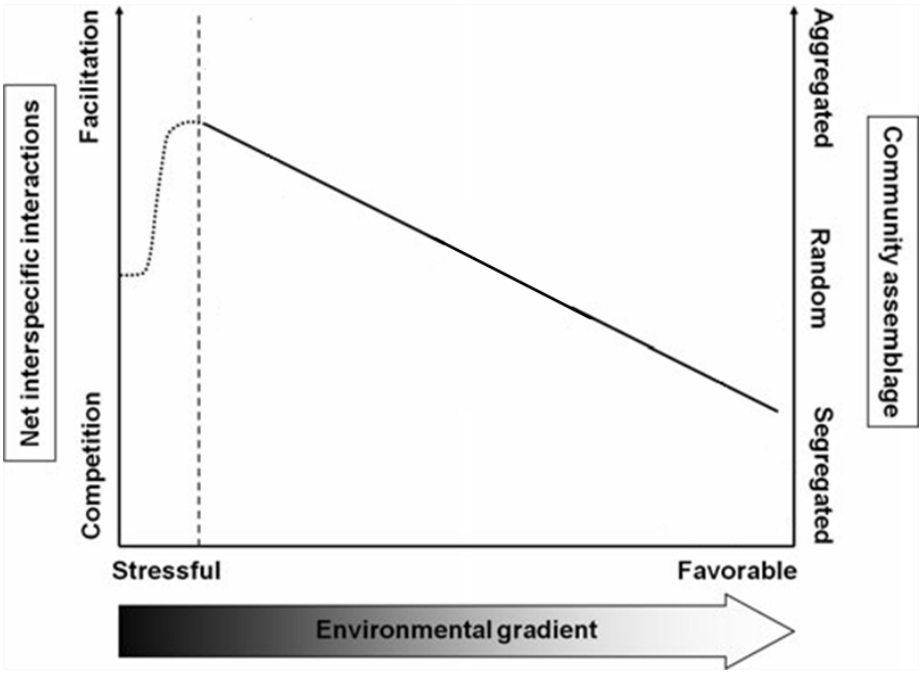

Fig. 1.7 - Theoretical diagram of the stress gradient hypothesis. The prevalence of facilitation under stressful conditions can be reverted under extreme environmental severity (adapted from Santoro *et al.*, 2012).

The SGH predicts an **increase in positive interactions** with increasing environmental stress and disturbance (Bertness & Callaway, 1994; He & Bertness, 2014). However, recent studies have provided evidence of a collapse in facilitation under severe conditions due to a decrease in the benefactor role of nurse plants (Michalet *et al.,* 2015a,b). Furthermore, other studies found evidence for the prevalence of competition even under high levels of environmental severity (e.g. Franks & Peterson, 2003; Maestre & Cortina, 2004; Armas & Pugnaire, 2009; Ariza & Tielborger, 2012; Vaz *et al.,* 2015)**.** Conversely, recent evidence suggests the absence of that facilitation collapse (Pugnaire *et al.,* 2015), highlighting the need of more tests of possible exceptions to the SGH under extreme environmental conditions (He & Bertness, 2014). This variety of results has stimulated refinements to the original SGH, with some authors even suggesting that competition may prevail at both ends of environmental severity gradients, while facilitation is likely most important at intermediate severity levels (e.g. Maestre *et al.,* 2009; Holmgren & Scheffer, 2010; Castanho *et al.,* 2015).

In this context, recent progress in SGH research highlights the need to **integrate functional ecology** for understanding the disparity of co-occurrence patterns of community assembly along gradients of abiotic severity (e.g. Michalet *et al.,* 2006; Callaway, 2007; Malkinson & Jeltsch, 2007; Brooker *et al.,* 2008; Biswas & Wagner, 2014). Abiotic factors can operate as environmental filters decreasing functional diversity (Cornwell *et al.,* 2006; Grime, 2006; Mouillot *et al.,* 2007; Bermudez, 2013). Those filters can additionally define how abiotic elements determine the **co-occurrence** of functional groups in a given community (Tilman, 1982; HilleRisLambers *et al.,* 2012). For instance, in coastal dunes, environmental filtering by the harsh environment is known to promote trait convergence (Bérmudez & Retuerto, 2013), with species co-occurrence patterns varying with spatial scale and with the focal abiotic stress gradient (Maltez-Mouro *et al.,* 2010; Vaz *et al.,* 2015). Additionally, the outcomes of biotic interactions may differ among functional groups, producing distinct effects on competitive or stress-tolerant plants (Liancourt *et al.,* 2005; Maestre *et al.,* 2009; Forey *et al.,* 2010; Schöb *et al.,* 2013a,b).

The integration of functional ecology in the analysis of patterns of species co-occurrence can be accomplished in the light of neutral or deterministic processes (Hubbell, 2001; Morlon *et al.,* 2009; McGill, 2010; Murrell, 2010; Maire *et al.,* 2012). While the neutral theory establishes that the existence of functional differences is not necessary to simulate observed patterns of diversity in natural conditions, the deterministic view considers that diversity patterns derive from deterministic processes such as habitat filtering or niche differentiation (MacArthur & Levins, 1967; Keddy, 1992; Adler *et al.,* 2010; Cornwell & Ackerly, 2010; Maire *et al.,* 2012; Wang *et al.,* 2015). H**abitat filtering** drives spatial convergence of plant species with similar traits, while **niche differentiation** promotes trait divergence and species with different niches occurring in a non-overlapping space (e.g. Grime, 2006; Kraft *et al.,* 2008; Schöb *et al.,* 2013a; Gross *et al.,* 2013). Habitat filtering and niche differentiation processes are not reciprocally exclusive, as traits may co-vary across space and time, often in relation to resources and niche availability (Suding *et al.,* 2008; Maire *et al.,* 2009; Devictor *et al.,* 2010; Gross *et al.,* 2013).

Area and spatial heterogeneity are also important when analysing community assembly patterns (Allouche *et al.,* 2012; Stein *et al.,* 2014). According to Seiferling *et al.* (2014), environmental heterogeneity is the «spatial or temporal variation of a given resource, structure, or biota in a given area». Besides biotic interactions, spatial variation of community assembly may be originated by environmental heterogeneity and **niche-based species sorting** (Foster *et al.,* 2011). Environmental heterogeneity includes three main components (environmental conditions, space, and time), with the spatial component considered to be the most important in connection with environmental gradients and biotic factors (Pausas & Austin 2001; Hofer *et al.,* 2008; Isermann, 2009). These components may promote species-environment sorting processes contributing to the heterogeneity of plant coexistence and turnover along gradients (Tilman & Pacala, 1993; Reynolds *et al.,* 2007; Questad & Foster, 2008; Williams & Houseman, 2013). Species sorting has actually been highlighted as one of the main processes of community structure in coastal dune vegetation, with species filtering related with abiotic preferences along major environmental gradients (Brunbjerg *et al.,* 2012a,b; Rajaniemi *et al.,* 2012; Vaz *et al.,* 2015).

1.3. Dune vegetation and changes in coastal dynamics

1.3.1. Change and governance in coastal areas

Coastal areas are among the most susceptible socio-ecological systems to natural hazards such as storms, erosion, flooding, landslides, rising salinity, and drought (EEA, 2013; Delgado-Fernández *et al.,* 2013). The resilience of coastal ecosystems is affected by human pressures (namely pollution, urban development, resource overexploitation, and tourism), which further enhance their **vulnerability** to extreme environmental events (EEA, 2013; Lavalle *et al.,* 2011a,b; Fernández *et al.,* 2013). Many coastal ecosystems have been managed unsustainably, suffering irreversible ecological changes, the anticipation of which is needed towards the implementation of sustainable governance processes (Craig & Ruhl, 2010).

Additionally, coastal areas have been suffering an increase of frequency and severity of extreme environmental events, mainly attributed to sea level rise and changes in the frequency and intensity of storms (Gray *et al.,* 2014). Continued sea level rise is due to impact coastal zones mainly through coastal erosion, increased coastal flooding and salinity intrusion, with implications for ecosystems, biodiversity and socio-economy (EEA, 2013; Lavalle *et al.,* 2011a,b; Delgado-Fernández *et al.,* 2013; Gray *et al.,* 2014). **Coastal erosion** may be defined as «the encroachment of land by the sea after averaging over a period which is sufficiently long to eliminate the impacts of weather, storm events and local sediment dynamics» (Salman *et al.,* 2004). The origin of each erosion phenomenon is diverse, and may emerge from the natural cyclic dynamics of the dune system or from several other factors, such as extreme storm and wind events, or sea level changes. Additionally, erosive processes can also be promoted by human factors, namely the development of infra-structures and resource exploitation (ANCORIM, 2012).

Coastal governance requires integrated actions for effective knowledge-based governance decisions, as well as for attaining robust and resilient systems (Clarke *et al.,* 2013). Given the inherent complexity of coastal zone governance, Integrated Coastal Zone Management (ICZM) approaches are essential to accomplish coastal sustainability as well as to prevent and mitigate negative consequences (Lavalle *et al.,* 2011b; Clarke *et al.,* 2013). Moreover, benefiting from the defensive role of coastal ecosystems is becoming gradually accepted by policy makers as an approach to develop coastal soft-defences based on integrated views involving coastal geomorphology, engineering and ecology (Hanley *et al.*, 2014). Thus, current restoration methodologies often involve the plantation of native plant species, e.g. *Ammophila arenaria*, which is an active dune builder through the stabilizing action of its rhizomatous system (Maun, 2009; Hanley *et al.,* 2014).

1.3.2. Responses of dune vegetation to changes in coastal dynamics

The **responses of ecological communities** to coastal pressures provide valuable indicators to evaluate the stability and resilience of these ecosystems (Honrado *et al.,* 2010; Mori *et al.*, 2014). In fact, ecosystem resilience is a promising concept to consider when dealing with the impact of environmental changes on the functioning and sustainability of ecosystems (Wang & Loreau, 2014). Resilience in coastal areas is strongly influenced by the distinct responses of vegetation to changes in the environment (Loreau & de Mazancourt, 2008, 2013; Hautier *et al.,* 2014; Wang & Loreau, 2014).

There is also strong evidence of a close connection between dune topography, plant community structure, and environmental conditions and gradients, thus highlighting **dune vegetation** as a potential source of indicators of prevailing coastal dynamics (García-Mora *et al.,* 1999; Feagin & Ben Wu, 2007; Honrado *et al.,* 2010). Recent research has revealed quantitative relations between topographic, geochemical and biological features of dune ecosystems, contributing with deeper insights on the determinants of spatial and temporal patterns of dune vegetation (Honrado *et al.,* 2010; Macedo *et al.,* 2010; Fidalgo *et al.,* 2014). Likewise, variations in coastal dynamics, particularly a shift from meta-stable to transgressive prevailing dynamics, is known to induce modifications in dune morphology (Henriques, 2007), as well as in plant

community structure and functional profiles (Honrado *et al.,* 2010; Macedo *et al.,* 2010), and even in the physiology of dune communities (Fidalgo *et al.,* 2014). Understanding the dynamics of dune systems and its relation with plant species and communities thus provides an important basis for the adaptive conservation and management of coastal dune habitats (Barrett-Mold & Burningham, 2010).

1.4. Research objectives, workflow, and thesis structure

Important insights on the roles of plant **species and their traits** on ecosystem functions and properties have been achieved by modern ecological research (Kazakou *et al.,* 2006). The investigation of functional changes and declining species richness as global drivers of alterations in ecosystem functioning has received a considerable attention (Loreau *et al.,* 2001). In coastal areas this is particularly important regarding the provision of ecosystem services and the mitigation of natural hazards (Lozoya *et al.,* 2011).

An important research avenue has been the one related with the interpretation of floristic changes through their consequences for the **representation of traits** in plant communities, identifying functional shifts in plant communities and thereby discriminating the effects of distinct environmental and ecological drivers (Grime, 2001). Specifically, plant communities in coastal dunes are harshly impacted by conditions of high stress (e.g., salinity, drought, and nutrient limitation) and frequent disturbance (e.g., sand burial, wind abrasion), with various and often synergistic effects (Forey *et al.,* 2008). Moreover, feedbacks between disturbance and stress gradient zonation constitute a distinct feature of coastal dune systems (Stallins & Parker, 2003), determining the patterns of species diversity and co-occurrence (Maltez-Mouro *et al.*, 2010).

The research developed for this thesis was outlined under a **general research question**: Can community ecological theory and its related analytical tools provide detailed insights on the responses of coastal dune ecosystems (and particularly of their plant communities) to environmental changes? Specifically, we aimed to evaluate the role of plant life strategies and functional types in shaping community structure of dune vegetation as well as in defining the responses of plant communities to a shift in prevailing coastal dynamics. We assessed the influence of key environmental gradients and of coastal dynamics on plant community structure and plant species diversity. The study was conducted in the Northern Portuguese coastline, at the transition between the Eurosiberian and the Mediterranean biogeographic regions of Europe. The final goal was to provide scientific bases for the adaptive management and monitoring of dune ecosystems under an ICZM framework.

This thesis reports the development and test of a framework to analyse **community assembly and dynamics** in coastal dune vegetation, based on the assessment of diversity and co-occurrence of plant species, life strategies and functional types along the main environmental gradients (regional and local). The following four questions were sequentially addressed:

(1) What patterns of **species diversity and co-occurrence** can be observed in plant communities along the local dune gradient?

(2) How are **plant strategies and functional types** distributed along the local dune gradient?

(3) How are the observed patterns of species diversity and co-occurrence **mediated by plant strategies and functional types**?

(4) Is this theoretical approach, based on co-occurrence patterns and functional profiles of species assemblages, **useful to identify ecological changes** induced by shifts in prevailing coastal dynamics?

The research workflow encompassed the study of vegetation in **five dune habitat types** organised in vegetation complexes from the beach towards inland in Northern Portugal: embryonic foredunes, foredunes, interior (grey) dunes, dry grasslands, and low scrub (see section 2.2 for a detailed description of these habitat types in the study area). Specifically, this research focused on the nature and relative importance of functional filters, biotic interactions and environmental heterogeneity in shaping the plant communities that colonize coastal dunes.

Sequentially, the **research workflow** involved: (1) assessing the patterns of diversity of plant species along regional and local environmental severity gradients; (2) analysing species co-occurrence patterns in all types of plant communities along the previous gradients; (3) characterising the dune flora of the study area from a functional perspective (plant strategies and functional types); (4) understanding the role of plant life strategies on the patterns of species co-occurrence in the focal plant communities; and finally (5) testing the ability of this theoretical approach, based on functional types

and strategies and on species interactions, to discriminate dune systems under contrasting coastal dynamics (i.e. meta-stability vs. transgression).

The thesis follows a classical structure and is organised in **four chapters**. In the current Chapter 1, the theoretical foundations and the objectives of the research developed for the thesis were described. In Chapter 2, a detailed description of the study area, sites and focal habitat types is provided, followed by a description of the analytical methods. The main results of the research developed for the thesis are presented and briefly discussed in Chapter 3. Finally, in Chapter 4 an integrative discussion as well the main conclusions and some suggestions for the way forward are presented.

2. Methods

2.1. The study area

The study was conducted along the **coast of Northern Portugal**, between Apúlia (Esposende), in the north to Cova Gala (Figueira da Foz), in the south, covering a shoreline distance of ca. 200 km (Fig. 2.1). The climate is Temperate, sub-Mediterranean to rainy Mediterranean, with strong oceanic influences. From north to south, total rainfall drops from ca. 1500 mm year^{-1} to ca. 800 mm year^{-1}, while mean annual temperature increase from ca. 14 °C to ca. 15 °C (Honrado *et al.,* 2010). The study area includes the transition between two biogeographic regions: the Eurosiberian (generally coincident with the Temperate sub-Mediterranean climate, and corresponding to the northern half of the study area), and the Mediterranean, with summer aridity and moderate rainfall throughout the rest of the year (Costa *et al.,* 1998, 2000, 2009; Honrado *et al.,* 2010; Fig. 2.1).

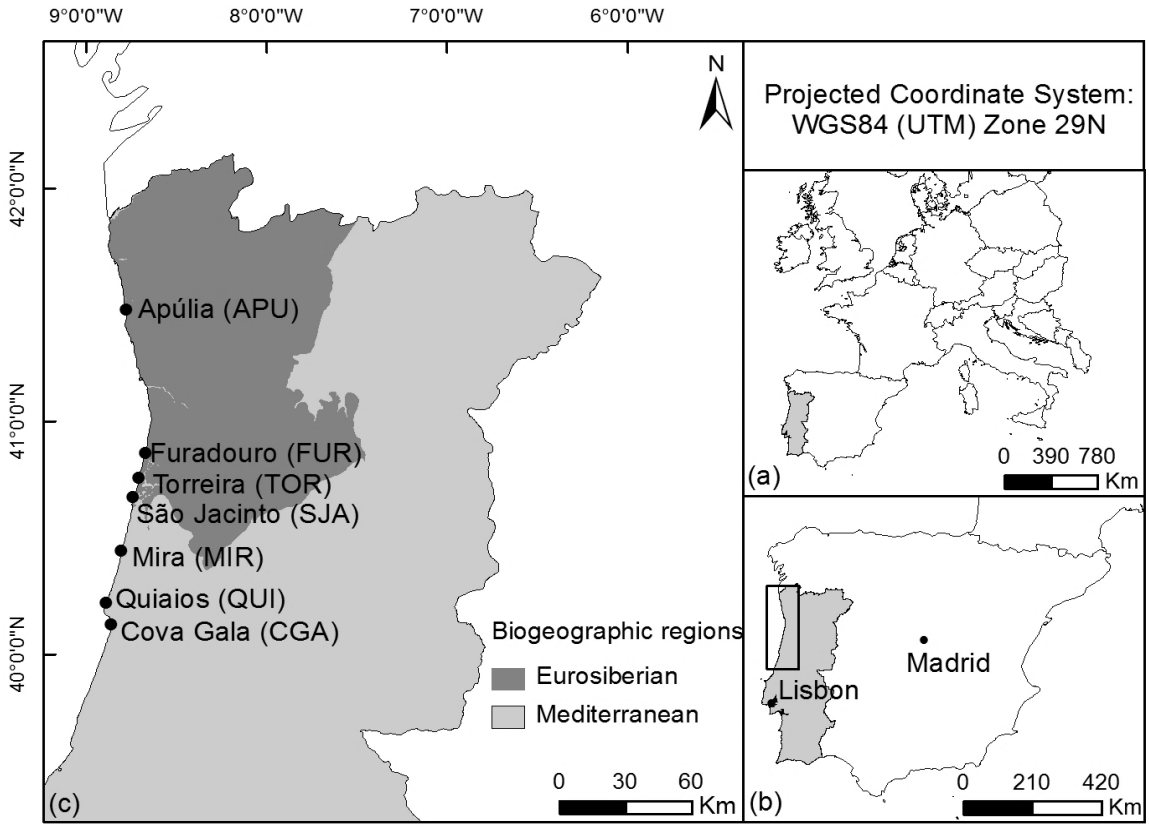

Fig. 2.1 - Study area in the European (a) and Iberian (b) contexts. The map in (c) also exhibits the location of the study sites and the two biogeographic regions in the northern half of Portugal (Costa *et al.*, 1998).

The coast of Northern Portugal is mesotidal (i.e. with mean spring tide ranging between 2 and 4 m; Bird, 2008), with an energetic wave regime and a dominant wave crest orientation from NW, thus generating a current from North to South (Granja *et al.,* 2011). Mostly due to urban and touristic development, the area has been under the effect of several engineering infrastructures (e.g. urban fronts, harbours, coastal defence structures). Coupled with the natural cyclic dynamics of dune ecosystems (e.g. mobility of sandy soils, sea-water flooding; Granja, 2002), impacts of sea level rise, and further human activity (e.g. leisure, fishery; Andrade *et al.,* 2007; Fortunato *et al.,* 2008), those structures have locally inverted the current and are recognised as disrupting the natural processes of coastal ecosystems (Carvalho *et al.*, 2006; Granja *et al.,* 2011). Therefore, **two main types** of beach-dune systems, related to local coastal dynamics, can be recognised along this coastline: (1) meta- stable, with balanced gains and losses in the sedimentary budget; and (2) transgressive, characterised by continuous sand removal and coastline regression (Veloso-Gomes *et al.,* 2004; Carvalho *et al.*, 2006; Honrado *et al.,* 2010).

As a result of the **biogeographic location** of the study area, its coastal flora (see Appendix 1 for a list of recorded taxa and complete taxonomic combinations) is quite diverse and includes several endemic taxa, such as *Jasione maritima* var. *sabularia* and *Coincya johnstonii* (Costa *et al.,* 2000; Neto *et al.,* 2007; Lomba *et al.,* 2008). The transition between the two biogeographic regions occurs around the “Ria de Aveiro” (Costa *et al.*, 1998, 2009), with plants dispersing and historically migrating between those biogeographic areas (Izco, 1989, 1992; Costa *et al.,* 2009). This transition is also signalled by the dominance of Atlantic syntaxa (i.e. vegetation types) northwards, and of Mediterranean syntaxa toward south (Costa *et al.*, 1998, 2000, 2009; Lomba *et al.,* 2008; Neto *et al.,* 2008). The study area includes several protected areas belonging to the National Network of Protected Areas (ICNF, 2012a) and/or to the European Natura 2000 Network (ICNF, 2012b).

2.2. The focal dune habitat types

2.2.1. The five habitat types along the local dune gradient

Five habitat types along the local dune gradient were considered and surveyed in this research (Fig. 2.2). Throughout the thesis, and in a sequence from the beach landward, these five habitat types were named: embryonic foredunes (EF), foredunes (FD), interior dunes (ID), dry grasslands (DG), and low scrub (LS). Specific vegetation types, dominated by different sets of species, are related to these habitats along a complex gradient of environmental stress and disturbance, as described in the following sections. The phytosociological nomenclature in those descriptions generally follows Costa *et al.* (2012).

Fig. 2.2 – The five habitat types surveyed in this research (adapted from Silva, 2006).

2.2.2. Embryonic foredunes

Embryonic foredunes (EF) correspond to the first seaward dunes, colonized by pioneer plant species, including prostrate grasses (namely *Elymus farctus* ssp. *boreali-atlanticus* in the study area) and succulent herbs with rhizomatous and stoloniferous development, responsible for sand fixing and foredune building (Brown & McLachlan, 2010). Initial stages of dune ecological succession are environmentally unstable, and are reflected in vegetation zonation and in the presence of dune species with wide ecological amplitudes within dune systems (Gray, 1985). Embryonic foredunes are temporary habitats that are either transformed by the colonization of *Ammophila arenaria* or removed by storms; hence new sand supplies are essential for the existence of this pioneer community (JNCC, 2006). Also, there is an intense influence of water, salt and substrate, with inputs of organic matter from the sea, enabling the frequent occurrence of *Cakile maritima* and other halo nitrophilous species (Gracia Prieto *et al.*, 2009). This close association to coastal dynamics justifies the use of embryonic foredunes as geo-indicators (Bush *et al.*, 1999; Favennec, 2002; Lomba *et al.,* 2008).

In the study area, embryonic foredunes are primarily colonized by halopsammophilous plants well adapted to water, temperature and salt stress, with hemicryptophytes and therophytes as dominant life forms (Lomba *et al.,* 2008; Honrado *et al.*, 2010). The perennial rhizomatous grass ***Elymus farctus* ssp. *boreali-atlanticus*** (syn. *Elytrigia juncea* ssp. *boreoatlantica*) is the most characteristic and abundant taxon, but some other specialized taxa also occur, such as *Calystegia soldanella, Eryngium maritimum*, *Euphorbia paralias* and *Pancratium maritimum*. Phytosociologically, the vegetation of embryonic foredunes throughout the study area is included in class *Euphorbio paraliae-Ammophiletea arundinaceae*, and in association *Euphorbio paraliae-Elytrigietum boreoatlanticae* (Costa *et al.,* 2012).

Embryonic foredunes and their associated plant communities in the study area (and in most of Europe) are listed in Annex I of the EU Habitats Directive (HD), under code **2110** (“Embryonic shifting dunes”). This habitat type does not host plant taxa of high conservation priority in our study area. Its current conservation status is variable (most often unfavourable), depending on local coastal dynamics and on touristic pressure (ICNF, 2012a,b; ALFA, 2004).

2.2.3. Foredunes

Foredunes (FD) usually develop parallel to the coastline (Tsoar, 2000) and can be defined as «shore-parallel dune ridges formed on the top of the backshore by aeolian sand deposition within vegetation», varying from «relatively flat terraces to markedly convex ridges» (Hesp, 2002). These are important geomorphological structures in dune systems, forming the first dune string, and exhibiting sand accretion supported by vegetation, and are related to loosely structured soils and incipient organic matter accumulation (ALFA, 2004; Gracia Prieto *et al.*, 2009). Foredune height is mainly determined by sand supply, and erosion processes have a disturbance effect on vegetation, leading to blowouts i.e. «wind-excavated gaps in the foredune ridges that channel sand transport landward» (Tsoar, 2000).

In the study area, foredune communities are perennial grasslands developing on foredune crests and dominated by ***Ammophila arenaria***. Other plant species are also present, e.g. *Medicago marina*, *Otanthus maritimus*, *Eryngium maritimum*, and *Calystegia soldanella* (Honrado *et al.,* 2006; Neto *et al.,* 2007; Lomba *et al.,* 2008). As in embryonic foredunes, species-poor annual grasslands dominated by *Silene littorea* can also be found (Neto, 1993; Neto *et al.,* 2007; Lomba *et al.,* 2008). Phytosociologically, foredune communities are included in class *Euphorbio paraliae-Ammophiletea arundinaceae*, and in associations *Otantho maritimi-Ammophiletum arundinaceae* and *Loto cretici-Ammophiletum arundinaceae* (Costa *et al.*, 2012).

Foredunes in the study area are included in the HD Annex I habitat **2120** ("Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)") and are also denominated *primary dunes* or *white dunes* due to the presence of open sandy spaces (ALFA, 2004). In general, their conservation status varies between unfavourable and medium, depending on important pressures such as hard coastal engineering structures and human trampling during summer (ALFA, 2004). Endemic taxa such as *Coincya johnstonii* and *Viola kitaibeliana* may occasionally occur in this habitat type (Neto, 1993; Neto *et al.,* 2007; Lomba *et al.,* 2008).

2.2.4. Interior dunes

Interior dunes (ID), also called *grey dunes* or *secondary dunes*, are more stable and more protected from wind and salt spray than foredunes, displaying a succession of smooth crests and intra-dune corridors (ALFA, 2004; Vick & Young, 2011). These are more "mature" dunes with neutral to acidic soil characteristics, higher concentration of organic matter, and higher influence of biotic factors, nutrients and space on shaping plant communities (Bunce *et al.*, 2010; Vick & Young, 2011).

Generally, interior dunes host **low shrub communities** with high cover, as well as communities dominated by therophytes, which can be nitrophilous or semi-nitrophilous (ALFA, 2004). Phytosociologically, its dominant vegetation belongs to class *Euphorbio paraliae-Ammophiletea* arundinaceae, and, in the study area, to associations *Iberidetum procumbentis* and *Armerio welwitschii-Crucianelletum maritimae* (Honrado *et al.*, 2006; Costa *et al.*, 2012).

These dunes are including the priority HD Annex I habitat **2130*** ("Fixed coastal dunes with herbaceous vegetation (grey dunes)"). Their conservation status ranges from unfavourable to medium, with human trampling, urban sprawl and invasion by alien plants as the main threats (ALFA, 2004). This habitat type hosts several endemic taxa, such as *Armeria welwitschii*, *Coincya johnstonii*, *Jasione maritima* var*. sabularia*, and *Verbascum litigiosum* (ALFA, 2004; Honrado *et al.*, 2006; Lomba *et al.*, 2008).

2.2.5. Dry grasslands

Dry grasslands (DG) are psammophilous and xerophytic open formations occurring landward in coastal interior dunes, developing on acidic and primarily water- and nutrient-limited sandy soils (Jentsch & Beyschlag, 2003; EC, 2013; Vaz *et al.*, 2015).

Dry grasslands, often occurring in mosaic with other vegetation types in the landward areas of interior dunes, are dominated by the caespitose grass ***Corynephorus canescens*** (ALFA, 2004; Lomba *et al.*, 2008) and exhibit a high

presence of annual plants, despite their generally low species richness (EC, 2013). Besides the dominant *Corynephorus canescens*, other common species are *Herniaria maritima* and *Carex arenaria* (ALFA, 2004). Concerning their phytosociology, these grasslands are included in class *Tuberarietea guttatae*, and in associations *Herniario robustae-Corynephoretum maritimi* (Costa *et al.*, 2012) and *Jasiono sabulariae-Corynephoretum maritimi* (Lomba *et al.*, 2008).

Dry grasslands are included in the HD Annex I habitat **2330** ("Inland dunes with open *Corynephorus* and *Agrostis* grasslands") (EC, 2013) and often host the Portuguese endemic *Jasione maritima* var. *sabularia* (Lomba *et al.*, 2008). In general, these grasslands show a favourable conservation status in the study area.

2.2.6. Low scrub

Low scrub (LS) formations occur in the most landward positions of the focal dune systems. These woody vegetation types usually colonize: (1) fixed decalcified dunes associated to oligotrophic soils with low water retention (ALFA, 2004), or (2) tertiary dunes or palaeodunes related to deep dry sandy soils (ALFA, 2004; Bunce *et al.*, 2012).

This habitat type corresponds to **psammophilous scrub communities** dominated in the study area by *Stauracanthus genistoides*, *Corema album* and/or *Ulex europaeus* ssp. *latebracteatus* (Espírito Santo *et al.*, 2000). Other frequent species are *Cistus salviifolius*, *Cistus psilosepalus*, *Carex arenaria* and *Corynephorus canescens* (Rivas-Martínez *et al.*, 2001, 2002a,b; ALFA, 2004; Neto *et al.*, 2007; Lomba *et al.*, 2008). These formations are included in classes *Calluno vulgaris-Ulicetea minoris* (association *Ulicetum latebracteato-minoris* subas. *cistetosum salviifolii*; Honrado *et al.*, 2006) and *Cisto-Lavanduletea* (association *Stauracantho genistoidis-Corematetum albi*) (Costa *et al.*, 2012).

Low scrub is included in two HD Annex I habitat types: **2150*** ("Atlantic decalcified fixed dunes (*Calluno-Ulicetea*)") and **2260** ("*Cisto-Lavanduletalia* dune sclerophyllous scrubs"). Their conservation status in the study area is most often unfavourable or medium.

2.3. Vegetation data

A pre-existing database was used for this work. The database consisted in **seven sites** surveyed along the north–south climatic and biogeographic gradient (see Fig. 2.1). At each site, a sea-landward transect, i.e. perpendicular to the shoreline, was established, encompassing the whole sequence of habitat types along the dune system (Carboni *et al.* 2009; Maltez-Mouro *et al.* 2010a; Fig. 2.3). The relative position of sites and plots was assumed to suitably express: (1) a **regional, climatic gradient** (reflecting a gradual transition between the Temperate and Mediterranean climates, along with the biogeographical transition between the Eurosiberian and Mediterranean regions; see Fig. 2.1), with increasing temperature and decreasing precipitation from north to south (Lomba *et al.,* 2008; Honrado *et al.,* 2010; Maltez-Mouro *et al.,* 2010a); and (2) a **local, sea–inland gradient** (Fig. 2.4), expressing a general decrease of abiotic stress (and disturbance), i.e. with decreasing levels of salt spray, sand burial and substrate mobility, as well as with increasing soil nutrients and organic matter content (Olff *et al.,* 1993; Maun & Perumal, 1999; Forey *et al.,* 2008; Maltez-Mouro *et al.,* 2010a).

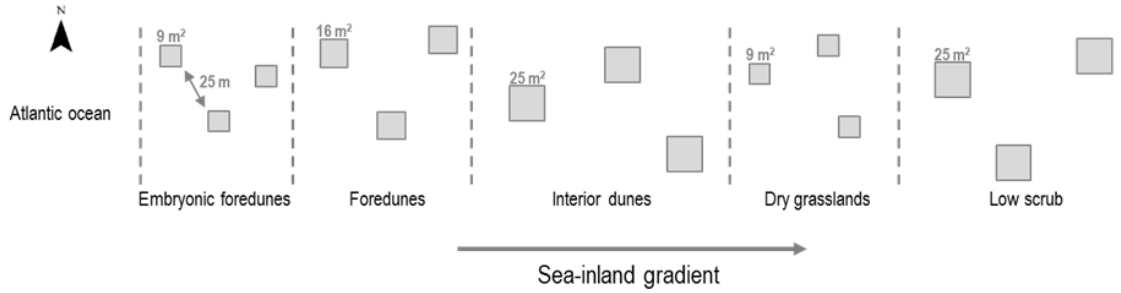

Fig. 2.3 - Schematic representation of the sampling design for field surveys conducted at each site. Squares represent the vegetation plots surveyed along the local dune system.

The seven sites were selected based on previous studies documenting the **prevailing coastal dynamics** (e.g. Granja & Carvalho, 1992; Granja, 1997; Henriques, 2007; Honrado *et al.*, 2010; Vaz *et al.*, 2014), which was further confirmed during field surveys. Those sites were thus included in two groups (Table 2.1) according to prevailing dynamics: those which displayed either meta-stable or progradant (i.e. with sediment accretion) dynamics, jointly called “meta-stable” (3 sites); and those with transgressive (i.e. erosive or in recession dynamics - 4 sites).

Table 2.1 – Name (north to south), coordinates (projected coordinate system: WGS84, zone 29N), biogeographic regions, and prevailing coastal dynamics of the seven sites surveyed in the study area.

Site	X_UTM	Y_UTM	Biogeographic Region	Prevailing Dynamics
Apúlia	518636.64	4591831.09	Eurosiberian	Transgressive
Furadouro	527090.90	4523845.37	Eurosiberian	Transgressive
Torreira	524220.63	4511902.09	Eurosiberian	Meta-stable
S. Jacinto	521598.31	4502758.09	Mediterranean	Meta-stable
Mira	516365.55	4477142.53	Mediterranean	Transgressive
Quiaios	509311.79	4452427.93	Mediterranean	Meta-stable
Cova Gala	511557.67	4442156.81	Mediterranean	Transgressive

In order to survey the vegetation along the local gradient, **three square plots** with a minimum distance of 25 m between them were placed, whenever possible, in each habitat type (Fig. 2.3). The final number of plots was dependent on the morphology and development of the dune system at each site. Thus, EF and LS habitats were absent from Mira, AG from Quiaios, and LS from Torreira, resulting in a total of 92 plots surveyed (sampling units, n = 92) belonging to five habitat types in the study area.

In field surveys for data collection were performed in late spring and early summer. The area of the plots followed the recommendations of the minimum area for vegetation surveys, and was expected to capture the most representative patterns and combinations of plant species in each habitat type (Kent & Coker, 1992; Chytry & Otypkova, 2003): 9 m^2 in ED, 16 m^2 in FD, 25 m^2 in ID, 9 m^2 in DG, and 25 m^2 in LS (Fig. 2.4). A complete list of vascular plant species was obtained for each surveyed plot (see Appendix 1) and the abundance of each species (measured as percentage cover) was estimated following a simplified version of the Domin scale (Kent & Coker, 1992): (1) <1%; (2) 1–5%; (3) 5–15%; (4) 15–25%; (5) 25–50%; (6) 50–75%; (7) 75–90%; and (8) 90–100%. Species nomenclature and classification of endemics generally followed Castroviejo *et al.* (1986–2014).

2.4. Data processing: classifications of plant species

2.4.1. Classification of dune plant species according to CSR strategies

The CSR classification corresponds to an equilateral triangular model which relies on three **primary, extreme strategies** (C, S, and R) and on four **secondary, intermediate strategies** (Grime, 1973, 1977, 2001; Al-Mufti *et al.*, 1977; Hodgson *et al.*, 1999; Tables 2.2 and 2.3; see Chapter 1). This classification has several valuable features, such as its simplicity, relation to several essential aspects of ecosystem functioning, suitability for impact studies, and strong relation with species composition along environmental gradients when complemented with multivariate analysis (Hunt *et al.,* 2004; Caccianiga *et al.,* 2006).

Table 2.2 – General description of the three CSR extreme strategies (Grime, 1973, 1977, 2001; Al-Mufti *et al.*, 1977; Hodgson *et al.*, 1999).

Primary strategy	Description
Competitors (C)	- Competitive dominants: large stature depending on a high rate of environmental resources; - Robust perennials of high potential growth rate with a dense, rapidly expanding biomass above and below ground; - Life forms: perennial herbs, shrubs and trees; - Extensive lateral spread above and below ground; - Longevity (established phase): long or relatively short; longevity (leaves/roots): relatively short.
Stress-tolerators (S)	- Stress-tolerant dominants with large stature related to the ability to sustain slow growth rates; - Seasonal growth or with short-term changes; - Life-forms: herbs, shrubs and trees; - Longevity (established phase): long-very long; longevity (leaves/roots): long.
Ruderals (R)	- Ruderal dominants (usually annual herbs): large stature depending on rapid rates of growth; - Prevailing annual life-cycles; also trend for short-lived perennial life-cycles; - Life-forms: herbs; - Longevity (established phase): very short; longevity (leaves/roots): short.

Each taxon recorded during in fields surveys was assigned to **one of the seven strategies**, based on the criteria synthetized in Tables 2.2 and 2.3, and using information mainly from specimen observations and ecological expert knowledge, as well as from Iberian floras - Castroviejo *et al.* (1986-2010), Franco (1971-1984) and Franco & Afonso (1994-2003) - and other scientific literature (e.g. Al-Mufti *et al.*, 1977; Grime *et al.,* 1977, 1992; Hodgson *et al.*, 1999; Grime, 2001). The resulting classification can be found in Appendix 2.

Table 2.3 – General description of Grime's secondary ecological strategies (after Grime 1977, 2001).

Secondary strategy	Description
C-R	- Competitive ruderals plants adapted to a low impact of stress where competition is reduced to a moderate intensity by disturbance; - Aptitude of some species to exploit environments already occupied by perennials whose co-existence may be merely viable under particular circumstances; - Includes annuals, biennials, and perennials.
C-S	- Stress-tolerant competitor plants adapted to undisturbed circumstances within a reasonable intensity of stress and associated to vegetation types exhibiting moderate productivity and low intensities of disturbance; - Species exhibit the capacity for lateral vegetative spread through rhizomes or expanding tussocks; - Comprises herbaceous and woody plant species.
S-R	- Stress-tolerant ruderals plants adapted to lightly disturbed unproductive habitats, within concomitant moderate intensities of stress and disturbance; - In general, growth and reproduction restricted to short periods, yet differentiated from R-strategists by their occurrence in habitats with an incidence of stress during the growth period with an ensuing reduction of the annual production; - Includes a substantial representation of small herbs and bryophytes.
C-S-R	- Species restricted to habitats in which competition is limited to moderate intensities due to the combined outcomes of stress and disturbance; - Small tussock grasses, deep-rooted and creeping, or stoloniferous forbs; - Grasses are able to exhibit narrow, folded, or rolled leaves and a shallower root penetration, under mineral nutrient stress; - Deep-rooted forbs to exhibit a distinct peak of shoot production in Summer with shoot biomass converted in rosettes, and thus the restriction of leaf canopy height and lateral spread.

2.4.2. Classification of dune plants according to functional types

Specifically for dune plants, García-Mora *et al.* (1999) proposed a classification with three **dune plant functional types**, related to the extent of plant adaptation to the dune conditions (see Chapter 1). Each taxon was assigned to **one of three functional types** (I, II or III) based on the criteria proposed by Garcia-Mora *et al.* (1999) in Tables 2.4 and 2.5, and using information gathered mainly from specimen observations and ecological expert knowledge, as well as following García-Mora *et al.* (1999) and the main Iberian floras (Castroviejo *et al.,* 1986–2010; Franco, 1971–1984; Franco & Afonso, 1994–2003). The resulting classification can be found in Appendix 2.

Table 2.4 – Ecological strategies for dune plants and their corresponding traits (after García-Mora *et al.*, 1999).

Characteristics	Plant Functional Type I	Plant Functional Type II	Plant Functional Type III
Life span	Winter annual	Perennial	Perennial or summer annual
Canopy height	≤ 15 cm	Indifferent	> 15 cm
Below-ground structures	Shallow fibrous or thin tap	Thick spreading or deep	Thick spreading or deep
Leaf adaptations to coastal stress	Absent	Present	Present
Ability to withstand deep sand burial	Absent	Absent	Present
Sea-water dispersion	Absent	Absent	Present

Table 2.5 – Synthetic description the three dune plant functional types (García-Mora *et al.*, 1999).

Plant functional type	Description
I	Winter annual plants with moderate size and soft leaves, with no presumed adaptations to the dune environment
II	Perennial plants with below-ground spreading root network and ough/succulent/pubescent leaves, with presumed adaptations to the coastal environmental stress
III	Plants strongly adapted to the foredune environment, with the ability of being dispersed by sea-water and of withstanding sand burial

2.5. Statistical analyses

2.5.1. Patterns of plant species diversity

In order to evaluate the patterns of plant species diversity across the considered dune gradients, **three diversity components** were considered: (1) species richness; (2) species evenness; and (3) species composition (Kent & Coker, 1992; Carboni, *et al.,* 2009; Baselga, 2010).

Species richness was computed from the complete list of plant species recorded at each vegetation plot, for the total species pool as well as for each CSR strategy and functional type (see section 2.4). **Species evenness** was computed based on species abundance data collected from each vegetation plot, considering the total pool as well as each CSR strategy and functional type, and evaluated through the Shannon's equitability index (E_H; Jost, 2007):

$$E_H = H/H'_{max},$$
$$H = -\sum (pi)\ln(pi)$$

where *pi* is the proportion of each species abundance (measured in a ranked cover scale) relative to the total abundance for all species recorded in the vegetation plot, *H* is Shannon's entropy index, and H'_{max} is the maximum *H* value found in the ensemble of vegetation plots being analysed.

The statistical distribution of the data was tested for normality and variance homoscedasticity through the Shapiro-Wilk's and the Levene's tests, respectively. Since data distribution did not follow a normal distribution and the variances were not homoscedastic, only **non-parametric tests and descriptive statistics** were used in subsequent data analysis (Dytham, 2010). Values for species richness or species evenness presented throughout the text are expressed as median ± inter-quartile range, and their distribution across vegetation plots is visually represented through box-and-whiskers plots. Significant differences among median values of species richness and species evenness across sites and habitat types were analysed through

Kruskal-Wallis (*H*) and post hoc Mann-Whitney (*U*) tests. All univariate statistical analyses were performed in the STATISTICA software (Version 8, 2008), considering the whole set of species and each individual set of species assigned to their CSR strategy and functional type. Based on values for species richness obtained for the whole study area, all CSR strategies and functional types were tested for pair-wise using Spearman tests. Though significant correlations were detected, correlation values were below 0.80, suggesting a rather independence between CSR and functional type classifications (see Appendix 3 for test results).

Multivariate analyses were used to assess the main gradients underlying variations in species composition (ter Braak & Smilauer, 2002; Leps & Smilauer, 2003; Carboni, *et al.* 2009). A Detrended Correspondence Analysis (DCA; ter Braak & Smilauer, 2002) was implemented in CANOCO version 4.5 using the default settings (ter Braak and Smilauer, 2002). DCA was first conducted to select the best multivariate model to apply to the surveyed data. According to ter Braak & Smilauer (2002), lengths of gradient for the first DCA axis above 4.0 standard deviation (SD) units allow the application of unimodal models, whereas lengths of gradient bellow 3.0 request the use of linear models for ensuring good results. For the analysed data, the gradient length of the first DCA axis was of 5.91 SD, so DCA methods were applied in subsequent analyses. This DCA was applied considering species abundances in each sampling unit for the whole study area (n = 92). For the analysis of data that considered only the floristic composition of mobile dunes (see section 2.5.3), the first DCA axis showed a gradient length of 2.88 SD units. Thus, in this case, a Principal Component Analysis (PCA) was used, based on species abundances in each sampling unit for embryonic foredunes (EF) and foredunes (FD) (n = 38).

For both cases (i.e., DCA and PCA), the **abundance** of each CSR strategy and functional type, expressed by the cumulative abundance of species belonging to a given strategy/functional type within each vegetation plot, was also calculated and projected on the ordination space to visualise variations across vegetation plots. To facilitate the visualisation of CSR strategy and functional type positions in the ordination space, each individual species, classified according to their respective CSR strategy and functional type, was also projected in the ordination space based on their abundance across vegetation plots. Additionally, the distribution of values for total

species richness across vegetation plots was visualised through the loess model option for visualisation (ter Braak & Smilauer, 2002).

Finally, in order to highlight specific environmental pressures on the coastal dune systems, the cover of *Ammophila arundinacea* per plot and the cover of *Vulpia alopecuros* per plot were used as **ecological proxies** of dune condition and projected in the ordination space (Costa *et al.,* 2000; Levin *et al.,* 2008; Honrado *et al.,* 2010; see section 2.3). *Ammophila arundinacea* is most typical from mobile dunes but may become frequent in more landward areas of the dune system under increased stress and disturbance triggered by transgressive coastal dynamics (Leven *et al.*, 2008; Honrado *et al.* 2010). *Vulpia alopecuros* tends to be favoured in by nutrient released due to disturbances (namely human trampling), especially in interior dune habitats (Costa *et al.,* 2000; Lomba *et al.,* 2008).

2.5.2. Patterns of plant species co-occurrence along gradients in the study area

To address the patterns of **species co-occurrence** in the analysed sand dune communities, a three-step approach was considering the relevant gradients (Vaz *et al.*, 2015; Fig. 2.4). By applying this approach, various co-occurrence patterns were expected to be detected along the climatic (i.e., regional) and sea-inland (i.e., local) gradients. To avoid the non-independence between plots and major scale-dependent effects, the presence or absence of a given species was considered for each habitat type (Kent & Coker, 1992). As a result, the 92 sampling units (see section 2.3) were aggregated in a total of 31 analysis units (i.e., m = 31; see section 2.3), which were used to analyse the patterns of species co-occurrence.

Overall, differences between the three steps of analysis related to the number of areas (k) considered in each step. **Step one** (Fig. 2.4) consisted of the analysis of co-occurrence patterns for the entire study area, thus considering the whole data set (i.e., k = 1, total area). **Step two** focused on the analysis of co-occurrence patterns along the climatic gradient by considering patterns of co-occurrence at each site and comparing them across the seven sites (i.e., k = 7 sites). Finally, **step three** focused on the analysis of co-occurrence patterns along the local sea-inland gradient,

analysing co-occurrence patterns in each habitat type and comparing them across the five habitat types (i.e., *k* = 5 habitat types).

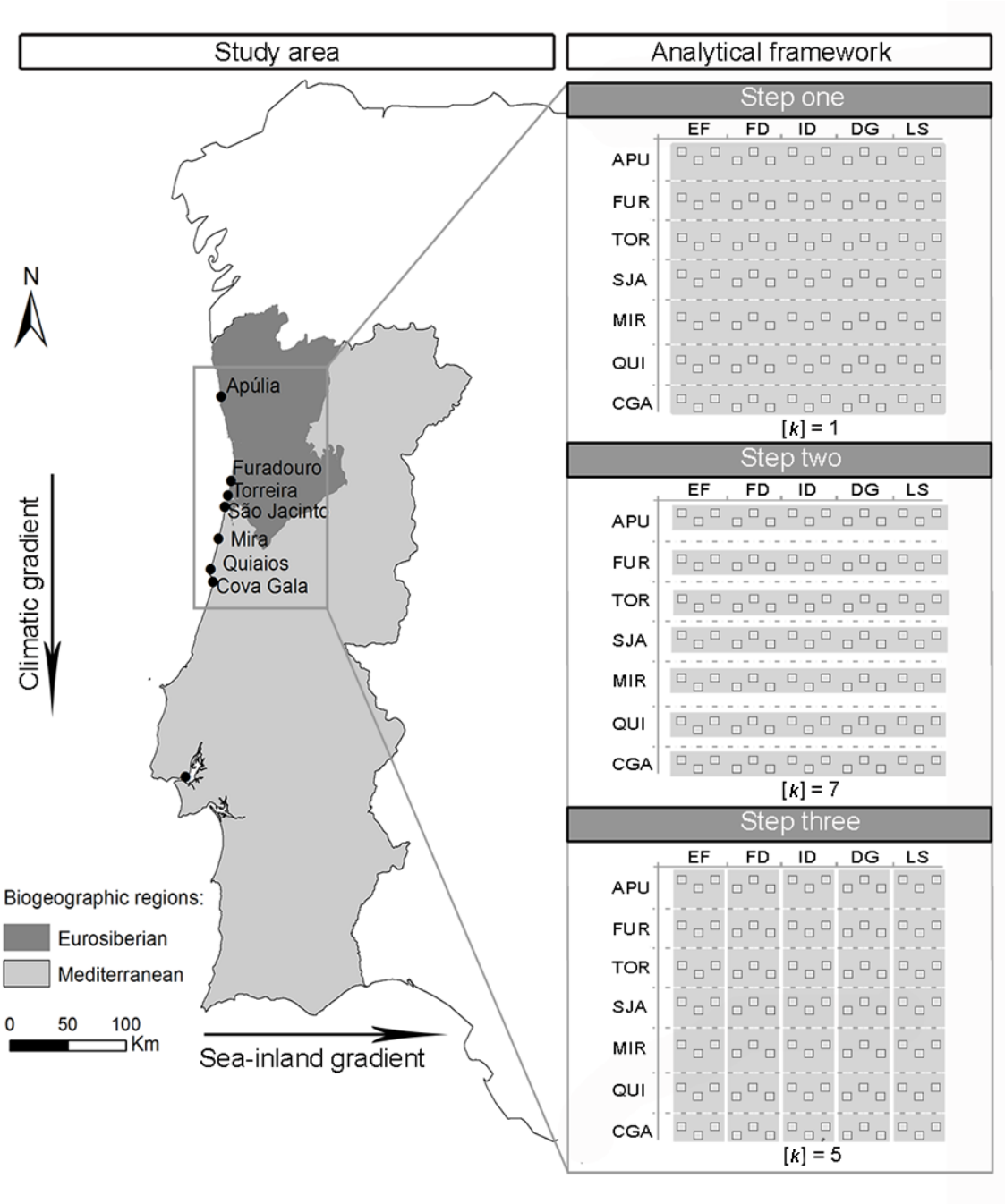

Fig. 2.4 – Schematic diagram of the analytical framework implemented to analyse co-occurrence patterns in the whole study area (step one), and along the climatic (step two) and the sea-inland gradients (step three). Column headers are for habitat types: embryonic foredunes (EF); foredunes (FD); interior dunes (ID); dry grasslands (DG); and low scrub (LS). Row headers indicate sites: Apúlia (APU); Furadouro (FUR); Torreira (TOR); São Jacinto (SJA); Mira (MIR); Quiaios (QUI); and Cova Gala (CGA). Data were surveyed from 92 plots (sampling units, *n* = 92) and co-occurrence

patterns were assessed from 31 aggregated units, *m* = 31); [*k*] stands for the number of areas analysed in each step of the framework (adapted from Vaz *et al.,* 2015).

Patterns of co-occurrence were assessed from **presence/absence matrices**, where each row or column represented a given species or surveyed unit, respectively. Co-occurrence analyses were performed considering either the whole set of plant species in the study area or each sub-set of plant species assigned to their respective CSR strategy and functional type (i.e., co-occurrence patterns within each strategy and type). The number of species in the matrices (*N*) was derived from the number of species recorded at each site or habitat type and was dependent on their classification regarding species strategies. Thus, in the first step of analysis (step one; Fig. 2.4), a matrix with *N* species by 31 units was considered for the whole study area. In step two (Fig. 2.4) a matrix with *N* species by five habitats was computed for each of the seven sites. In step three (Fig. 2.4), a matrix with *N* species by seven sites was obtained for each of the five habitat types.

Co-occurrence patterns were assessed through the checkerboard score (***C-score***), which expresses the mean number of checkerboards for all possible pairs of species (Gotelli, 2000; Ulrich & Gotelli, 2010) and is computed from the equation:

$$\text{C-score} = (Ri-S)(Rj-S)$$

where *Ri* and *Rj* refer to the row totals (where each row represents a given species) for species *i* and *j*, respectively, and *S* refers to the number of matrix squares where both species occur (Gotelli, 2000).

All C-score values calculated for the input matrices were statistically compared to scores computed for **10 000 simulated matrices**, by comparing the number of times that the simulated scores were higher or lower than the input matrix scores (Gotelli & McCabe, 2002). Those simulated matrices were obtained by randomising the input matrices (in this case, using 10 000 randomisations) by fixed column and row sums null models implemented in EcoSim version 7 (Gotelli, 2000). Null models were applied as they have low type I error and good power for detecting aggregation and

segregation patterns (Gotelli, 2000; Ulrich & Gotelli, 2010). To facilitate the comparison and interpretation of the results, the obtained scores were standardised by computing:

$$\text{Standardised C-/CA-score} = (I^{obs} - I^{sim})/S^{sim}$$

where I^{obs} is the score of the input matrix, and I^{sim} and S^{sim} are the mean and standard deviation of the scores obtained for the simulated matrices, respectively (Gotelli & McCabe, 2002).

The standardisation of the co-occurrence indices allowed detecting statistically significant deviations from a random species distribution, regardless of the sampling size. **Standardised *C*-score values** higher or lower than 0 indicate respectively segregation or aggregation among species within the whole community or within each CSR strategy or functional type (Gotelli & McCabe, 2002; Götzenberger *et al.,* 2012). Furthermore, Standardized *C*-score values greater than 2 or lower than -2 are statistically significant (for a confidence interval of 95%), indicating a significant aggregation or segregation of species, respectively.

To **test for significant differences** in the co-occurrence patterns across sites or habitat types, the Guild Structure Module was applied as suggested by Gotelli & Entsminger (2001). This procedure was conducted following the previously described settings in EcoSim version 7. This allowed testing whether the variability of patterns of species co-occurrence within each site or habitat type was significantly larger or smaller than the variability of species co-occurrence among sites or habitat types (Gotelli & Entsminger, 2001). All values for standardised *C*-scores are visually represented by column plots or by their respective values throughout the text. The representation of some species groups may be absent as the low number of species in the analysis did not allow for computing their respective *C*-score values (as a minimum of two co-occurring species is required for the analysis).

The previously described steps were also applied to assess co-occurrence patterns among all **CSR strategies** and **functional types**, as well as between pairs of CSR strategies and functional types. Again this was accomplished by applying the

Guild Structure Module to evaluate strategies' co-occurrences (Gotelli & Entsminger, 2001). In this module, all plant species in a group are assigned to only one specific classification, therefore the analyses are applied considering a *priori* hypotheses on the existence of species groups with distinctive ecological requirements. This module allows testing if the mean co-occurrence indices among all, or between pairs of CSR strategies and functional types, are larger or smaller than those expected by chance, while also including the variability of species co-occurrences within each group. Consequently, a large variability indicates that groups are significantly different in levels of co-occurrence and that some CSR strategies or functional types within each group include species with high levels of co-occurrence, while others include species with low levels of co-occurrence. Groups with small variability indicate that they are similar in the levels of co-occurrence. Therefore, if a random result for the final index is found, then it suggests that the level of co-occurrence among (or between pairs of) CSR strategies or functional types is similar to the co-occurrence patterns expected if the species were randomly assigned to different CSR strategies or functional types (Gotelli & Entsminger, 2001).

2.5.3. Effects of coastal dynamics on community structure

Following results from previous research on the link between dune vegetation and coastal dynamics (Honrado *et al.*, 2010; Macedo *et al.*, 2010; Fidalgo *et al.*, 2014), the community-level responses of dune vegetation to shifts in prevailing coastal dynamics were assessed based only on the floristic data collected from **mobile dune habitats**, i.e. embryonic foredunes (ED) and foredunes (FD).

In order to test for significant differences in the patterns of **species richness and species evenness** across types of coastal dynamics (meta-stable *versus* transgressive sites), Kruskal-Wallis (*H*) and post-hoc Mann-Whitney (*U*) tests were computed using the STATISTICA software (Statsoft, 2008).

Significant differences in plant **species composition** between meta-stable and transgressive sites, were evaluated through the non-parametric test ANalysis Of SIMilarities (one-way ANOSIM), based on the Euclidean distance measure. The test considers the variability within groups (each set of meta-stable and transgressive plots)

and allows comparing such variability to the variability between groups. To do so, 9999 randomisations under Monte-Carlo permutation of the input matrices were implemented in PAST version 3 (Hammer *et al.,* 2001). Significant test results indicate dissimilarity between types of coastal dynamics (based on the Euclidean distance), whereas non-significant values indicate that the level of similarity between meta-stable and transgressive sites is identical to the similarity expected if the vegetation plots were randomly assigned to any type of coastal dynamics (Hammer *et al.,* 2001).

Additionally, a Principal Component Analysis (PCA) was conducted to highlight the main gradients underlying variations in **species composition** of mobile dunes (ter Braak & Smilauer, 2002; Leps & Smilauer, 2003; Carboni, *et al.* 2009). The Principal Component Analysis (PCA) was conducted based on species abundances in each sampling unit for embryonic foredunes (EF) and foredunes (FD). The visualization settings adopted were similar to those described in section 2.5.1.

An identical approach to the one described in section 2.5.2 was followed to test for significant differences in the **co-occurrence patterns** between meta-stable and transgressive sites, using, in this case, each vegetation plot as the analysis unit (m = 38). Following the procedure suggested by Gotelli & Entsminger (2001), the Guild Structure Module was applied to test differences across the two types of coastal dynamics. Such procedure allowed testing if the variability of patterns of species co-occurrence within each type of coastal dynamics was significantly larger or smaller than the variability of species co-occurrence between types of coastal dynamics (Gotelli & Entsminger, 2001).

In the case of **CSR strategies and functional types** for which the analyses indicated statistically different co-occurrence patterns across types of coastal dynamics, standardised *C*-score values were calculated for each individual set of meta-stable and transgressive sites. Identically to the information described in section 3.5.2., presence/absence matrices with *N* species by two habitats were computed for each set of sites classified as meta-stable or transgressive. The procedure was implemented in EcoSim version 7. All analyses were performed for the whole set of species as well as for each set of species assigned to a specific group (i.e. CSR strategy or functional type; see section 3.5.2 for details).

3. Results and discussion

In this chapter, the main results of the research developed for this thesis are **presented and briefly discussed** in the broader context of the relevant literature and state of knowledge. It is followed by an integrative discussion and main conclusions, which will be presented in chapter 4.

The chapter includes **five main sections**. The first section (**3.1**) briefly describes the species plant pool recorded in the dune system, especially regarding the representation of the several CSR strategies and functional types. The second section (**3.2**) describes patterns of dune plant diversity along regional and local gradients, based on detailed analyses of patterns of species richness for the whole plant community, as well as for individual plant strategies and functional types. The third section (**3.3**) analyses community-level species composition and relates the observed patterns with regional and local gradients and processes. In a fourth section (**3.4**), patterns of species co-occurrences are analysed for the total species pool as well as for CSR strategies and dune plant functional types. Finally, the fifth section (**3.5**) provides a test of the approach described in the first four sections, by applying it to assess the effects of changes in prevailing coastal dynamics on mobile dune vegetation.

3.1. Plant strategies and functional types in the study system

Overall, **80 vascular plant taxa** were recorded in the whole set of plots (see Appendix 1 for a full list of taxa). Two taxa are endemic to Portugal (*Jasione maritima* var. *sabularia* and *Verbascum litigiosum*) and four others are wider Iberian endemics (*Iberis procumbens*, *Linaria polygalifolia* ssp. *polygalifolia*, *Stauracanthus genistoides* and *Ulex europaeus* ssp. *latebracteatus*).

Considering **CSR plant strategies** (Grime 1977, 2001), *Ammophila arenaria* ssp. *arundinacea* (67% of all plots), *Artemisia crithmifolia* (53%) and *Calystegia soldanella* (50%) were the most taxa regarding the CS strategy, which was the most common strategy in the species pool (25 taxa) (Table 3.1). The most frequent species found for the SR strategy were *Silene niceensis* (41%) and *Lagurus ovatus* (34%). The S strategy exhibited a clear dominance of *Pancratium maritimum* (53%) and *Crucianella maritima* (47%), followed by *Euphorbia paralias* and *Medicago marina* (both 38%). For the C strategy, the most frequent species was *Quercus suber,* though it only occurred in 3% of the surveyed plots. This is consistent with the fact that dune environments are not ideal for pure competitors due to their weak capacity to respond to stress and disturbances (Grime, 1984, 2001). For the CR strategy, *Cistus salviifolius* (19%) and *Senecio gallicus* (16%) were the species which exhibited the highest frequency values. Finally, *Leontodon taraxacoides* ssp. *taraxacoides* was the most representative taxon for the CSR strategy (46%). The R strategy was mostly represented by *Vulpia alopecuros* (41%) and was more abundant in landward dune habitats, where anthropogenic disturbances are frequent and the nutrient levels are higher than in more seaward dune habitats (Van der Valk, 1975; Brunbjerg *et al.,* 2012a).

Concerning **dune plant functional types** (García-Mora *et al.,* 1999), their distribution was also not equitable (Table 3.2). The expectable dominance of functional Types II and III, holding adaptations to the dune environment (García-Mora *et al.,* 1999; Macedo *et al.,* 2010), was confirmed. The most common strategy was by far Type II (41 taxa), which includes perennial species adapted to the coastal environment but that cannot stand harsh environmental conditions such as sand burial (García-Mora *et al.,* 1999). This strategy, which corresponds mostly to pioneer perennial rhizomatous grasses or chamaephytes (García-Mora *et al.,* 1999), is mainly represented by *Artemisia crithmifolia* (53% of all plots) and *Leontodon taraxacoides* ssp. *taraxacoides*

(47%). Dune specialists capable of tolerating severe stress and disturbance (Type III; 21 taxa) and annual ruderal species specialized in colonizing disturbed environments (Type I; 18 taxa) were represented by fewer species but jointly comprised about half of the total pool. *Vulpia alopecuros* (41%), *Silene niceensis* (41%) and *Lagurus ovatus* (34%) were the most frequent species of Type I, which are generally semi-nitrophilous ruderals forming ephemeral, spring-blooming communities on nutrient-poor soils (García-Mora *et al.*, 1999; Houston, 2008). *Ammophila arenaria* ssp. *arundinacea* (67%), *Pancratium maritimum* (53%) and *Calystegia soldanella* (50%), three well-known coastal dune specialists (Garcia-Mora *et al.*, 1999; Lomba *et al.,* 2008; Honrado *et al.,* 2010), were the most frequent taxa regarding Type III.

Table 3.1. Frequency of plant strategies in the total species pool, with the most frequent species recorded in the surveyed plots.

Plant strategy	**Total number of taxa**	**Most frequent taxon**	
		Taxon	**% of plots**
CS	25	*Ammophila arenaria* ssp. *arundinacea*	67
SR	24	*Silene niceensis*	41
R	10	*Vulpia alopecuros*	41
S	8	*Pancratium maritimum*	53
CR	7	*Cistus salviifolius*	19
CSR	3	*Leontodon taraxacoides*	46
C	3	*Quercus suber*	3

Table 3.2. Dune plant functional groups in the total species pool recorded in the surveyed plots.

Functional group	**Total number of taxa**	**Most frequent taxon**	
		Taxon	**% of plots**
II	41	*Artemisia crithmifolia*	53
III	21	*Ammophila arenaria* ssp. *arundinacea*	67
I	18	*Vulpia alopecuros; Silene niceensis*	41

3.2. Patterns of species richness along local and regional gradients

3.2.1. Species richness for the total species pool

A gradual increase in species richness was observed from the seaward end to the middle of the local sea-inland gradient, followed by a landward decrease (Fig. 3.1). Thus, **interior dune (ID) habitats** displayed the highest median value of species richness per plot (15 ± 5), followed by foredunes (FD), dry grasslands (DG), low scrub (LS), and finally embryonic foredunes (EF). Kruskal-Wallis test resulted in significant differences for the median values of species richness among habitat types (Fig. 3.1). More specifically, post hoc Mann-Whitney tests identified significant differences between EF and all other habitat types (between ID and all the other habitat types ($p < 0.05$; Fig. 3.1).

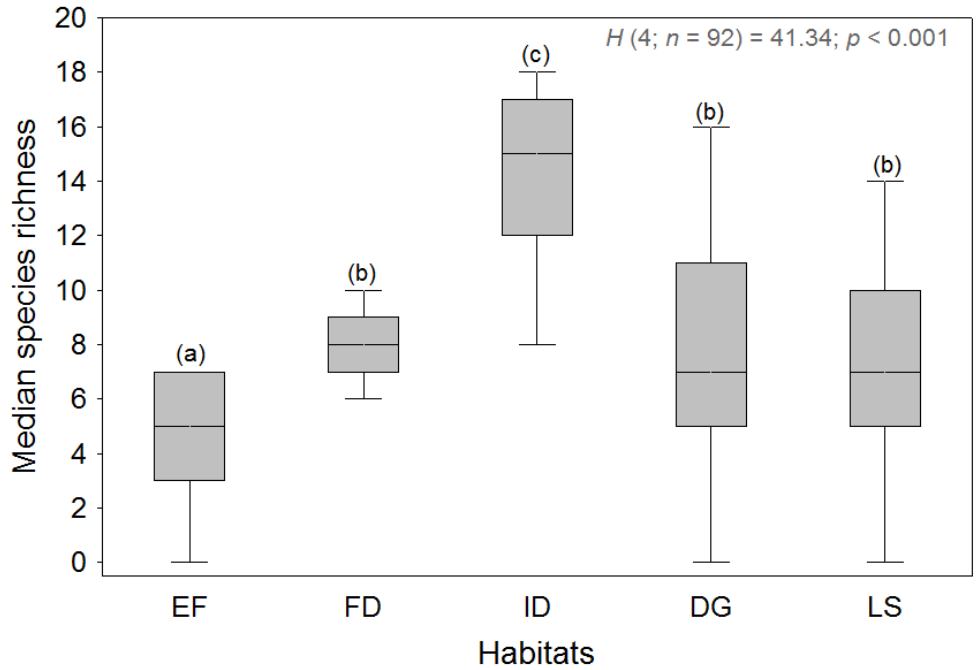

Fig. 3.1 - Median values of species richness per vegetation plot for each habitat type. Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Codes in the horizontal axis are for habitat types: embryonic foredunes (EF); foredunes (FD); interior dunes (ID); dry grasslands (DG); and low scrub (LS). Results for Kruskal-Wallis (H and p) and post hoc Mann-Whitney tests are included in the figure. Distinct letters indicate significant differences between habitat types, whereas similar letters stand for non-significant differences ($p < 0.05$).

Species richness was thus highest at **the centre of local gradient** (i.e. in ID) and decreased towards both ends, with the lowest values reached towards the seaward end of the gradient (Fig. 3.1). This pattern can be explained by the different combinations of stress and disturbance along the dune gradient (Forey *et al.,* 2008; Peyrat, 2011). The levels of nutrient availability and ecological stability typical of interior dune (ID) habitats seem to favour plant diversity (Pianka, 1994; Schwartz *et al.,* 2000; Bonte *et al.,* 2004), in agreement with the humped-back relation between resources and species diversity (Michalet *et al.*, 2006; Isermann, 2011; Peyrat, 2011). Conversely, in the seaward mobile dunes, the harsh conditions of stress and disturbance prevent the occurrence of most species while enabling few specialized taxa (namely *Ammophila arenaria* and *Elymus farctus* ssp. *boreali-atlanticus*) to become dominant (Ciccarelli *et al.,* 2012). The observed decrease of species richness in the more landward habitats may be associated to the reduced environmental stress and instability (Stankeviciute, 2001; Peyrat & Fichtner, 2011), with few competitor species becoming dominant and excluding others (Nielsen *et al.,* 2011; Dwyer *et al.,* 2015).

This hypothesis of increased dominance at the two ends of the local gradient was further confirmed by analyses of **species evenness** (evaluated through Shannon's index). The median value across all plots was 0.68 ± 0.23. More importantly, the index showed a humped-back pattern across habitat types (Fig. 3.2), with ID holding the highest species evenness (0.88 ± 0.11), followed by DG, FD, LS, and finally by EF, in which the dominance by one highly adapted species (*Elymus boreali-atlanticus*) was more pronounced. Again, Kruskal-Wallis tests revealed significant differences in species evenness per plot between ID and all other habitat types and between EF and all other habitat types (Fig. 3.2).

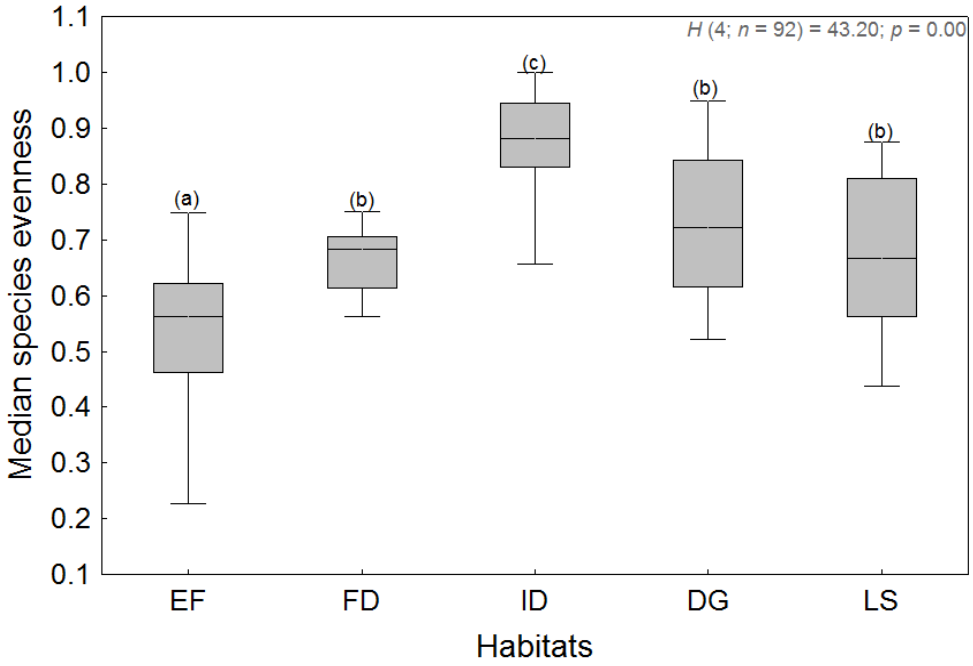

Fig. 3.2 - Median values of species evenness per plot for each habitat. Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Codes in the horizontal axis are for habitat types: embryonic foredunes (EF); foredunes (FD); interior dunes (ID); dry grasslands (DG); and low scrub (LS). Results for Kruskal-Wallis (*H* and *p*) and post hoc Mann-Whitney tests are included in the figure. Distinct letters indicate significant differences between habitat types, whereas similar letters stand for non-significant differences ($p < 0.05$).

Along the regional biogeographic/climatic gradient (i.e. across sites), Furadouro (13 ± 8) and Torreira (11 ± 7) showed the highest median values for species richness per plot, followed by Apúlia, Cova Gala, Quiaios, Mira, and finally São Jacinto. However, differences across sites were not statistically significant ($p > 0.05$). Also, a clear regional pattern for species richness per plot did not seem to emerge (Fig. 3.3). Nonetheless, a tendency for the **northern sites** to host higher median numbers of species than the southern ones was observed (Fig. 3.3). This may be due to the lower water stress suffered by plants under Temperate and sub-Mediterranean climates when compared to those under Mediterranean climates (Forey *et al.,* 2008; Fidalgo *et al.,* 2014; Vaz *et al.,* 2015), especially during the dry summer growth season (Weltzin & McPherson, 2000; Monge & Gornish, 2014).

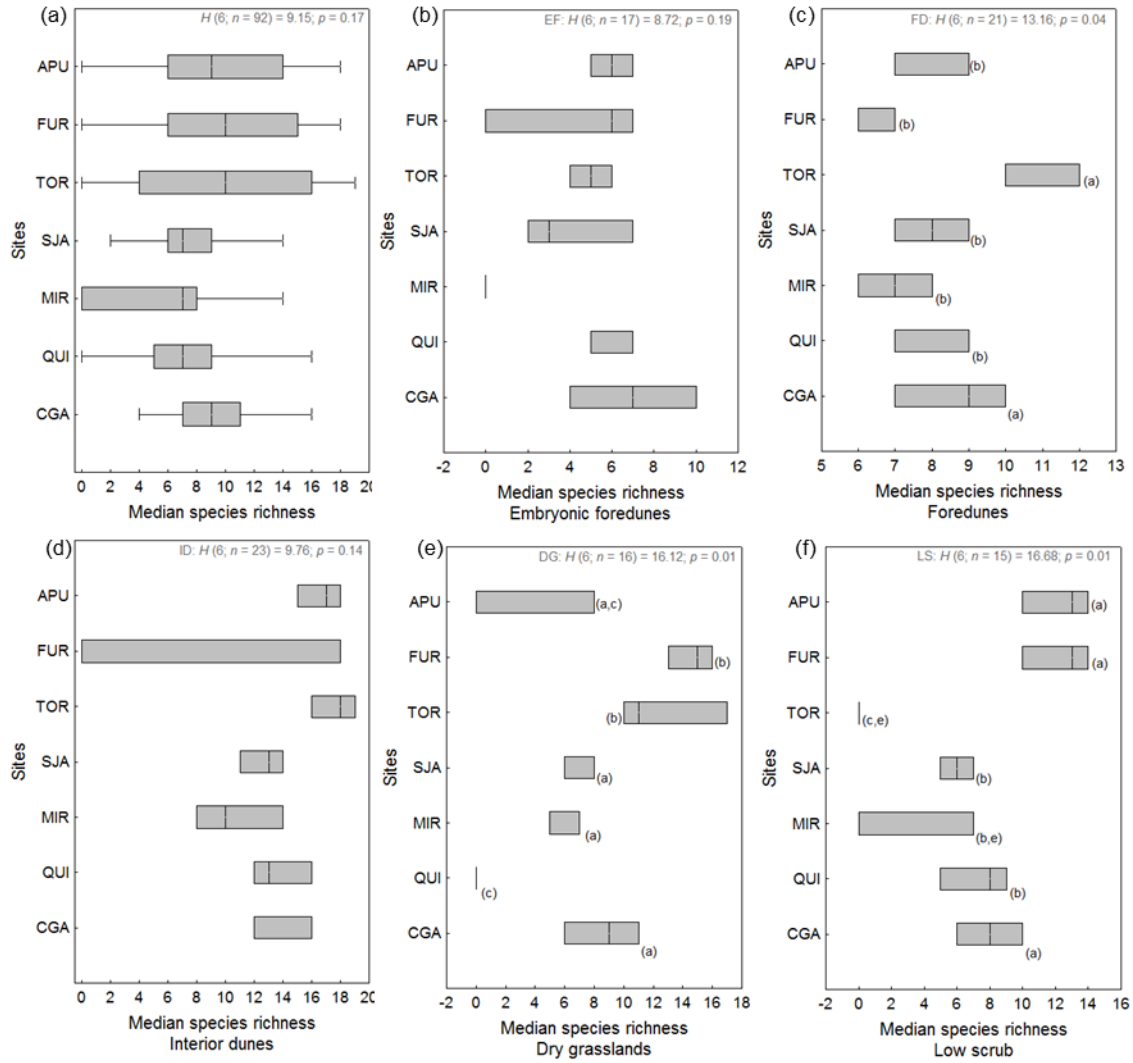

Fig. 3.3 - Median values of species richness per vegetation plot for each site considering the whole study area (a) and each habitat type: embryonic foredunes (b); foredunes (c); interior dunes (d); dry grasslands (e); and low scrub (f). Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Codes in the vertical axis are for the sites of Apúlia (APU); Furadouro (FUR); Torreira (TOR); São Jacinto (SJA); Mira (MIR); Quiaios (QUI) and Cova Gala (CGA). Results for Kruskal-Wallis (*H* and *p*) tests are included in the figure. Different letters indicate statistically significant differences between sites (Mann-Whitney test: $p < 0.05$).

3.2.2. Species richness for CSR strategies

In the whole study area, the highest median values of species richness per plot were observed for the strategies with a **S (stress-tolerant) component** (Fig. 3.4), consistently with the expected dominance of this component in the specialized dune flora (Grime, 2001; Macedo *et al.,* 2010; see Table 3.1). The dominance of the S component was more evident in the seaward habitats (EF and FD), with a gradual (and significant) replacement by plants with a R or C component towards the most landward habitats (DG and LS; Fig. 3.4).

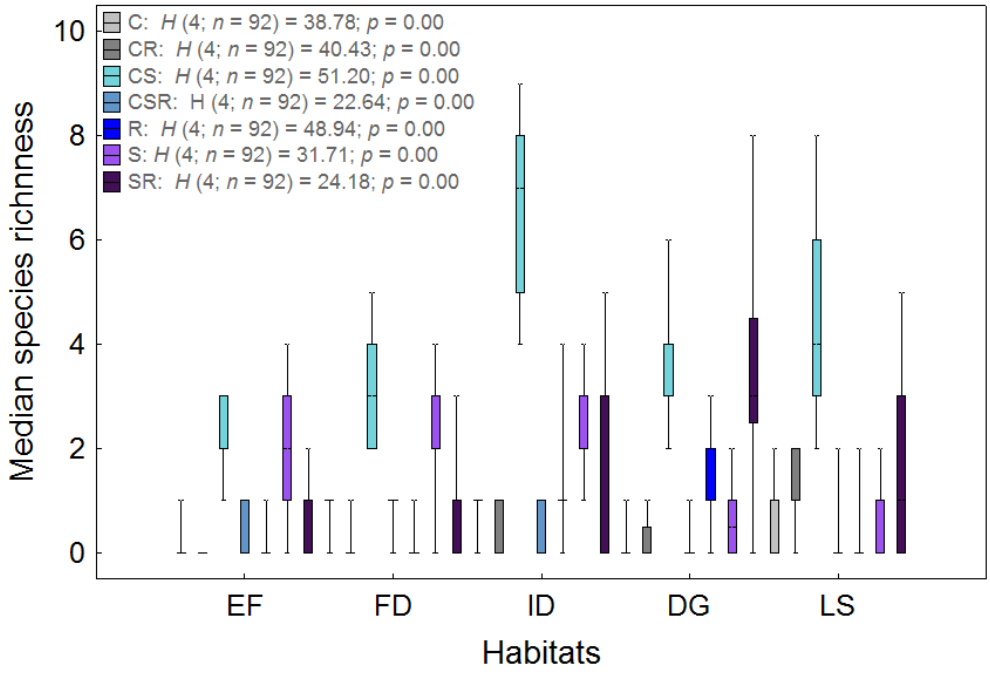

Fig. 3.4 - Median values of CSR species richness per vegetation plot for each habitat type. Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. **C**odes in the horizontal axis are for habitat types: embryonic foredunes (EF); foredunes (FD); interior dunes (ID); dry grasslands (DG); and low scrub (LS). Results for Kruskal-Wallis (*H* and *p*) tests are included in the figure.

Along the sea-inland gradient, a general **humped-back curve** for species richness was observed for most strategies along the local gradient, with higher values observed at the centre of the gradient (ID; Fig. 3.4). This suggests that ID habitats are transitional zones where conditions allow the coexistence of plants from the several habitat types along the gradient, explaining the highest values of species richness for most plant strategies (Isermann, 2005; Peyrat & Fichtner, 2011; Álvarez-Molina *et al.,*

2012). In the more landward habitats, the C component becomes more frequent in response to the lower levels of stress, especially regarding nutrient availability (Grime, 2001; Kuiters *et al.,* 2009; Maun, 2009).

Though there was **no clear regional pattern** for any individual strategy, the highest median values were attained at the northernmost sites, whereas the southernmost sites seemed to exhibit a higher heterogeneity of species richness values (Fig. 3.5). However, a tendency was observed of CS and S strategists to become more frequent in the southernmost sites (Fig. 3.5), which may be connected with an increase in water stress, as described above (Grime, 1984; Otto *et al.*, 2006; Ricalde *et al.*, 2010). Overall, these results suggest an interaction between regional and local stress gradients (Forey *et al.,* 2008; Macedo *et al.,* 2010; Vaz *et al.,* 2015), not only for the total species pool but also for individual strategies.

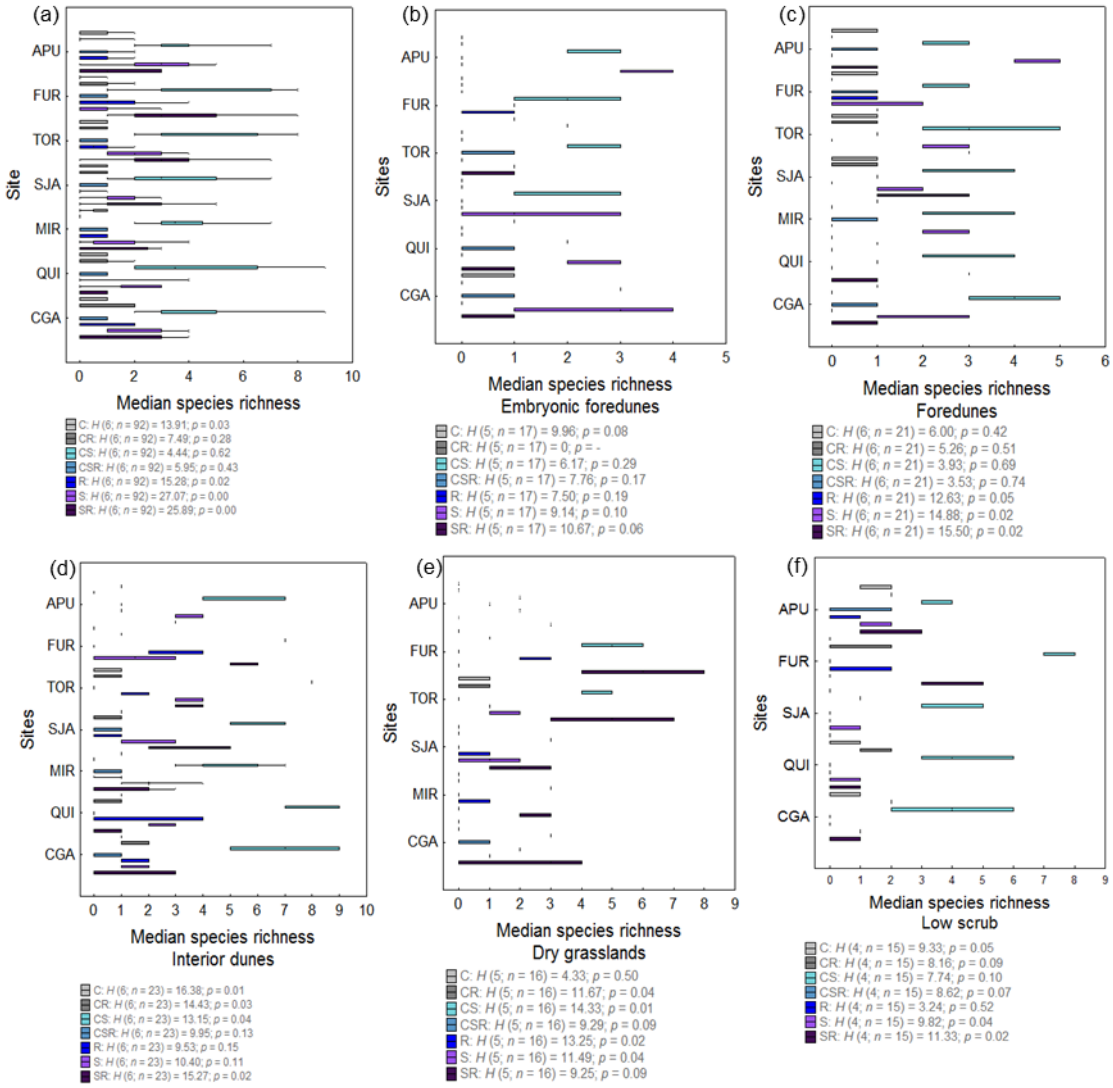

Fig. 3.5 - Median values of CSR species richness per vegetation plot for each site considering the whole study area (a) and each habitat type: embryonic foredunes (b); foredunes (c); interior dunes (d); dry grasslands (e); and low scrub (f). Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Codes in the vertical axis are for the sites: Apúlia (APU); Furadouro (FUR); Torreira (TOR); São Jacinto (SJA); Mira (MIR); Quiaios (QUI) and Cova Gala (CGA). Results for Kruskal-Wallis (H and p) tests are included in the figure.

3.2.3. Species richness for dune plant functional types

The analysis of dune plant functional types (García-Mora *et al.,* 1999) along the local sequence of five habitat types (Fig. 3.6) revealed an expected dominance of **Type III** species (dune specialists) in seaward habitats (EF and FD) and of **Type II** species in the more landward habitats (ID, DG and LS). Conversely, Type I species (generalist ruderals) were most frequent in intermediate positions along the gradient (ID and DG; Fig. 3.6), where the particular balance of stress and disturbance seems to be more suitable for generalist plants (García-Mora *et al.,* 1999, 2000).

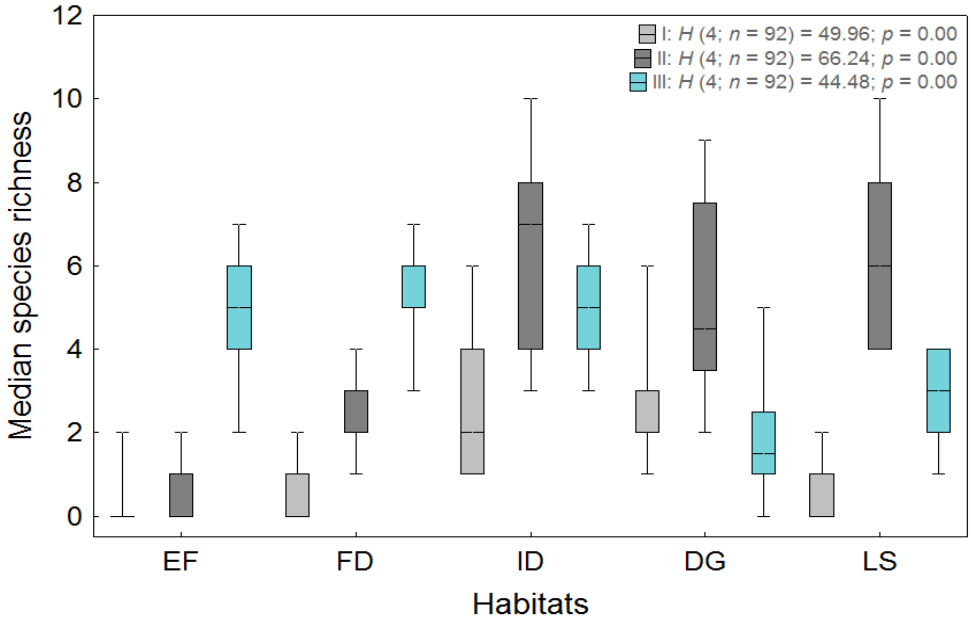

Fig. 3.6 - Median values of species richness for plant functional types per vegetation plot for each habitat type. Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Codes in the horizontal axis are for habitat types: embryonic foredunes (EF); foredunes (FD); interior dunes (ID); dry grasslands (DG); and low scrub (LS). Results for Kruskal-Wallis (*H* and *p*) tests are also included.

Again, **no clear pattern** for species richness per functional type was observed along the regional climatic gradient. Yet, Type I was always the functional type represented by fewer species while Types II and III exhibited the most heterogeneous values of species richness (Fig. 3.7).

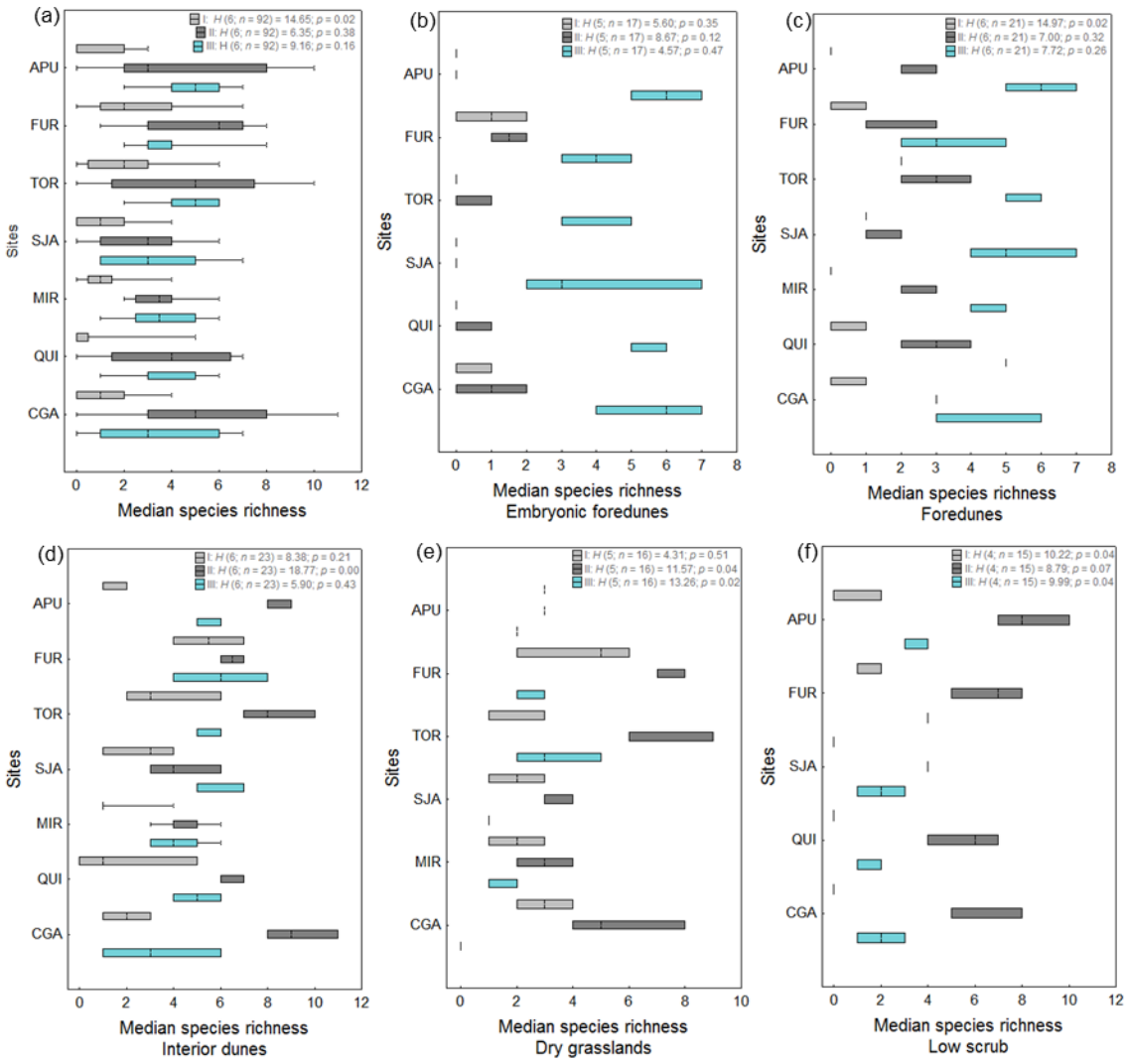

Fig. 3.7 - Median values of species richness for plant functional types per vegetation plot for each site considering the whole study area (a) and each habitat type: embryonic foredunes (b); foredunes (c); interior dunes (d); dry grasslands (e); and low scrub (f). Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Codes in the vertical axes are for sites: Apúlia (APU); Furadouro (FUR); Torreira (TOR); São Jacinto (SJA); Mira (MIR); Quiaios (QUI) and Cova Gala (CGA). Results for Kruskal-Wallis (*H* and *p*) tests are included in the figure.

3.3. Patterns of species composition and their relation with environmental gradients

3.3.1. Species composition for the total species pool

Detrended Correspondence Analysis (DCA) revealed a **high floristic heterogeneity among plots**, reflected in the gradient length of the first DCA axis (DCA1, 5.91 standard deviation units, ter Braak & Smilauer, 2002; Leps & Smilauer, 2003; Fig. 3.8). The cumulative variation explained by the first four DCA axes was 25.3%.

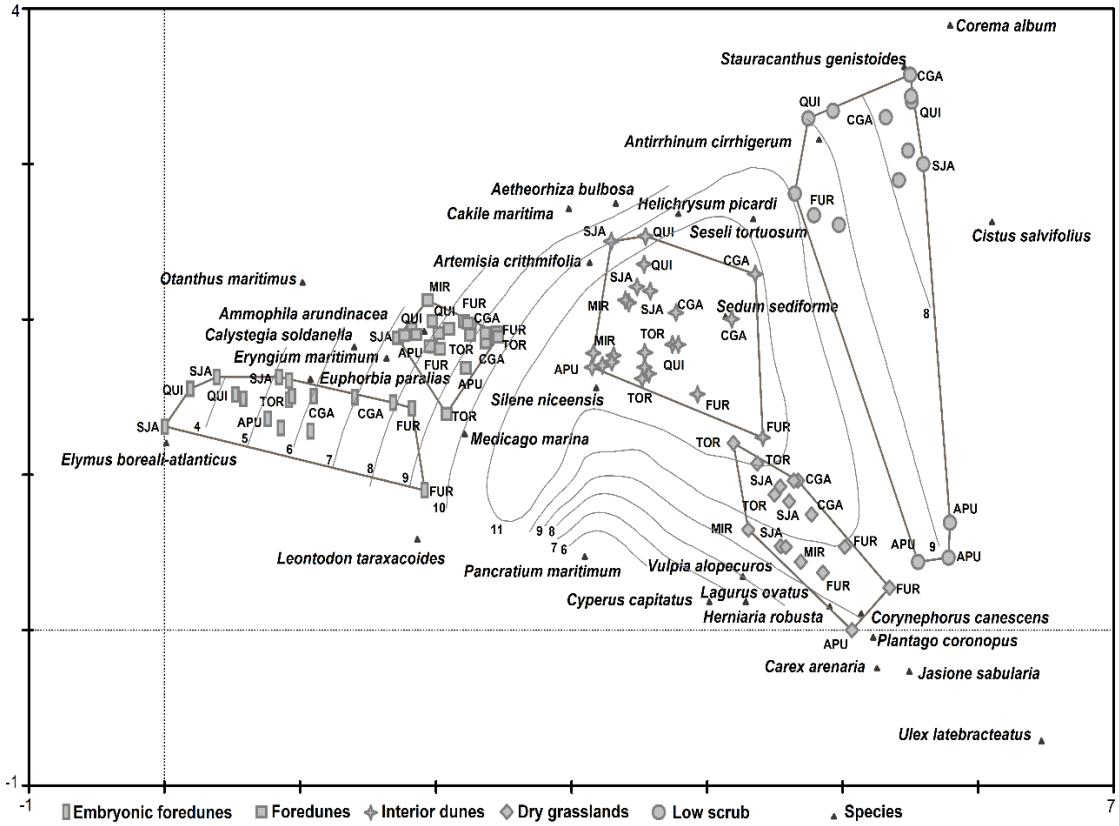

Fig. 3.8 - Detrended Correspondence Analysis plot (DCA1/DCA2) based on species composition (total pool) across the surveyed plots. Isolines represent the variation of species richness in the ordination space range, through the loess model option for visualisation (ter Braak & Smilauer, 2002). Only species with a minimum weight range of 7% are shown (ter Braak & Smilauer, 2002). Habitat types (embryonic foredunes, foredunes, interior dunes, dry grasslands and low scrub) are represented by distinct symbols and enclosed by the drawn polygons. Sites in the figure are: Apúlia (APU); Furadouro (FUR); Torreira (TOR); São Jacinto (SJA); Mira (MIR); Quiaios (QUI); and Cova Gala (CGA).

The first DCA axis (DCA1, 11.2%; Fig. 3.8) depicted the effect of the **sea–inland gradient**, expressed by the position of samples of each habitat type in the ordination space and also by the segregation of species along the axis (from left to right), from those typical of EF (e.g. *Elymus boreali-atlanticus*) and FD (e.g. *Ammophila arundinacea*) to those of ID (e.g. *Artemisia crithmifolia*), DG (e.g. *Corynephorus canescens*) and LS (e.g. *Stauracanthus genistoides*; Lomba *et al.,* 2008). The second axis (DCA2, 7.3%) appeared to express the effect of the **regional climatic gradient**, reflected in the position of samples of each site along a north–south arrangement, with the northernmost site of Apúlia (APU) at one end of the axis and the southernmost sites of Quiaios (QUI) and Cova Gala (CGA) at the other. This was especially evident in the more landward habitat types (Fig. 3.8), in which the higher stability may enable a stronger effect of regional climate on community structure (Honrado *et al.*, 2006). This could further be inferred from the relative position of typical Eurosiberian (or Atlantic) species (e.g. *Jasione maritima* var. *sabularia* and *Ulex europaeus* ssp. *latebracteatus*) and Mediterranean species (e.g. *Stauracanthus genistoides* and *Corema album*; Costa *et al.,* 2000; Lomba *et al.,* 2008; Costa *et al.,* 2009).

3.3.2. Species composition and CSR strategies

The projection of CSR strategies in the ordination space confirmed that stress-tolerant species are more common in the seaward positions of the **local dune gradient** (DCA1), whereas strategies with C or R components are dominant in landward habitats (Fig. 3.9), in line with previous results and consistently with ecological theory (Grime, 2001; Jiménez-Alfaro *et al.*, 2015).

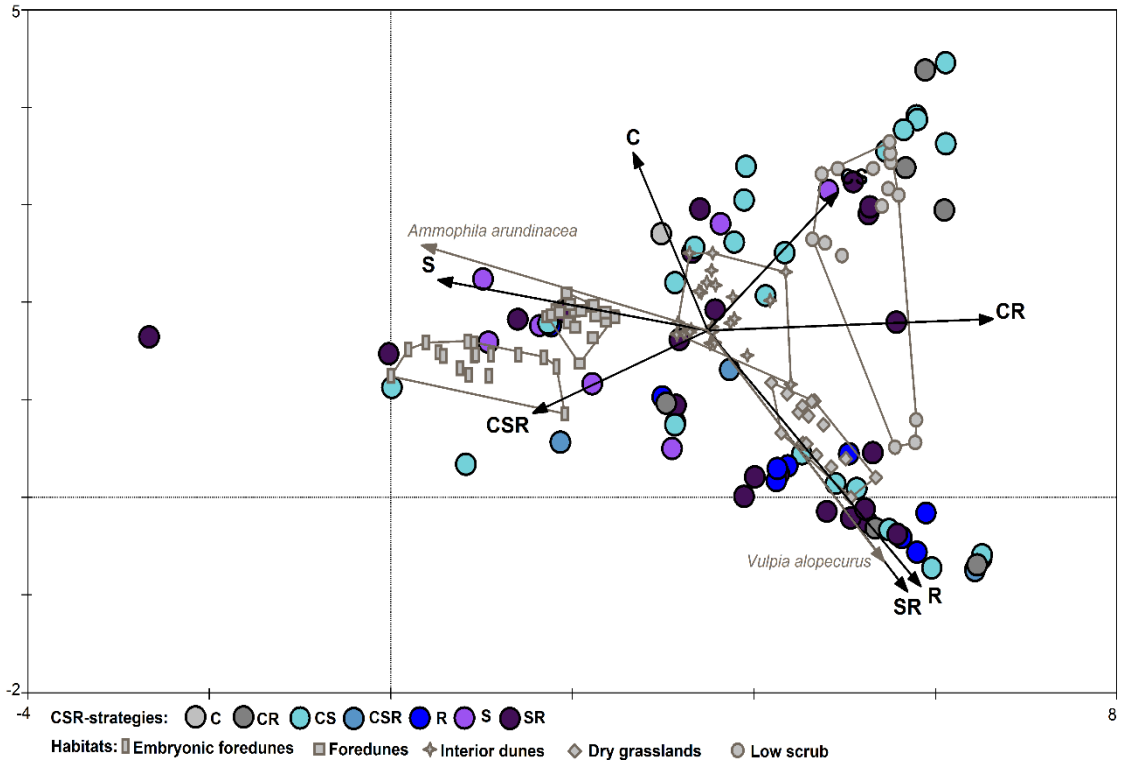

Fig. 3.9 - Detrended Correspondence Analysis plot (DCA1/DCA2) based on species composition (total pool) across the surveyed plots. Habitat types (embryonic foredunes, foredunes, interior dunes, dry grasslands and low scrub) are represented by distinct symbols and enclosed by the drawn polygons. Each species in the plot is represented by a circle with a distinct color according to its CSR strategy. The frequency of each CSR strategy and the abundance of each environmental proxy (*Ammophila arundinacea* and *Vulpia alopecuros*) are represented by arrows.

Along the **regional climatic gradient** (DCA2), species with the C (rare in the overall dataset) or the S component were confirmed to be more common in southernmost sites. Conversely, the R component had a higher expression in the northern sites (Fig. 3.9). This suggests better conditions for survival of ruderal annuals under temperate climate, but also a possible north-south gradient of disturbance, consistent with the abundance of *Vulpia alopecuros*, an indicator of nutrient release due to disturbance in interior dunes (Costa *et al.,* 2010; Lomba *et al.,* 2008; Martins *et al.,* 2013). Thus, in northern sites an increase in generalist annuals was observed (McIntyre *et al.* 1995; Kuiters *et al.,* 2009; Honrado *et al.,* 2010), whereas in southern sites the more prevalent drought stress creating conditions for a higher incidence of the S component (Grime, 1984; McIntyre *et al.,* 1999; Honrado *et al.,* 2010; Macedo *et al.,* 2010).

3.3.3. Species composition and dune plant functional types

The projection of plant functional types (García-Mora *et al.,* 1999) in the ordination space confirmed the gradual replacement of dune specialists (Type III) by dune species that are less adapted to the harsh environment (Type II) and by generalist ruderals (Type I) along the **sea-inland gradient** (DCA1; Fig. 3.10). This confirms a close connection between Type III species and seaward habitats, and between Type II species and landward habitats (García-Mora *et al.,* 2001; Ferreira *et al.,* 2006; Macedo *et al.,* 2010). The pattern observed for Type I species (Fig. 3.10) was consistent with the one discussed above for ruderal and stress-tolerant ruderal species, and reflects much of their weaker tolerance to salt spray, waves and wind, as well as their adaptation to nutrient-rich, disturbed environments (García-Mora *et al.,* 2001; Macedo *et al.,* 2010).

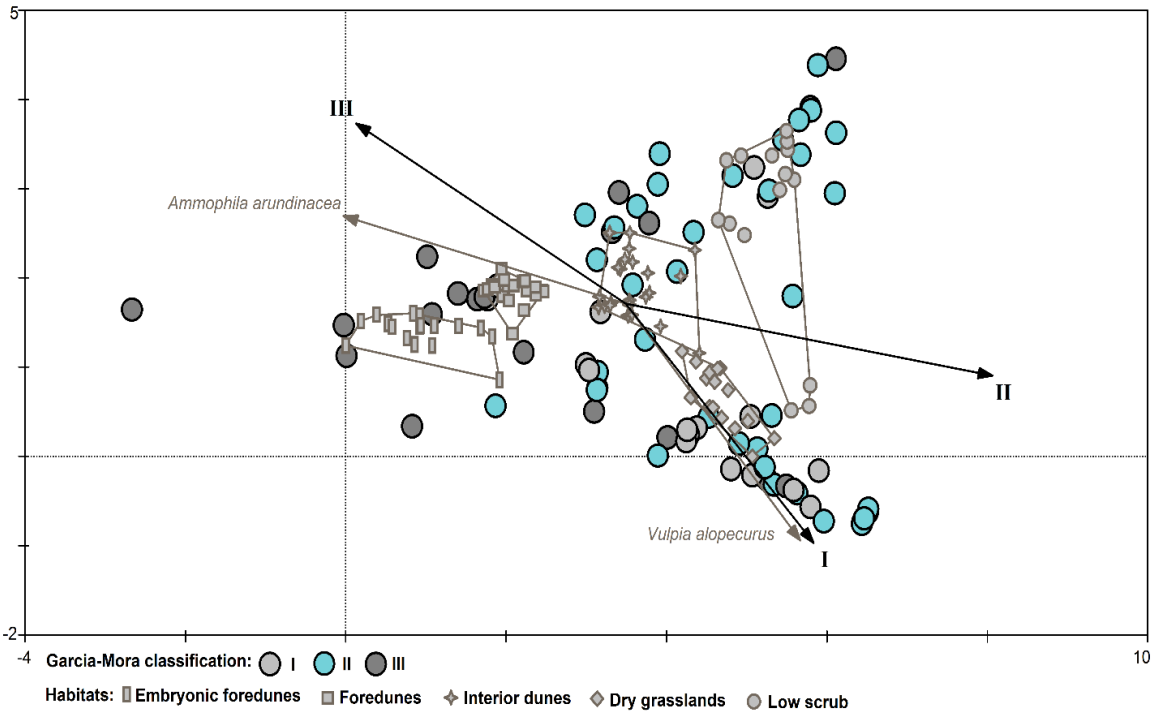

Fig. 3.10 - Detrended Correspondence Analysis plot (DCA1/DCA2) of species composition (total pool) across the surveyed plots. Distinct habitat types (embryonic foredunes, foredunes, interior dunes, dry grasslands and low scrub) are represented by distinct symbols and enclosed by the drawn polygons. Each species in the plot is represented by a circle with a distinct color according to its plant functional type. The frequency of each plant functional type and the abundance of each considered environmental proxy (Ammophila arundinacea and Vulpia alopecuros) are represented by arrows.

Along the **north-south climatic gradient** (DCA2), there was a southwards tendency for species of Types I and II to be gradually replaced by species of Type III (Fig. 3.10). This is consistent with conditions of increasing environmental stress towards south and with a decrease in the effectiveness of facilitation (Brooker *et al.,* 2008; Castanho *et al.,* 2015a,b), whereas highly adapted dune specialists are favoured (Bagousse-Pinguet *et al.,* 2014), in line with the results described above for S strategists.

3.4. Co-occurrence of species, life strategies and functional groups in dune vegetation

3.4.1. Species co-occurrence for the total species pool

Considering the whole dataset, the C-score obtained for the input matrices exhibited a positive and significant value (8.62; $p < 0.05$), compared with the scores obtained for the 10 000 simulated matrices, suggesting the prevalence of (significant) **segregation among species** across the study area. Overall, this expresses the prevailing effects of the strong environmental gradients throughout the study area, and suggests a predominant effect of species sorting along those gradients in shaping dune plant communities (Vaz *et al.,* 2015).

Along the local sea–inland gradient, significantly different patterns of species co-occurrence were found among the five habitat types ($p < 0.01$). **Within each habitat type**, co-occurrence analyses revealed negative (but non-significant) C-scores for EF and ID, but positive and significant values for FD, DG and LS (Fig. 3.11). This suggests the prevalence of species segregation in these three habitat types, expressing species sorting among sites (Lomba *et al.,* 2008; Honrado *et al.,* 2010; Brunbjerg *et al.,* 2012a,b; Vaz *et al.,* 2015).

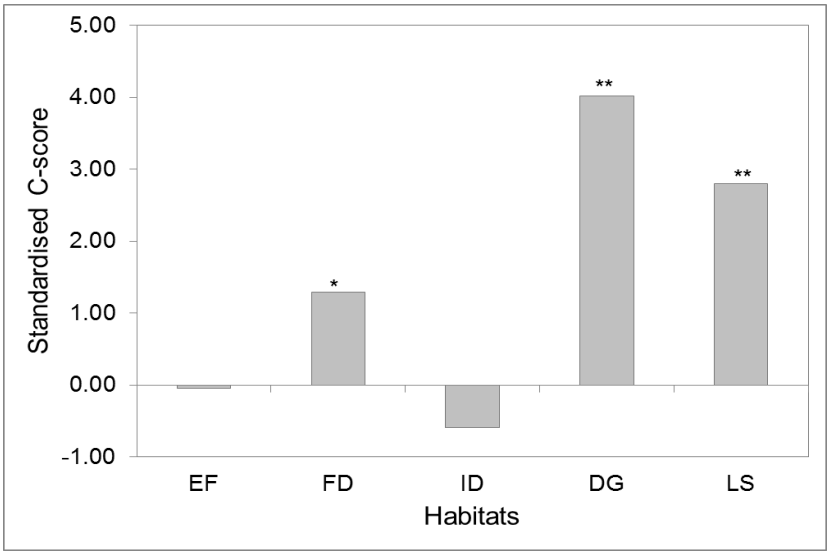

Fig. 3.11 - Standardised C-scores calculated for each habitat type along the local sea-inland gradient. Statistical significance: *, $p < 0.05$, **, $p < 0.01$.

The analysis of co-occurrence patterns **at each site** along the climatic gradient resulted in positive and significant C-scores at all sites (Fig. 3.12), revealing species segregation across habitats. This segregation likely expresses the sorting of species with distinct requirements along the local gradient, and possibly also some interspecific competition in the more landward positions along that gradient (Brunbjerg *et al.,* 2012b; Vaz *et al.,* 2015).

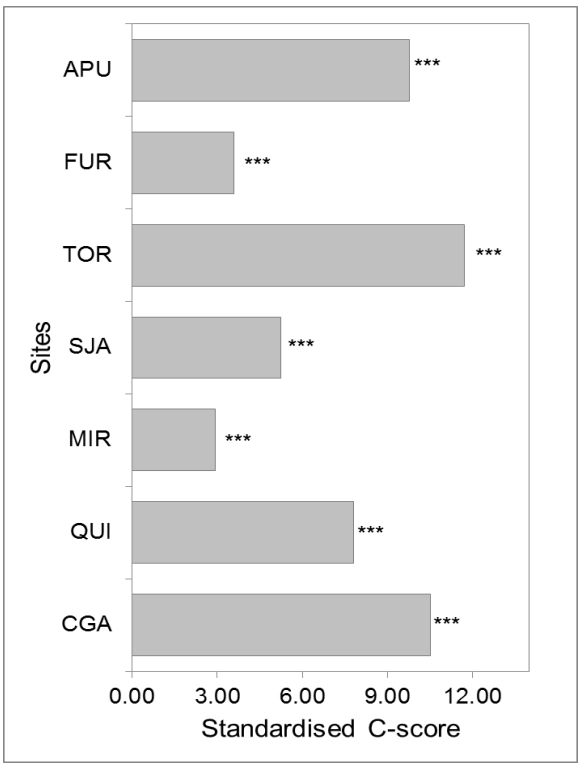

Fig. 3.12 - Standardised C-scores calculated for each site along the climatic gradient. Statistical significance: ***, $p < 0.01$.

Though no clear pattern was observed for the variation of C-scores along the regional gradient (Fig. 3.12), species co-occurrences **among sites** were found to be significantly different compared to the variability of species co-occurrence within sites ($p < 0.05$), suggesting the predominance of species segregation, not only within but also between sites. This may express the effects of the regional climatic gradient on species sorting (e.g. Forey *et al.* 2008), as discussed above, but also the effects of other factors discriminating conditions at the several sites, such as those related with coastal dynamics (e.g. Honrado *et al.,* 2010; Fidalgo *et al.*, 2014; see section 3.5).

3.4.2. Species co-occurrence for CSR plant strategies

Overall, co-occurrence analysis **among the different CSR strategies** resulted in a low value for the C-score (0.27) with no statistical significance ($p > 0.05$), suggesting that the level of co-occurrence among the seven strategies is similar to the patterns expected if the species were randomly assigned to different strategies (Ulrich & Gotelli, 2010; Götzenberger *et al.,* 2012).

When analysing the C-scores obtained for **pairs of strategies**, several negative and positive values were observed (though mostly non-significant; Fig. 3.13). However, positive and significant C-score values were found between the R and S strategies (R-S; 1.67; $p < 0.05$), and between the SR and S strategies (2.36; $p < 0.05$), suggesting a (significant) segregation between those pairs of strategies (Fig. 3.13). The segregation of two extreme strategies, R and S, could be expected considering that plants with these strategies are adapted to quite distinct conditions of stress and disturbance, and will thus be sorted along the regional and local dune gradients (Grime, 1974, 1984, 2001). The segregation between the SR and S strategies likely expresses their distinct positions along the disturbance gradient, with SR species occupying areas where stress is joined by some level of disturbance, accordingly (Grime, 1984, 2001; Brunbjerg *et al.,* 2014a,b; Jiménez-Alfaro *et al.*, 2015).

Also, a (non-significant) tendency for aggregation was detected between the R and SR strategies (-1.19), and between the CS and R strategies (-0.96) (Fig. 3.13). In the first case, this aggregation likely expresses the responses of species with an R component to a same set of conditions, namely regarding nutrient release from disturbances (Grime, 1984, 2001; Maestre *et al.,* 2009). In the second case, it may reflect the **facilitation** of ruderals by the dominant (nurse) plants of the CS strategy (Callaway, 1995; Castanho *et al.,* 2012).

Within each CSR strategy, a general tendency for species segregation was observed, as C-scores were found to be positive and significant for most strategies (Fig. 3.13). This within-strategy segregation, which likely reflects competition among species with similar traits and resource requirements (Bertness & Callaway, 1994; Maestre *et al.,* 2009), was statistically stronger for strategies with the S or the R components, which are the most common in the data set (Fig. 3.13).

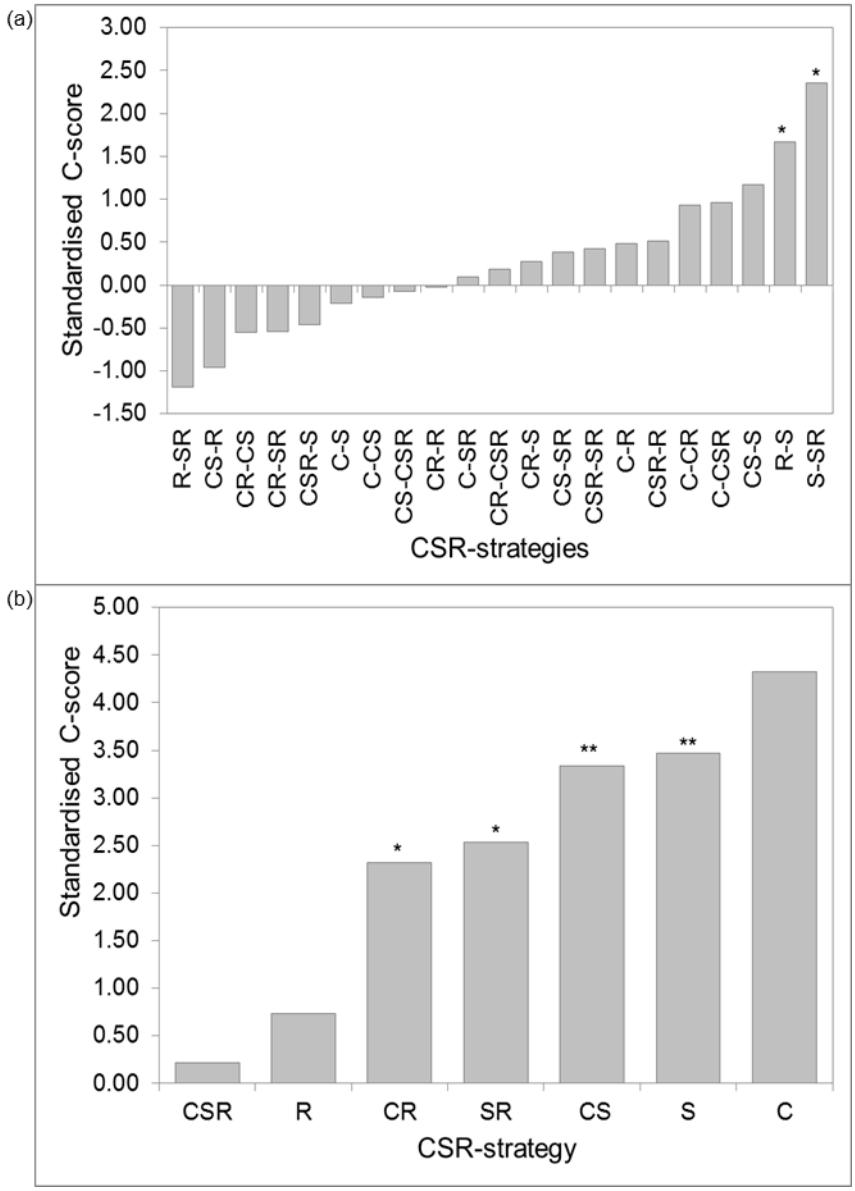

Fig. 3.13 - Standardised C-scores calculated for the whole study area, and considering co-occurrences between pairs of CSR strategies (a) and within each CSR strategy (b). Statistical significance: *, $p < 0.05$; **, $p < 0.01$.

Along the **sea-inland gradient**, both negative and positive values were obtained for the co-occurrence of CSR strategies in each habitat type (Fig. 3.14a). EF and ID showed trends for the segregation among CSR strategies, whereas FD, DG and LS exhibited evidence for aggregation among strategies. Interestingly, and although the obtained C-score values were not statistically significant, the pattern observed along the sea-inland gradient was rather symmetric to the one observed for the total species

pool (cf. Fig. 3.11). This suggests that species co-occurrence is at least partially mediated by plant strategies, with habitat filtering mechanisms determining the range of viable strategies in coastal dunes (Cornwell & Ackerly, 2009; Katabuchi *et al.,* 2012).

Again, C-score values for **pair-wise relations** among CSR strategies revealed both species aggregation and segregation (mostly non-significant; Fig. 3.14b), suggesting that within each habitat type the overall community assembly is at least partially mediated by plant strategies. This may include the sorting of strategies along gradients (Gitay & Wilson, 1995; Waugh & Aarssen, 2011; Brunbjerg *et al.,* 2012b) as well as the development of both negative and positive interactions (Pugnaire *et al.*, 2011). Our results also suggest that co-occurrence patterns are dependent of each pair of strategies being analysed, which in turn will influence the prevailing co-occurrence pattern detected at the community level (Maltez-Mouro *et al.*, 2010; Waugh & Aarsen, 2011).

For each CSR strategy, differences for species co-occurrences among habitat types were statistically significant for CS ($p < 0.001$) and C ($p < 0.05$) strategies. Conversely, **within each strategy** there was a clear dominance of species segregation (i.e. positive C-score values) within a given habitat type, especially in the case of SR and S species (Fig. 3.14c). Again, these results are likely the joint expression of strategy sorting along gradients through trait selection (Douma *et al.,* 2012a,b) and of local competition between species with similar adaptations and requirements (Craine *et al.*, 2013; Vaz *et al.,* 2015).

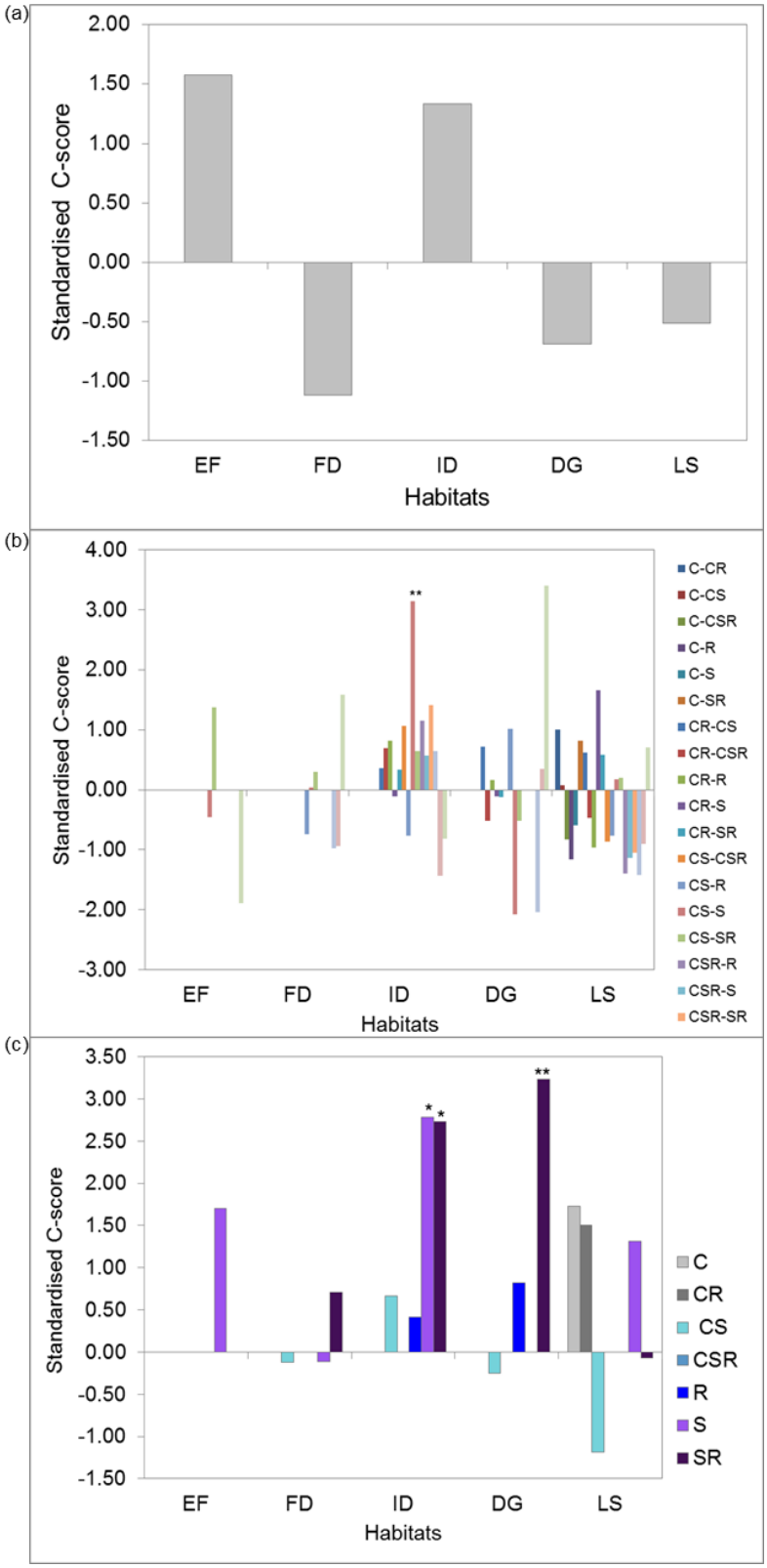

Fig. 3.14 - Standardised C-scores calculated for each habitat type, and considering co-occurrences among CSR strategies (a), between pairs of strategies (b), and within each strategy (c). Statistical significance: *, $p < 0.05$, **, $p < 0.01$.

No clear co-occurrence pattern was observed along the **regional, climatic gradient** (Fig. 3.15). Negative but non-significant (p > 0.05) C-score values were obtained for the majority of sites when analysing the co-occurrence patterns among all CSR strategies (Fig. 3.15a), suggesting randomness or some tendency for aggregation, possibly due to facilitative interactions among strategies (Ulrich & Gotelli, 2010). Contrastingly, Furadouro (0.95) and São Jacinto (1.07) showed evidence of segregation (also non-significant; p > 0.05) among CSR strategies, which is consistent with the sorting of species with different strategies along the local dune gradient (Gitay & Wilson, 1995; Waugh & Aarssen, 2011; Brunbjerg *et al.,* 2012b; Vaz *et al.,* 2015).

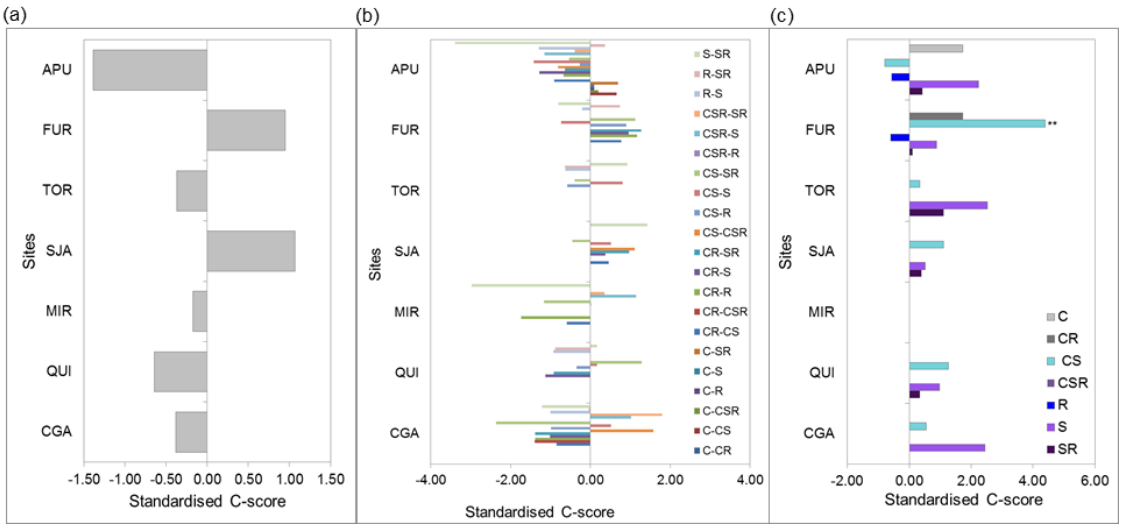

Fig. 3.15 - Standardised C-scores calculated for each site, and considering co-occurrences among CSR strategies (a), between pairs of strategies (b), and within each strategy (c). Statistical significance: **, p < 0.01.

The **pair-wise analysis** of co-occurrence also yielded non-significant C-score values (Fig. 3.15b). Yet, the observed values confirm that the relations among all strategies are the result of distinct pair-wise co-occurrence relations. In other words, in one same site both segregation and aggregation patterns occur between distinct pairs of CSR strategies, resulting in an overall non-significant value for the co-occurrence among strategies (Fig. 3.15a).

Finally, co-occurrence patterns among species **within each CSR strategy** in the several sites revealed a prevalence (non-significant in most cases) of species segregation (Fig. 3.15c), suggesting an effect of competitive interactions among plants within one same strategy (Grime, 1977; Maestre *et al.* 2009; Bowker *et al.,* 2010)

together with fine-scale sorting along the steep local gradients (Brunbjerg *et al.,* 2012b; Vaz *et al.,* 2015).

3.4.3. Species co-occurrence for dune plant functional types

Among all the dune plant functional types (García-Mora *et al.,* 1999), C-score value was also low (0.83) and non-significant ($p > 0.05$). When focusing on the analysis of co-occurrence patterns between **pairs of plant functional types**, both positive and negative C-score values were attained (Fig. 3.16a). Specifically, a tendency for species from the Type I strategy to be aggregated relatively to the other two plant functional types was observed, suggesting that annual generalists may be facilitated by the more adapted plants of Types II and III (Garcia-Mora *et al.,* 1999; Bertness & Callaway, 1994; Cavieres *et al.,* 2014). Conversely, a significant segregation between species belonging to Types II and III (2.28; $p < 0.05$) was detected. This likely reflects the gradual replacement of dune specialists (Type III) by other dune plants (Type II) along the local dune gradient, through competition and/or species sorting along the stress gradient (García-Mora *et al.,* 1999; Jiménez-Alfaro *et al.*, 2015; Vaz *et al.,* 2015).

Finally, results from the co-occurrence tests among species **within each functional type** revealed positive and significant C-score values, for all three functional types (Fig. 3.16b), suggesting species segregation regardless of the strategy type. This suggests that, within each strategy, different plant species take advantage of the specific conditions in each position along the local or regional gradients, including competition and species sorting (e.g. Maestre *et al.,* 2010).

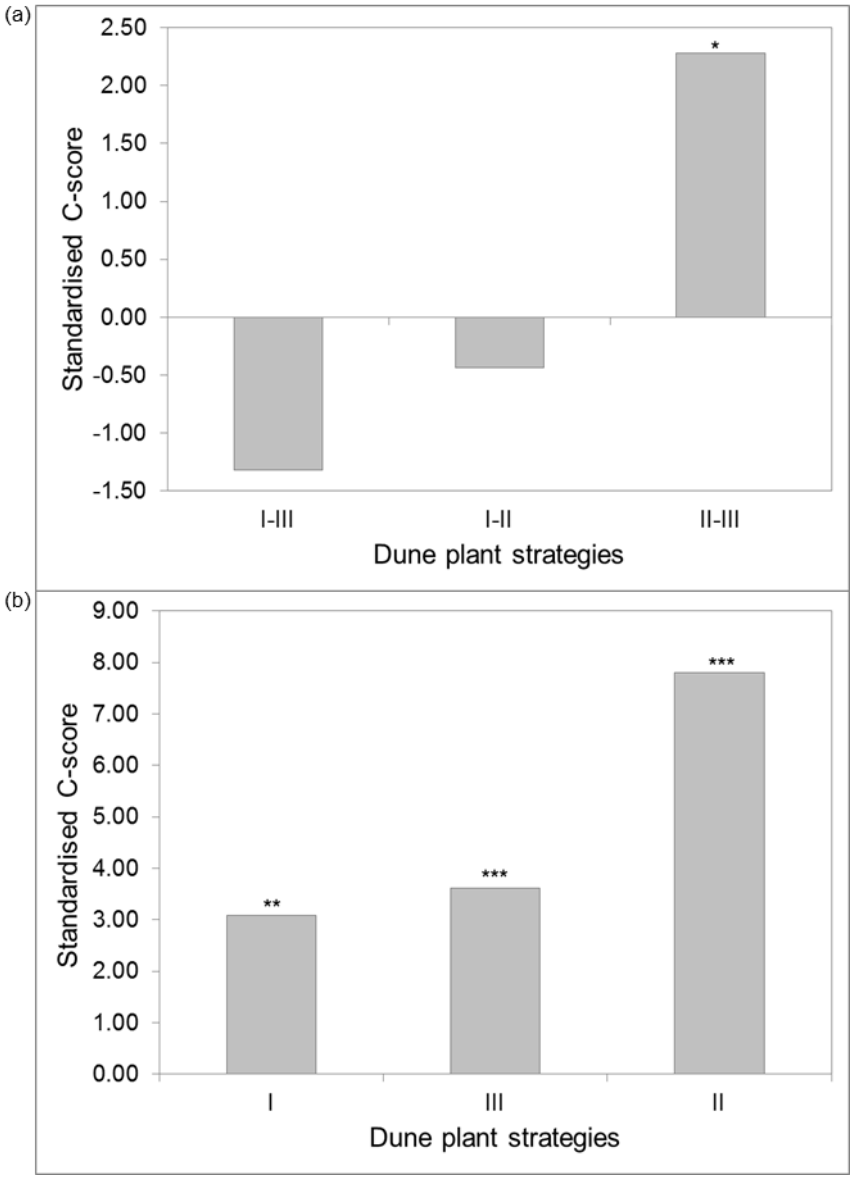

Fig. 3.16 - Standardised C-scores calculated for the whole study area, and considering co-occurrences between pairs of strategies (a), and within each strategy (b). Statistical significance: *, $p < 0.05$, **, $p < 0.01$; ***, $p < 0.001$.

Co-occurrence analyses among habitat types revealed significant differences in C-score values ($p < 0.001$) for functional Type II. This suggests that, **along the sea-inland gradient**, Type II species are more segregated across habitat types than randomly expected, possibly reflecting a strong adaptation of individual species to certain positions along the gradient (Gallego-Fernández & Martínez, 2011; Guerin *et al.,* 2014)**.** Considering species co-occurrences within each habitat type (Fig. 3.17a), co-occurrence analyses for plant functional types exhibited non-significant C-score values.

Yet, a possible local pattern was observed (Fig. 3.17a), with a tendency for aggregation of plant functional types at both extreme ends of the sea-inland gradient (i.e. EF and LS habitats), whereas strategies seem to occur segregated from each other in the centre of the gradient (FD, ID and DG).

This pattern also reflects the results obtained for the **pair-wise analyses** of co-occurrence (Fig. 3.17b). Plants of functional Types II and III tend to occur aggregated in EF, but segregated in more interior habitats (Fig. 3.17b), possibly reflecting a gradual increase of local competition as the two groups become more frequent and species diverse (Mouchet *et al.,* 2010; Lewis *et al.,* 2014a,b). Conversely, plants of Types I and II tend to segregate in FD and DG (Fig. 3.17b), again suggesting local competition for resources, but occur aggregated in LS habitats, where competition may be lower as Type II is here mainly represented by shrubs, which have deeper rooting systems compared with Type I ruderal annuals (García-Mora *et al.,* 1999; Lucrezi *et al.,* 2014).

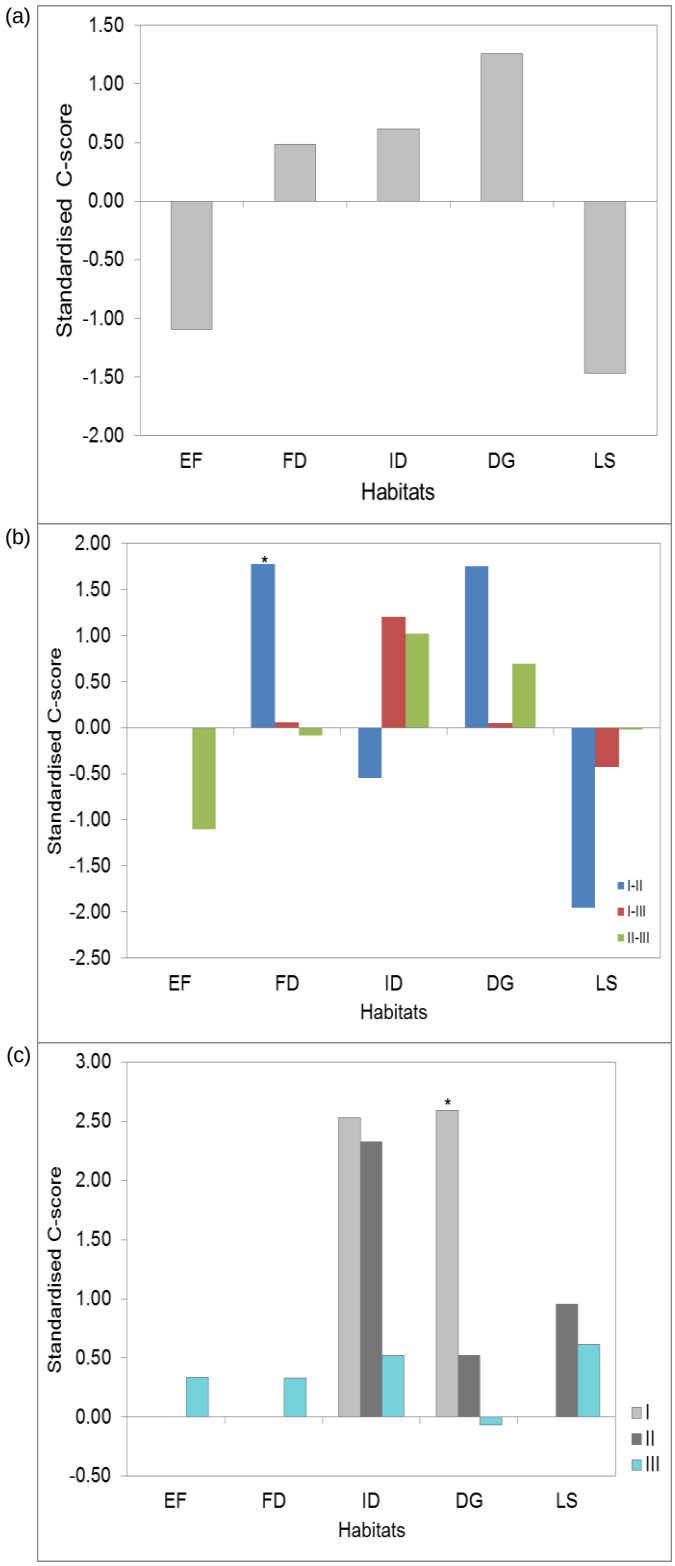

Fig. 3.17 - Standardised C-scores calculated for each habitat type, and considering co-occurrences among plant functional types (a), between pairs of strategies (b), and within each strategy (c). Statistical significance: *, $p < 0.05$.

When analysing co-occurrence patterns **within each functional type**, there was a clear prevalence of within-strategy species segregation (Fig. 3.17c). Again, however, most C-scores were non-significant. In fact, Type I species were the only ones with a significant segregation among species, specifically in one of the habitats where they are more common (DG; see Fig. 3.6), which may be associated to some niche overlap among annual plants and thus increased local competition (Coomes *et al.,* 2002; Turnbull *et al.,* 2004).

Along the **regional climatic gradient**, a tendency for aggregation of functional types was observed, especially in the southward sites (Fig. 3.18a). This prevalence of aggregation was also evident in pairwise comparisons (Fig. 3.18b), and may overall express the occurrence of facilitative interactions between species with distinct levels of adaptation to the dune environment, which would be more important in the southern, more stressful sites (Caldeira *et al.,* 2005; Maestre *et al.,* 2009; Gross *et al.,* 2013).

Conversely, but in line with previous results, the analysis of co-occurrence patterns **within each plant functional type** (Fig. 3.18c) revealed that the most common pattern was species segregation. This pattern was found to be significant in most sites, especially within Types II and III, and is consistent with strong competition for resources among species with similar requirements and adaptations (García-Mora *et al.,* 1999; Kikvidze & Armas, 2010). In opposition, species of the Type I strategy showed a tendency for aggregation in the northernmost sites (Fig 3.18c). Here these species are more frequent and probably occur together due to their dependence on facilitative interactions with more adapted dune specialists (Tirado & Pugnaire, 2003; Cushman *et al.,* 2010; Pugnaire *et al.,* 2011), and/or to their similar response to disturbances towards inland habitats (Lewis *et al.,* 2014a,b). These two processes would explain the observed patterns by enabling coexistence of ruderal plants (Cavieres & Badano, 2010).

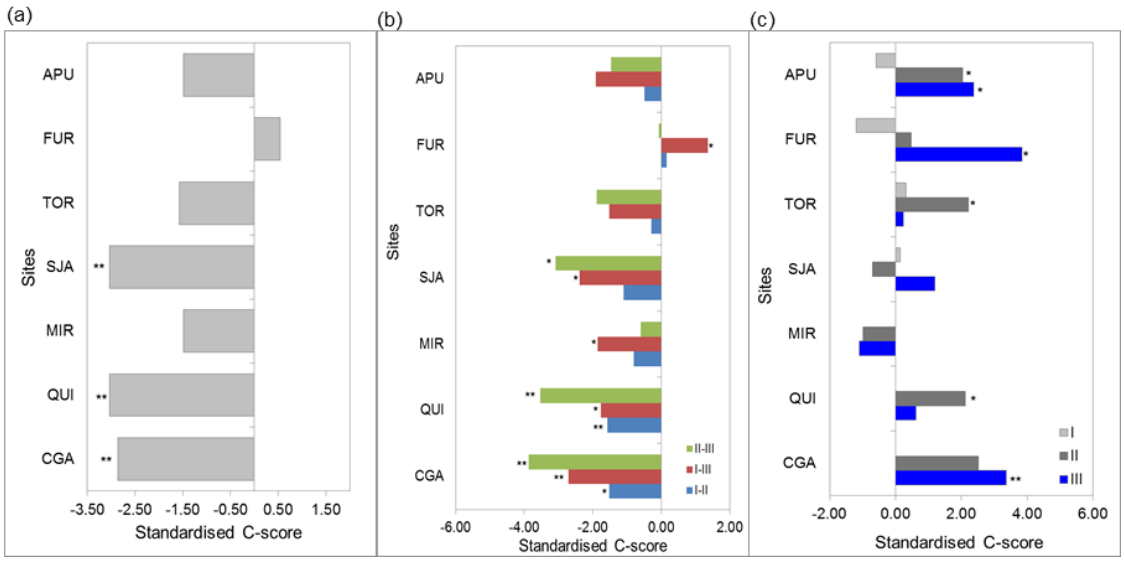

Fig. 3.18 - Standardised C-scores calculated for each site, and considering co-occurrences among plant functional types (a), between pairs of strategies (b), and within each strategy (c). Statistical significance: *, $p < 0.05$, **, $p < 0.01$.

3.5. Community-level responses of dune vegetation to changes in coastal dynamics

The results described in this section compare patterns of dune plant community structure between **two contrasting types of coastal dynamics** occurring in the surveyed coastal areas, i.e. transgressive *versus* meta-stable dunes. Based on previous research conducted in the study area (Granja, 1997; Carvalho *et al.*, 2006; Macedo, 2008; Honrado *et al.,* 2010; Macedo *et al.,* 2010; Vaz *et al.,* 2014) and elsewhere (e.g. Rubinstein *et al.,* 2013; Hernández-Cordero *et al.*, 2015), we assumed that vegetation changes induced by a shift in coastal dynamics would be more evident in **the mobile dune complex** (i.e. the EF and FD habitats) due to its seaward-most position (e.g. García-Mora *et al.,* 1999; Hesp, 2002; Lemauviel & Rozé, 2003; Lucrezi *et al.,* 2014; Zuo *et al.,* 2014).

Thus, the present section includes a comparative analysis of changes in the patterns of diversity and co-occurrence of the total species pool in the complex of mobile dunes under either transgressive or meta-stable coastal dynamics, followed by an outline of the main changes in CSR strategies and in dune plant functional types. In this regard, it points a test of the usefulness of information on plant community structure to signal changes on prevailing coastal dynamics.

3.5.1. Patterns for the total species pool under contrasting coastal dynamics

Twenty one plant species were found in the ensemble of meta-stable plots, and 23 in the set of transgressive plots. Comparisons of median values of **species richness** between transgressive and meta-stable sites resulted in non-significant differences (Fig. 3.19a). However, values of species richness were more similar across transgressive plots, suggesting a homogenising effect of disturbance on community structure (Honrado *et al.* 2010). Meta-stable plots displayed the highest prevalence of species that are most typical of EF habitats, such as *Calystegia soldanella* and *Otanthus maritimus* (Ciccarelli *et al.,* 2009), while transgressive plots showed the highest dominance of typical FD species, especially *Ammophila arenaria* (Fig. 3.19b). These are not surprising results since under transgressive dynamics some loss of

vegetation zonation is expected to occur, often resulting in the destruction of the seaward-most biotopes and associated vegetation (Rodwell *et al.,* 2000; Honrado *et al.,* 2010; Martins *et al.,* 2013).

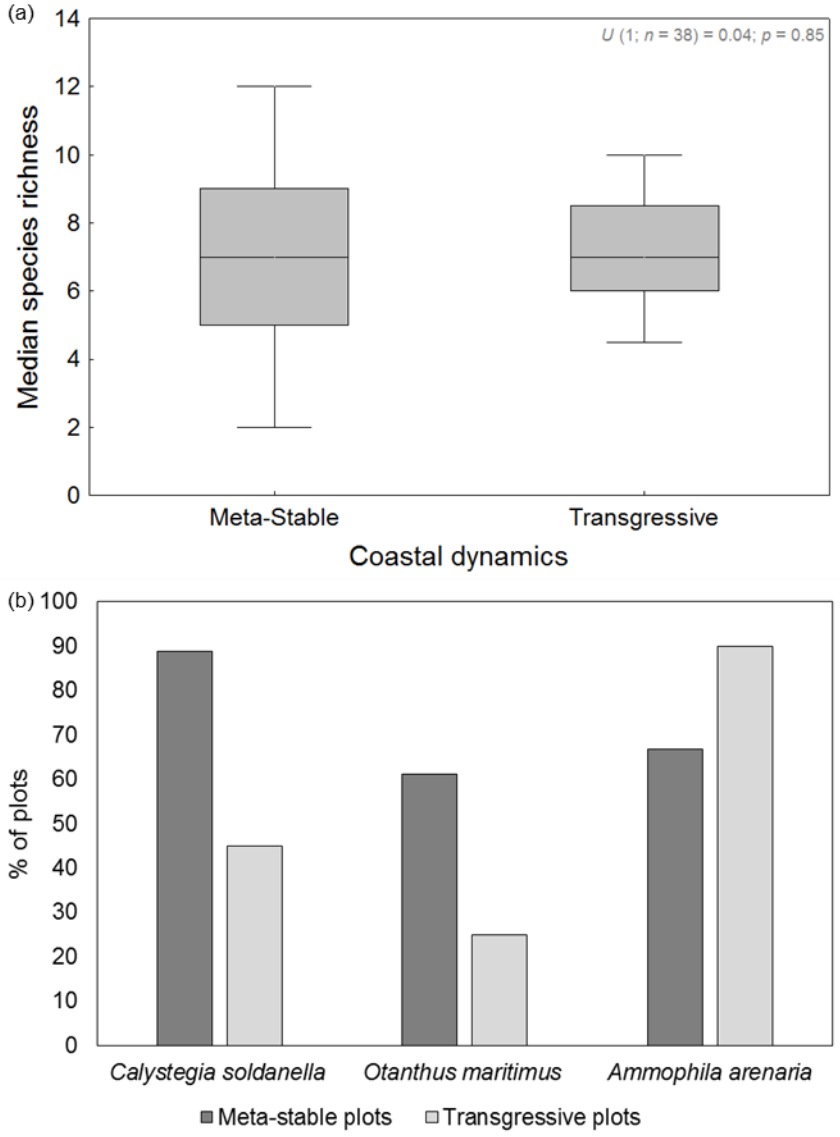

Fig. 3.19 - Median values of species richness considering the ensemble of plots from meta-stable and transgressive sites (a), and percentage of meta-stable and transgressive plots in which the three most frequent species occur (b): *Calystegia soldanella*, *Otanthus maritimus* and *Ammophila arenaria*. Boxes depict the 25th and 75th percentiles and whiskers represent the 5th and 95th percentiles. Results for Mann-Whitney (*U* and *p*) tests are included in the figure.

Focusing on **species composition** in the mobile dune complex, the Principal Component Analysis (PCA; Fig. 3.20) showed that a cumulative variation of 83.8 % was explained by the first four DCA axes. The first PCA axis (PCA1, 51.1%), mostly depicts a sea-inland gradient expressed by the segregation of samples and species of EF (right side of the plot; e.g. *Elymus boreali-atlanticus* and *Polygonum maritimum*) from those of FD (left side of the plot; e.g. *Ammophila arundinacea*, *Crucianella maritima*; Mateus, 1992; Lomba *et al.,* 2008).

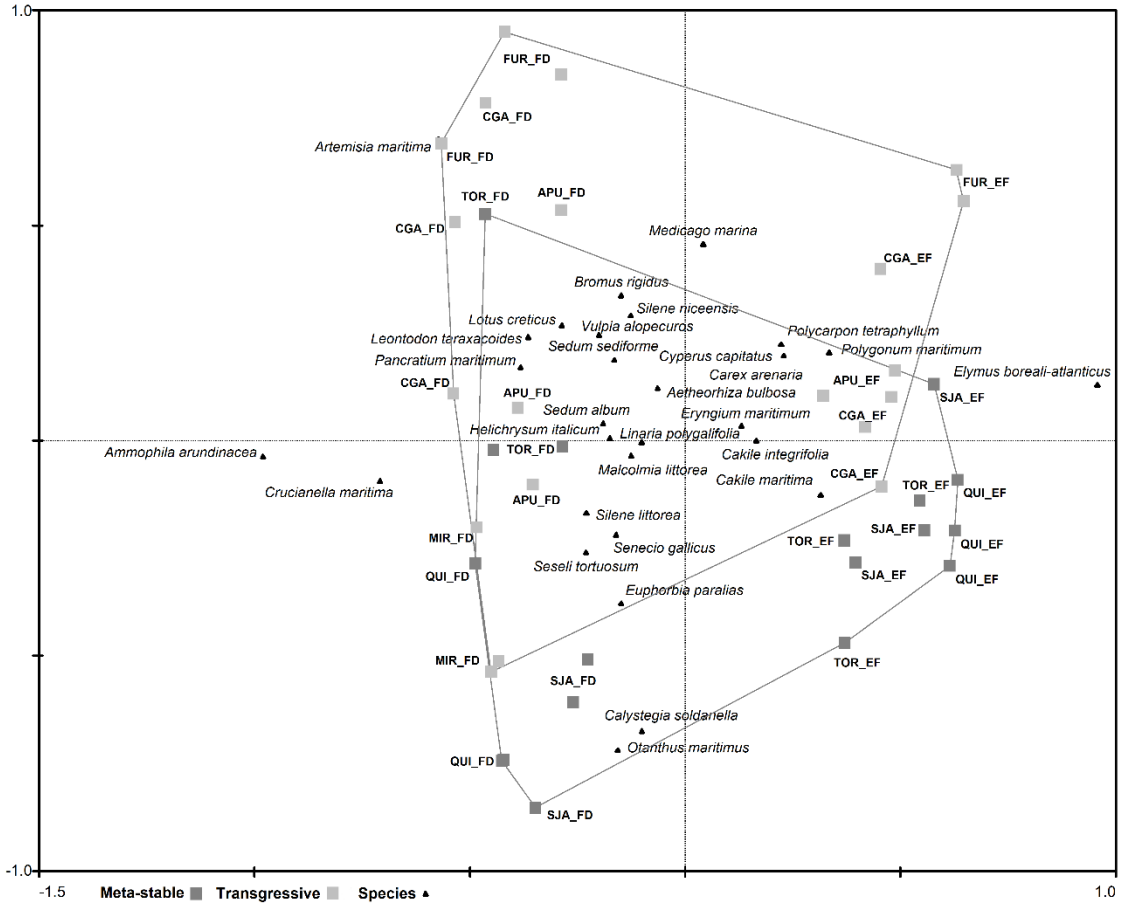

Fig. 3.20 - Principal Correspondence Analysis plot (PCA1/PCA2) based on species composition across plots from meta-stable and transgressive sites (represented by distinct symbols and enclosed by the drawn polygons). Only species with a minimum weight range of 7% are shown (ter Braak & Smilauer, 2002).Sites designations are as follows: Apúlia (APU); Furadouro (FUR); Torreira (TOR); São Jacinto (SJA); Mira (MIR); Quiaios (QUI); and Cova Gala (CGA). Habitat types: embryonic foredunes (EF) and foredunes (FD) are also exhibited.

The second PCA axis (PCA 2: 14%) seemed to reflect the **segregation of vegetation plots under meta-stable (bottom) or transgressive (top) dynamics** (Fig. 3.20). This was also accompanied by the segregation of *Artemisia maritima* or *Medicago marina* (at the top of the ordination plot) from *Calystegia soldanella* and

Otanthus maritimus (at the bottom). These results are consistent with the fact that *Artemisia maritima* and *Medicago marina* are well-adapted to situations of coastal instability in foredune crests (Henriques & Neto, 2002), whereas *Calystegia soldanella* and *Otanthus maritimus* are more frequent in the typical communities of embryonic foredunes and early stages of foredune formation (Lomba *et al.,* 2008; Ciccarelli *et al.,* 2012).

In fact, ANOSIM tests confirmed **significant differences** in species composition between meta-stable and transgressive coastal dynamic types ($R = 0.078$; $p < 0.05$). Contrastingly to the results obtained for species richness, coastal dynamics seems to act as an important filter for species composition, promoting the prevalence of species with distinct dominance levels and ecological requirements under contrasting coastal dynamics (Tissier *et al.,* 2013; Timmermann *et al.,* 2014).

Significant differences in the co-occurrence patterns were also observed between the two types of coastal dynamics ($p < 0.001$). Specifically, positive and significant standardised C-scores were found for meta-stable sites (C-score: 6.01; $p < 0.001$) and positive, yet non-significant values for transgressive sites (C-score: 1.68; $p > 0.05$). These results suggest the prevalence of species segregation in meta-stable sites, most likely driven by the diversity of niches and thus species sorting across well-developed EF and FD habitats. This segregation pattern is however modified in disturbed transgressive sites, where the collapse of EF habitats and the alteration of FD habitats due to erosion processes result in a more homogeneous community structure (Fig. 3.21; Honrado *et al.,* 2010).

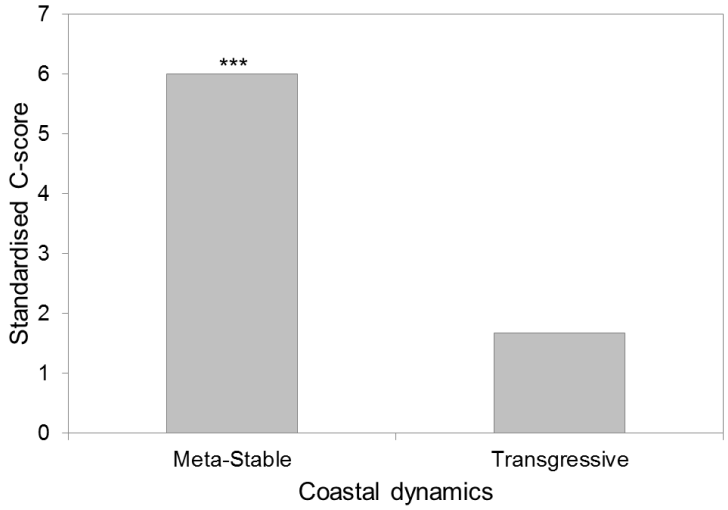

Fig. 3.21 - Standardised C-scores calculated for plots from meta-stable and transgressive sites. Statistical significance: ***, $p < 0.01$.

3.5.2. Patterns for CSR plant strategies under contrasting coastal dynamics

Differences in species richness between meta-stable and transgressive sites were found to be non-significant for most CSR strategies ($p < 0.05$; Fig. 3.22). An exception was found for the values of species richness of the SR strategy (Fig. 3.22). These **stress-tolerant ruderal plants** may be severely affected by overwash and aeolian sand deposition (Costa, 1991; Costa *et al.*, 1996; Hesp, 1991). In fact, this halonitrophilous pioneer vegetation dominated by *Honckenya peploides* and *Cakile maritima* ssp. *integrifolia* is found, not only in open sand across the upper beach, but also in EF habitats (Lomba *et al.,* 2008; Acosta *et al.,* 2009; Fenu *et al.*, 2013a,b), which are severely affected by transgressive dynamics (Honrado *et al.*, 2010).

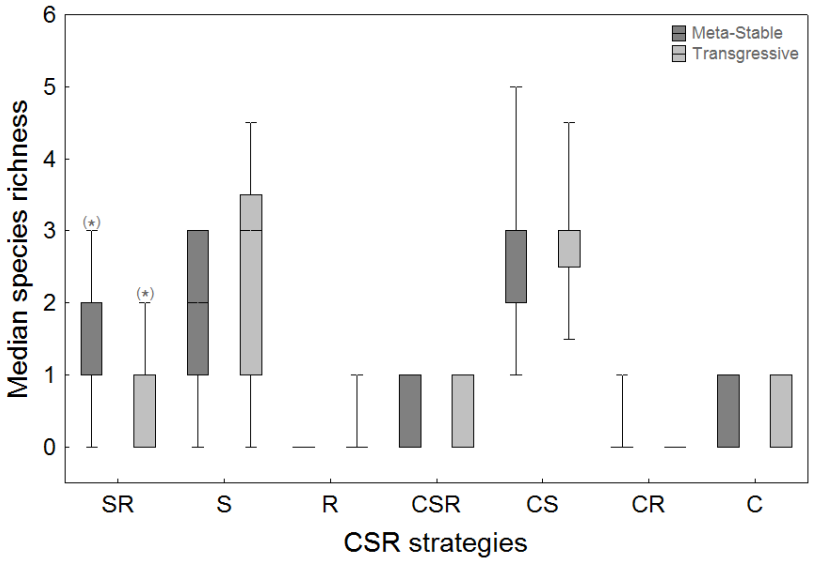

Fig. 3.22 - Median values of species richness considering the ensemble of plots from meta-stable and transgressive sites for CSR plant strategies; (*) stands for statistically significant differences ($p < 0.05$) according to Mann-Whitney tests.

For the patterns of **species composition**, the only significant difference between meta-stable and transgressive plots was observed for the S ($R = 0.15$; $p < 0.001$) and the SR ($R = 0.04$; $p < 0.05$) strategies. In fact, the projection of strategies in the ordination space (Fig. 3.23) suggests that species from the S strategy are more dominant in meta-stable plots than in transgressive plots. Contrastingly, species with an R strategy (both R and SR species) seem to be more predominant in transgressive plots (Fig. 3.23). Thus, in meta-stable sites, where the effect of stress gradients is more prominent, there is a higher incidence of stress-tolerant species, in contrast with sites where the effect of disturbance is likely more pronounced (transgressive sites), allowing ruderal plants to become more abundant (Grime, 1974, 2001; Michalet *et al.,* 2014).

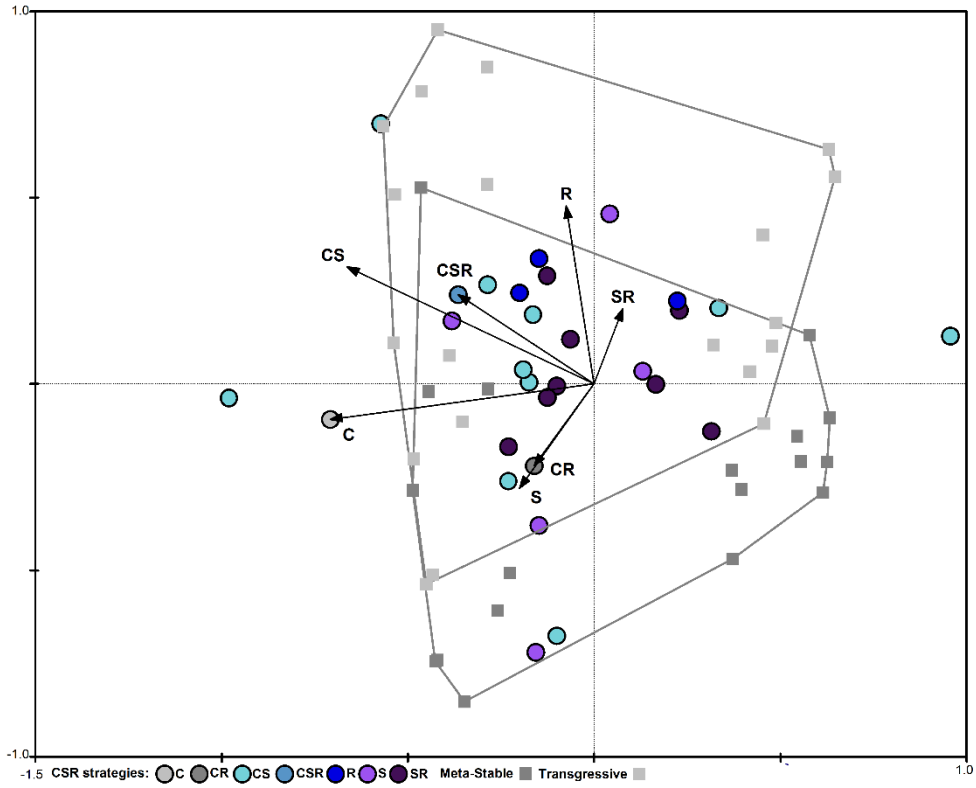

Fig. 3.23 - Principal Component Analysis plot (PCA1/PCA2) based on species composition across plots from meta-stable and transgressive sites (represented by distinct symbols and enclosed by the drawn polygons). Each species in the plot is represented by a circle with a distinct color according to its CSR strategy. The abundance of each CSR strategy is also represented by arrows.

Differences in **co-occurrence patterns** of each CSR strategy were found to be non-significant across types of coastal dynamics (Fig. 3.24). Exceptions were found for the CS ($p < 0.001$) and the S ($p < 0.001$) strategies, which differed between the two types of coastal dynamics. In meta-stable sites**,** the CS and S strategies exhibited a significant **aggregation of species** (in both cases: C-score = 2.09; $p < 0.05$; Fig. 3.24), suggesting the effect of positive environmental filtering on species that are strongly adapted to the mobile dune environment (Gallego-Fernández & Martínez, 2011; Ciccarelli, 2015).

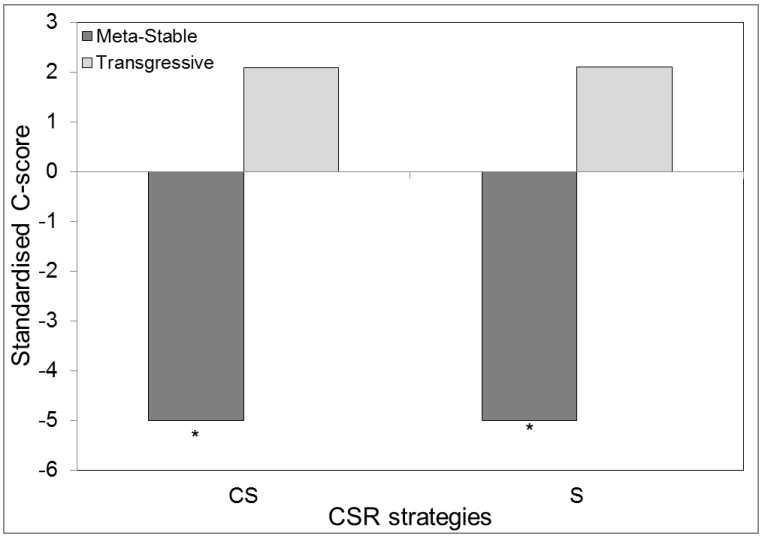

Fig. 3.24 – Significant differences for standardised C- scores for the CS and S strategies across plots from meta-stable and transgressive sites. Statistical significance: *, $p < 0.05$.

3.5.3. Patterns for dune plant functional types under contrasting coastal dynamics

Regarding the median values of **species richness** for each plant functional type, only non-significant values were found between transgressive and meta-stable sites, with Type III specialists as the dominant functional type under both types of coastal dynamics (Fig. 3.25).

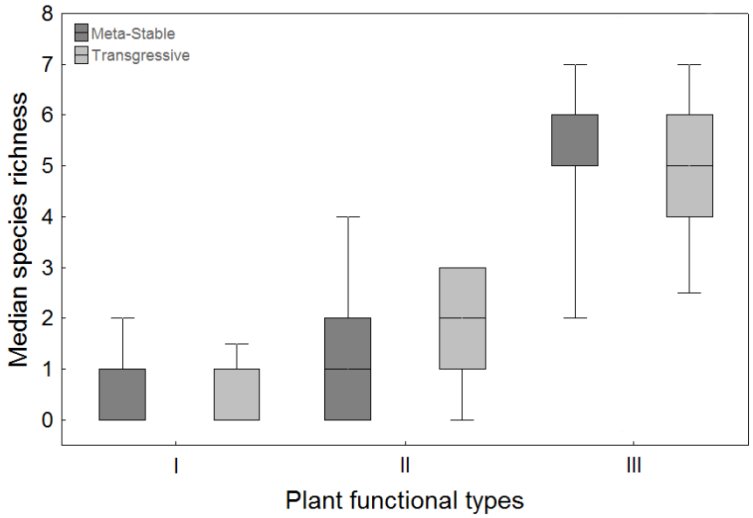

Fig. 3.25 - Median values of species richness considering the ensemble of plots from meta-stable and transgressive sites plant functional types.

However, when focusing on **species composition**, only Type II species showed significant differences between meta-stable and transgressive sites (R = 0.09; p < 0.05). As reported before (García-Mora *et al.*, 1999; see Fig. 1.6), the projection of species in the PCA plot suggests a higher affinity of Type I and II species with transgressive plots. Type III species, in contrast, have a higher expression on meta-stable plots (Fig. 3.26), in agreement with results for S strategists described above. These results, together with those obtained for species richness suggest important changes in plant diversity for the functional types, likely due to the fact that these include taxa with analogous ecological functions (da Silva *et al.,* 2008; Gallego-Fernández & Martínez, 2011).

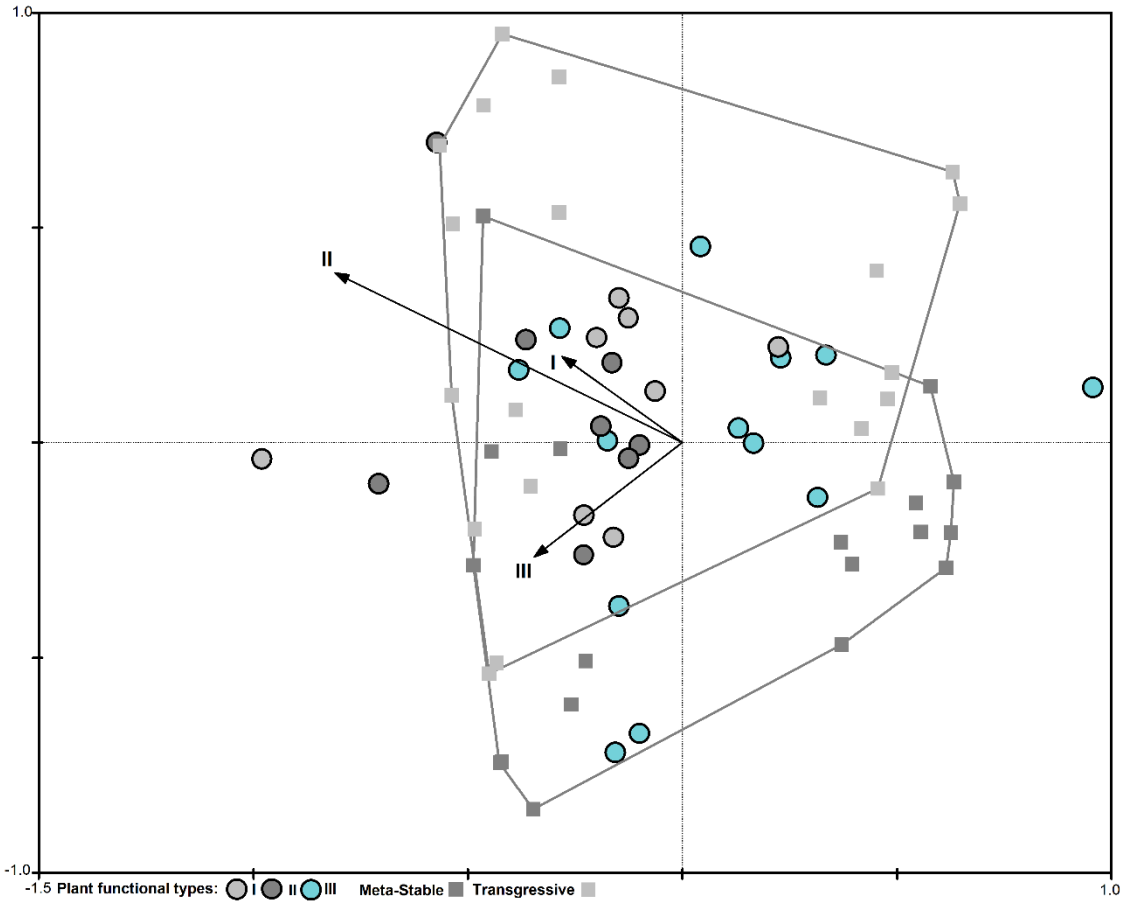

Fig. 3.26 – Principal Component Analysis plot (PCA1/PCA2) based on species composition across plots from meta-stable and transgressive sites (represented by distinct symbols and enclosed by the drawn polygons). Each species in the plot is represented by distinct colors according to their plant functional type. The abundance of each plant functional type is also represented by arrows.

Finally, when focusing on **co-occurrence patterns** (Fig. 3.27), both Type II ($p < 0.001$) and Type III ($p < 0.001$) species showed significant differences between the C-score values obtained for meta-stable and transgressive sites. Despite the fact that co-occurrence analysis within each type of coastal dynamics showed non-significant values, some aggregation of Type II (C-score = -0.41; $p > 0.05$) species and some segregation of Type III (C-score = 1.26; $p > 0.05$) species were observed in meta-stable sites. In transgressive sites, a tendency for species segregation were observed for both Type II (C-score = 0.55; $p > 0.05$) and Type III (C-score = 1.52; $p < 0.05$) species. Accordingly, a transition from aggregated patterns of Type II species in meta-stable sites to segregated patterns in transgressive ones was observed. These results, together with the ones for species composition, suggest that Type II species may be more greatly impacted by overwashing under transgressive conditions, leading to species spatial segregation both within and among sites (Martínez *et al.*, 2006; Carvalho *et al.,* 2012).

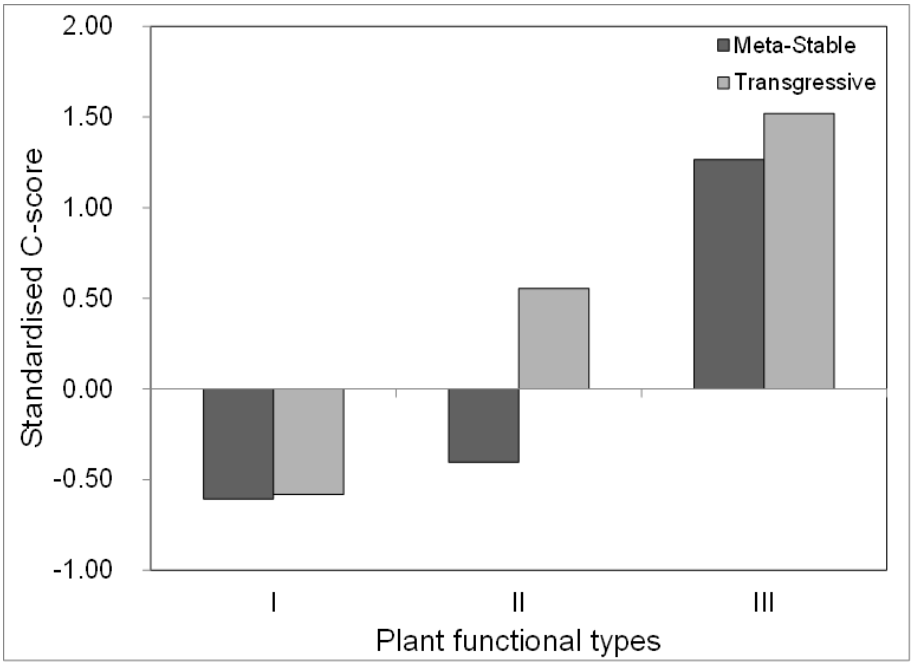

Fig. 3.27 - Standardised C-scores calculated for each plant functional types in plots from meta-stable and transgressive sites.

4. Integrative discussion and conclusions

In this final chapter, the main findings reported in chapter 3 are combined and discussed under the proposed research objectives and questions (outlined in section 1.4). More specifically, this chapter provides an **integrative discussion** of those results that most highlight the usefulness of community ecology theory to predict responses of dune ecosystems (and particularly of their plant communities) to environmental gradients and to changes in those gradients.

The chapter includes **two main sections**. The first section (4.1) presents an integrative overview and discussion of the core results, following the brief topic-by-topic discussion provided in chapter 3. In a second section (4.2), the overarching conclusions of this study are presented in line with the research questions raised in section 1.4, and perspectives are outlined for future research aiming to further develop this approach and test it in a practical context of coastal change assessment and monitoring.

4.1. Summary and integrative discussion of the main findings

This section discusses the core results of the research developed for the thesis under a theoretical, community-based approach. An **integrative discussion** is done of the diversity and co-occurrence patterns in the whole dune plant community, considering the total species pool as well as plant strategies and functional types. These patterns are discussed considering not only the underlying regional and local environmental gradients, but also the community-level effects of changes in prevailing coastal dynamics.

4.1.1. Plant community structure along local dune gradients

Along the sea-inland gradient, **dune plant diversity (species richness, evenness and abundance) exhibited a humped-back pattern**, translated in the highest diversity values in habitats located at the centre of the gradient and the lowest values towards both ends of the gradient (see Figures 3.1 and 3.2). This pattern seems to follow the humped-back model of species richness and biomass production (Grime 1973, 2001; Al-Mufti *et al.*, 1977; Forey *et al.*, 2009, 2010; Pierce, 2014), which predicts the highest taxonomic richness at intermediate conditions of biomass production and of its limiting factors, including disturbance and stress (Pierce, 2014). Also, these results seem to be in line with the stress-gradient hypothesis (SGH; Bertness & Callaway, 1994, Michalet *et al.*, 2015a,b), which relates intermediate levels of abiotic severity with the highest values of species diversity (Grime, 2001; Isermann, 2011) and with an increase in facilitative interactions (Michalet *et al.*, 2015a). Along the local dune gradient, the peculiar combination of stress and disturbance conditions of interior dunes (located at the centre of the gradient) can promote environmental diversity at finer scales (Provoost *et al.*, 2011; Gratani *et al.*, 2013). Under such fine-scale heterogeneity of conditions, more species can find suitable conditions and dune plants may expand their realized niches (Bruno *et al.*, 2003; Michalet *et al.,* 2006; Forey *et al.*, 2010), resulting in the occurrence of species-rich vegetation mosaics (Levin *et al.*, 2008; Pintó *et al.*, 2014).

This humped-back response was **more evident for (semi-)ruderal strategists with no, or only moderate, specific adaptations to the dune environment** (i.e. SR, CR and Type I species; see figures 3.4 and 3.6). These plants seem to respond positively to the intermediate environmental conditions and highest niche diversity at the middle of the gradient (Grime, 1977; García-Mora *et al.*, 1999, Grime, 2001; García-Mora *et al.*, 2000). Here they may benefit from the moderate conditions of stress and disturbance that characterize interior dune habitats, as well as of the niche diversity resulting from such fine-scale environmental heterogeneity (Grime, 1974, 1984; Grime *et al.*, 2007; Isermann, 2011; Nylén *et al.*, 2013). This is not the case in other dune habitats with more stable and uniform abiotic conditions, i.e., landward dunes colonized by scrub or woodland (Dolman *et al.*, 2010; Ciccarelli *et al.*, 2012; Tobias, 2014), where species with a stress-tolerant (S) and especially a competitor (C) component become more common and even dominant (Grime, 2001; Jentsch & Beyschlag, 2003; Bossuyt *et al.*, 2007).

At both ends of the local gradient, species diversity displayed the lowest values of plant diversity and the dominance of distinct plant strategies and functional types. **In the seaward, mobile dune habitats, species of functional Type III and with an S-component prevailed**, such as the dominant perennial grasses *Ammophila arenaria* and *Elymus boreali-atlanticus* (see Figures 3.8-3.10). The adaptive syndromes characteristic of these plant groups (including dispersal by sea-water and sand burial tolerance; García-Mora *et al.*, 1999, 2000) allow them to thrive under the harsh conditions of mobile dunes (Wilson & Sykes, 1999; Houle, 2002). Also, those harsh conditions act as severe filters for species with no or only moderate adaptations to the dune environment (Gallego-Fernandez & Martínez, 2011), and often even facilitative interactions with well-adapted nurse plants are not enough to allow those species to survive under the severe combination of stress and disturbance conditions that characterise highly energetic coastal areas (Toledo *et al.*, 2015).

Conversely, **the more landward habitats were dominated by widespread and/or generalist species, mostly with an R component and included in the Type II functional type**, such as *Vulpia alopecuros*, *Corynephorus canescens*, *Ulex europaeus* ssp. *latebracteatus* or *Cistus salvifolius* (Figures 3.8-3.10). These species are well adapted to prevail under less stressful conditions (Grime, 1977; García-Mora *et al*, 1999; Grime, 2001) but still with some level of disturbance due to sand blowing

from the seaward dunes (Dodd, 2013) or to anthropogenic perturbations (Grunewald, 2006). Dominance by one or few species was also found to be more pronounced here than in interior dune habitats (see Fig. 3.2), which may contribute to the low values of species richness observed in dry grassland and scrub habitats (Hillebrand *et al.*, 2008; Peyrat & Fichtner, 2011).

4.1.2. Co-occurrence of species, life strategies and functional groups in dune vegetation

Along the local dune gradient, species segregation was the predominant pattern at both the community and the whole dune system level, suggesting the prevalence of species sorting and competitive interactions along the sea-inland gradient. These results seem to disagree with the original SGH assumptions (Bertness & Callaway, 1994), in the sense that segregation was the predominant pattern, and significant aggregation could be expected but was not observed under severe conditions of mobile dunes (see Figure 3.11). Nonetheless, a general tendency for increasing species segregation was observed along with a decrease of environmental severity (i.e., in a sea-inland direction). As described in Vaz *et al.* (2015), the predominance of segregation suggests that competition and especially species sorting along gradients are the key processes in dune community assembly and dynamics. Moreover, the results reported in chapter 3 suggest that facilitative interactions may be infrequent in coastal dunes and restricted to few habitat types along the local gradient.

A tendency for species aggregation was perceived in embryonic foredune and interior dune habitats. As described before, in embryonic foredunes only habitat specialists (Type III) and stress-tolerant plants (S strategists) were found to dominate. According to Maestre *et al.* (2009), under high levels of non-resource severity (which is the case in embryonic foredunes due to tidal nutrient input; Labuz & Grunewald, 2007; Labuz, 2013), aggregation among stress-tolerant species can prevail due to the local improvement of environmental conditions by benefactor plants (Michalet *et al.,* 2006; Holmgren & Scheffer, 2010). Contrastingly, in foredunes, more stable conditions prevail at fine scales, e.g. due to soil stabilisation under *Ammophila arenaria* tussocks (Forey *et al.,* 2009, 2010). This allows progressive foredune colonisation by competitive species (i.e., those with a C component and a Type II strategy) from

landward positions, promoting local species diversity (e.g. Wilson & Gitay, 1995; Tilman *et al.,* 1997; Michalet *et al.,* 2006) and a shift from aggregation to segregation likely due to increased competition and fine-scale species sorting along the steep local gradient (Holmgren & Scheffer, 2010; Vaz *et al.*, 2015). In interior dunes, where SR, CR and Type I species prevail, species aggregation could be explained by the combination of intermediate levels of environmental stress and disturbance, promoting complex variations of environmental conditions at fine scales, where benefactor plants may allow other stress-tolerant or stress-intolerant species to expand their realised niches (Michalet *et al.*, 2006, 2010; Holmgren & Scheffer, 2010; Piston *et al.*, 2015).

These patterns were **further explored by interpreting pair-wise and intra-group/strategy co-occurrence patterns**. The observed patterns among species within strategies with an S-component (the prevailing component in the dune species pool) were inverse (but consistent) with the ones obtained for the whole community (see Figures 3.11 and 3.14). In seaward habitats, there was a dominance of aggregation among and between plant functional types (see Fig. 3.17), suggesting the occurrence of facilitative interactions under harsh conditions (Michalet *et al.*, 2006, 2015a), especially sand burial that may even significantly filter stress-tolerant plants (Franks & Peterson 2003; Maestre *et al.*, 2009) and dune specialists (Type II and Type III; García-Mora *et al.*, 1999). In ID habitats, species with SR and S strategies exhibited the prevalence of inter-specific segregation. This was also observed for species within the Type I and II functional types (see Fig. 17). These results may relate with competition for similar resources among species with partially similar strategies, combined with fine-scale sorting of species with partially distinct resource needs and tolerances (Reich *et al.*, 2003; Kumordzi *et al.*, 2015). Those same processes may also be responsible for the segregation between CS and S species, and between functional Types I-II and II-III, observed in the innermost habitats. Overall, these results are consistent with the expected occurrence of stronger negative interactions among species within functional groups than among species belonging to distinct groups (Grime, 2006; Gross *et al.*, 2007; Adler *et al.*, 2013).

4.1.3. Community-level responses of mobile dune vegetation to changes in coastal dynamics

The typical zonation of plant species and vegetation along the local gradient is modified by a shift in coastal dynamics (Honrado *et al.,* 2010). In the seaward-most vegetation, biomass is often totally or partially destroyed in the process (Rodwell *et al.*, 2000; Honrado *et al.*, 2010; Martins *et al.*, 2013), thus causing a significant decrease in embryonic foredune characteristic species (e.g. *Calystegia soldanella*), as evidenced by plant composition analyses (see Figure 3.20). Nonetheless, overall plant diversity in mobile dunes does not seem to suffer significant changes following a shift to transgressive coastal dynamics. Still, there was a higher homogeneity for species diversity in eroding sites than in meta-stable sites (see Fig. 3.19). Honrado *et al.* (2010) had already reported lower species turnover values along the local gradient in transgressive sites compared with meta-stable dune systems. Overall, this suggests that the increased disturbance (and stress) in transgressive dunes will have a homogenizing effect on species composition in mobile dune vegetation (Honrado *et al.*, 2010), both within and between individual communities. Biotic homogenization processes act by selecting those species that are better adapted to ecological changes, which then reflects on community compositional patterns (Olden & Poff, 2003; Olden & Rooney, 2006; Devictor *et al.*, 2010).

The analysis of co-occurrence patterns revealed **a shift from species segregation in meta-stable sites to random patterns in transgressive sites** (see Figure 3.21). On the one hand, this highlights the importance of species sorting as a key process underlying community assembly and vegetation zonation along the steep local environmental gradients of meta-stable mobile dunes (Honrado *et al.*, 2010). Moreover, this change in co-occurrence patterns highlights the disruption of stress gradients, biotic interactions and vegetation zonation due to the more intense and/or frequent disturbances, resulting in more random spatial structures of species assemblages in transgressive sites (Lomba *et al.*, 2008; Acosta *et al.*, 2009; Honrado *et al.* 2010).

In general, **no significant differences were observed in species diversity for CSR strategies between the two types of coastal dynamics**. Still, stress-tolerant ruderals (SR) suffered a reduction of species richness with the shift to transgressive dynamics (see Figure 3.22). However, the SR strategists that could cope with erosive dynamics (as well as ruderals) became relatively more abundant in the assemblages resulting from transgressive dynamics (see Figure 3.23). Conversely, stress-tolerant (S) species and competitive ruderals (CR) were more predominant in meta-stable dunes than in transgressive plots, confirming previous reports for S-strategists in the study region (Macedo *et al.,* 2010) and suggesting facilitation of CR plants by foredune specialists (Maestre *et al.*, 2009). Overall, meta-stable sites, which are mainly structured by stress gradients (Grime, 2001; Michalet *et al.*, 2014), usually host more plants with stress-tolerant and competitive strategies, in comparison with transgressive sites (more affected by disturbance), where ruderal plants become more frequent (Grime, 1974, 2001; Michalet *et al.*, 2010; see Fig. 3.23). Differences in co-occurrence patterns of each CSR strategy were predominantly non-significant under the two types of dynamics. Exceptions were found for the CS and the S strategies, which exhibited a significant aggregation of species in meta-stable sites, but random patterns in transgressive sites (see Figure 3.27), in line with the results obtained for the total species pool.

Regarding plant functional types, **Type II species were the ones responding more significantly to changes in coastal dynamics**, showing a higher diversity and abundance under transgressive conditions compared to meta-stable sites (see Figure 3.26). This is consistent with the combination of stress and disturbance conditions under transgressive dynamics, which is expected to favour the prevalence of species with moderate adaptation to stress and disturbance rather than pure stress specialists (García-Mora *et al.*, 1999; Carboni *et al.*, 2010; Gallego-Fernández & Martínez, 2011). A tendency for higher prevalence of Type III species in meta-stable dunes and of Type I species in transgressive habitats was also perceived (see Figure 3.26). Thus, the modified environmental conditions in transgressive mobile dunes can promote the replacement, to some extent, of species tolerant to sand burial and salinity (i.e. species of functional Type III) by plants from the other two functional groups (García-Mora *et al.*, 2000).

4.1.4. Interactions between local and regional gradients

Along the regional climatic gradient, there was a general trend for **community-level species diversity to decrease from north to south**, with the lowest values observed at the Mediterranean sites (see Figure 3.3). The decrease of precipitation and the increase of temperature observed along this direction (Costa, 2000, 2009; Loidi *et al.,* 2007) may promote harsher environmental conditions, decreasing the effectiveness of facilitative interactions (Michalet *et al.,* 2006; Holmgren & Scheffer, 2010) and reducing the diversity of species in the dune systems (Harpole & Tilman, 2007; Lu *et al.*, 2014). In fact, a gradual replacement of typical Atlantic species by Mediterranean species was observed along the regional, climatic gradient (see Figure 3.8), with stress-tolerant ruderals, a group of specialized species showing higher abundances in the southernmost sites (see Figure 3.12). Under more severe conditions at the regional scale, a loss of unspecialized plants from dune systems seems to be promoted, while specialized plants become more prevalent (Maestre & Cortina, 2004; Brooker *et al.,* 2008; Honrado *et al.,* 2010), suggesting some influence of regional heterogeneity and the prevalence of multi-scale co-occurrence patterns (Zeleny *et al.*, 2010; Fidalgo *et al.*, 2014; Redon *et al.*, 2014).

No clear patterns of species co-occurrence could be perceived along the regional climatic gradient. As discussed before, species segregation was the prevailing pattern at each site, suggesting competition and species sorting as main processes for community structure within sites (Brunbjerg *et al.*, 2012b; Vaz *et al.*, 2015). In fact, co-occurrence patterns observed at the community level seemed to be related to the local sorting of, and interactions between strategies and functional types at each site. The prevalence of segregation between species with similar strategies or functional types, as well as the aggregation between pairs of distinct CSR strategies, strongly suggests that **biotic interactions and species sorting at local scales are the main processes driving the spatial structure of communities** (Forey *et al.*, 2008; Maltez-Mouro *et al.*, 2010; Brunbjerg *et al.*, 2012a,b), with only a minor role played by regional gradients. Community structure in the studied mobile dunes is thus primarily driven by the local, sea-inland gradient, and therefore also by the coastal dynamics prevailing at each site, in line with other studies conducted in the study area (Lomba *et al.*, 2008; Honrado *et al.*, 2010; Fidalgo *et al.*, 2014) and elsewhere (Provost *et al.*, 2004; Forey *et al.,* 2008; Brunbjerg *et al.,* 2012a,b).

No significant influence of the regional climatic gradient was perceived when evaluating responses of mobile dune vegetation to shifts in coastal dynamics. This could partially be attributed to the fact that the study focused on a specific part of the dune system (mobile dunes along a relative short biogeographic gradient), which allowed capturing a rather stable species composition in these habitat types (Forey *et al.*, 2008; Kim *et al.*, 2014; Vaz *et al.,* 2015), thus masking any potential effect of the regional gradient. Nonetheless, Fidalgo *et al.* (2014) were able to identify interactions between biogeographic location and local conditions when analysing eco-physiological responses of dune plants to changes in coastal dynamics along the same study area. Based on those findings, the authors advocated that such interactions among processes operating at different scales should be clearly elucidated before applying the resulting framework in the assessment and monitoring of prevailing coastal dynamics. Here, we could successfully discriminate meta-stable from transgressive sites based on selected features of community structure in mobile dunes (see Figures 3.22-3.27), even if the regional gradient did influence some features of community structure when the whole set of habitats along the dune gradient was analysed.

4.2. Conclusions and future perspectives

In section 4.1, an integrative discussion of the main results was provided, connecting functional plant ecology with co-occurrence and biotic interactions to assess plant community structure and dynamics. In this final section we outline the overarching conclusions of the study, in line with the research questions defined in chapter 1, and identify some promising avenues for future research. Even if the research design may have suffered from a few caveats (small number of sites, relatively narrow biogeographic gradient), we were able to draw some important conclusions that may contribute to advance the state-of-knowledge and to outline future research directions.

4.2.1. Overarching conclusions

Our first research question was: What patterns of species diversity and co-occurrence can be observed in plant communities along the local dune gradient?

We were able to conclude that:

- Overall, **dune plant species diversity exhibits a humped-back pattern along the local dune gradient**, with the highest values recorded in the middle of the gradient, in agreement with the various combinations of stress and disturbance and with predictions of core ecological theory.

- **Along the local dune gradient there is a clear vegetation zonation**, with spatial segregation of plant species typical of seaward habitats from those of landward habitats, mainly determined by environmental sorting of species with specific resource needs and ecological preferences.

- **Species segregation is the predominant pattern of co-occurrence within and between habitat types**, suggesting an overall prevailing role of species sorting and competition over facilitation in the assembly and dynamics of dune plant communities.

Concerning our second research question: How are plant strategies and functional types distributed along the local dune gradient?

We obtained evidence to support the following conclusions:

- In general, **plant species of functional Type III and of strategies with an S-component prevail in the seaward, mobile dune habitats**, confirming the adaptation and ability of those species to thrive under severe environmental conditions.

- When moving landward from the beach along the local gradient, **a gradual replacement of strategies with an S-component by those with an R-component** occurs, highlighting the role of environmental stress and resource availability in locally sorting species and thereby structuring plant communities.

- Concurrently, **Type III species were gradually replaced by Type I and II species in a landward direction**, confirming that the harsh conditions in the dune system act as effective filters for species with no or moderate adaptations to the combined effect of stress factors and disturbances that characterise coastal dunes.

For our third research question: How are the observed patterns of species diversity and co-occurrence mediated by plant strategies and functional types?

We were able to conclude that:

- **The humped-back response of plant species diversity was more evident for (semi-)ruderal strategists** with no specific adaptations to the dune environment (i.e. SR, CR and Type I species), consistently with the moderate conditions of stress and disturbance that characterize, with various small-scale combinations, interior dune habitats.

- The predominance of species segregation across plant strategies and functional types confirms a key role of species sorting according to stress-tolerance and also of competitive interactions, and confirms that **facilitation may, in fact, not be**

so frequent in coastal dunes (due to the extreme levels of environmental severity), as well as ineffective and restricted to specific habitat types.

- A tendency for species aggregation was perceived in the embryonic foredune and interior dune habitats, where **localized facilitation and fine-scale heterogeneity of conditions may enable species and strategies that are less adapted** to the dune environment.

Finally, regarding our fourth research question: Is this theoretical approach, based on co-occurrence patterns and functional profiles of species assemblages, useful to identify ecological changes induced by shifts in prevailing coastal dynamics?

We found evidence to conclude that:

- **Plant diversity in mobile dunes does not seem to suffer significant changes following a shift to transgressive coastal dynamics**, suggesting that this component of community structure may not be an effective indicator of ecological change driven by modifications in coastal dynamics.

- Different plant strategies and functional profiles exhibited contrasting co-occurrence patterns under the two types of coastal dynamics, highlighting that **interactions between abiotic filters, species traits, and biotic factors will drive vegetation responses to shifts in coastal dynamics**.

- The typical zonation of species, plant strategies and functional types in mobile dune communities along the local gradient was changed under transgressive coastal dynamics, suggesting that **indicator selection for ecological assessment and monitoring should focus on the functional profile of plant communities**.

- **No significant regional influence was observed in local responses of mobile dune plant communities to changes in coastal dynamics**. Still, some interactions between local and regional processes were perceived for the whole set of dune habitats, confirming previous reports. Those interactions should be carefully

elucidated before the actual application of our findings in coastal assessment and monitoring.

4.2.2. Avenues for future research

From the many possible research avenues, five can be highlighted due to their potential contribution to build upon our results and advance the application of ecological theory in the assessment and anticipation of ecological changes in coastal zones:

- *Functional ecology:* A promising line of research would involve refining the analysis of functional profiles of species assemblages, by complementing the analysis based on plant strategies and functional groups with assessments based on the **distribution of traits** (Bernhardt-Römermann *et al.*, 2011; Sterk *et al.*, 2013). The emphasis should be on those traits that are more closely related with adaptation to the dune environment, and especially with dune resilience under environmental change.

- *Spatial ecology:* Analysing the **fine spatial patterns** of species, life strategies, functional groups and/or traits would add significantly to the assessment of co-occurrence, species sorting and biotic interactions (Dullinger *et al.,* 2007; Maltez-Mouro *et al.,* 2010; Waugh & Aarssen, 2011). The recent advances in the use of unmanned airborne vehicles (UAVs, or “drones”) for ecological and environmental assessment opens a new avenue for exploring all the potential of very-high spatial resolution imagery (Anderson & Gaston 2013), including in coastal areas (Mancini *et al.,* 2013; Calviño-Cancela *et al.,* 2014; Chikhradze *et al.*, 2015; Gonçalves & Henriques, 2015). The potential of very-high resolution imagery has recently been tested, with promising results, in the exploratory analysis of spatial co-occurrence between plant species in coastal dune habitats (Gomes, 2012).

- *Experimental ecology:* Experimental approaches to analyse community assembly and dynamics under controlled conditions have been a fruitful field in ecological research (Tilman *et al.*, 1997; Dormann, 2008; Castanho *et al.*, 2015b). Experimental designs can be used to **simulate focal gradients or processes**, as well as the effects of changes in environmental conditions on community structure and

functional profile, and downstream on ecosystem functioning and properties such as productivity or resilience. The focus in this case should be on analysing quantitative variations of traits, types and intensity of biotic interactions, and the resulting community structure along quantified or simulated gradients of dune stress factors (Mori *et al.*, 2014; Laughlin *et al.*, 2015)

- *Long-term research and monitoring:* Long-term ecosystem research (LTER) has emerged as an attempt to analyse processes operating over long time frames as well as their effects on biological or ecological attributes of ecosystems (Turner *et al.* 2003). Applying an **LTER-like approach** to coastal dunes, based on frequent surveillance of core ecological indicators, could allow a "(near-)real-time" analysis of species- and community-level responses to gradual or abrupt changes in the prevailing coastal dynamics as well as to discrete catastrophic events, while at the same yielding data time-series against which the general model described in this thesis could be validated.

- *Resilience and ecosystem services:* The more refined analyses of spatially- and temporally-explicit and multi-scalar processes, allowed by an LTER-like approach, could offer a significant contribution for identifying and anticipating **critical transitions** towards new, possibly undesired system states (Scheffer *et al.,* 2012). An integrative approach to community dynamics, identifying tipping points in species interactions and the functional profiles of species assemblages, would allow assessing and promoting dune ecosystem resilience to shifts in coastal dynamics, stimulating the provision of ecosystem services and thereby minimizing coastal hazards (Lozoya *et al.*, 2011).

5. References

Acosta A, Carranza ML, Izzi CF. 2009. Combining land cover mapping of coastal dunes with vegetation analysis. *Applied Vegetation Science* 8(2): 133-138.

Acosta A, Stanisci A, Ercole S, Blasi C. 2003. Sandy coastal landscape of the Lazio region (Central Italy). *Phytocoenologia* 33(4): 715-726.

Adler PB, Ellner SP, Levine JM. 2010. Coexistence of perennial plants: an embarrassment of niches. *Ecological Letters* 13(8): 1019-1029.

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJ. 2013. Trait-based tests of coexistence mechanisms. *Ecological Letters* 16(10): 1294-1306.

ALFA. 2004. Tipos de Habitat Naturais e Semi-Naturais do Anexo I da Directiva 92/43/CEE (Portugal continental): Fichas de Caracterização Ecológica e de Gestão para o Plano Sectorial da Rede Natura 2000. Lisboa: ICNF - Instituto da Conservação da Natureza e das Florestas.

Allouche O, Kalyuzhny M, Moreno-Rueda G, Pizarro M, Kadmon R. 2012. Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences* 109(43): 17495-17500.

Al-Mufti MM, Sydes CL, Furness SB, Grime JP, Band SR. 1977. A Quantitative Analysis of Shoot Phenology and Dominance in Herbaceous Vegetation. *Journal of Ecology* 65(3): 759.

Álvarez-Molina LL, Martínez ML, Pérez-Maqueo O, Gallego-Fernández JB, Flores P. 2012. Richness, diversity, and rate of primary succession over 20 year in tropical coastal dunes. *Plant Ecology* 213(10): 1597-1608.

Amici V, Geri F, Csontos P, Neteler M, Rocchini D. 2010. Fuzzy and Boolean Forest Membership: On the Actual Separability of Land Cover Classes. *Applied Ecology and Environmental Research* 8: 39–50.

ANCORIM 2012. ANCORIM - Atlantic Network for Coastal Risk Management. http://ancorim.aquitaine.fr/: Regional Council of Aquitaine, France.

Anderson K, Gaston KJ. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Frontiers in Ecology and the Environment* 11(3): 138-146.

Andrade C, Pires HO, Taborda R, Freitas MDC. 2007. Projecting future changes in wave climate and coastal response in Portugal by the end of the 21st century. *Journal of Coastal Research* SI 50(50): 263-257.

Anthony EJ, Ruz M-H, Vanhée S. 2009. Aeolian sand transport over complex intertidal bar-trough beach topography. *Geomorphology* 105(1-2): 95-105.

Ariza C, Tielbörger K. 2012. Biomass explains the intensity of facilitative – not competitive – interactions: three intraspecific tests with annuals. *Web Ecology* **12**: 49–55.

Armas C, Kikvidze Z, Pugnaire FI. 2009. Abiotic conditions, neighbour interactions, and the distribution of Stipa tenacissima in a semiarid mountain range. *Journal of Arid Environments* 73(12): 1084-1089.

Armas C, Pugnaire FI. 2009. Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system. *Journal of Vegetation Science* 20(3): 535-546.

Arteaga C, Juan de Sanjosé J, Serrano E. 2008. Terrestrial photogrammetric techniques applied to the control of a parabolic dune in the Liencres dune system, Cantabria (Spain). *Earth Surface Processes and Landforms* 33(14): 2201-2210.

Baas ACW, Nield JM. 2010. Ecogeomorphic state variables and phase-space construction for quantifying the evolution of vegetated aeolian landscapes. *Earth Surface Processes and Landforms* 35(6): 717-735.

Balestri E, Lardicci C. 2013. The impact of physical disturbance and increased sand burial on clonal growth and spatial colonization of Sporobolus virginicus in a coastal dune system. *PLoS One* 8(8): e72598.

Barbosa LM, Dominguez JML. 2004. Coastal dune fields at the São Francisco River strandplain, northeastern Brazil: morphology and environmental controls. *Earth Surface Processes and Landforms* 29(4): 443-456.

Barbour MG, Jong TMD, Pavlik BM 1985. Marine beach and dune plant communities. In: Brian F. Chabot HAM ed. *Physiological Ecology of North American Plant Communities*: Springer Netherlands, 296-322.

Barrett-Mold C, Burningham H. 2010. Contrasting ecology of prograding coastal dunes on the northwest coast of Ireland. *Journal of Coastal Conservation* 14(2): 81-90.

Bartels D, Sunkar R. 2005. Drought and Salt Tolerance in Plants. *Critical Reviews in Plant Sciences* 24(1): 23-58.

Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19(1): 134-143.

Bermúdez R, Retuerto R. 2013. Living the difference: alternative functional designs in five perennial herbs coexisting in a coastal dune environment. *Functional Plant Biology* 40(11): 1187.

Bermudez R, Retuerto R. 2014. Together but different: co-occurring dune plant species differ in their water- and nitrogen-use strategies. *Oecologia* 174(3): 651-663.

Bermúdez Villanueva R. 2013. *Spatio-temporal variability in ecophysiological determinants of performance: a study in perennia herbs of coastal foredunes.*PhD Thesis, University of Santiago de Compostela, Santiago de Compostela, Spain.

Bernhardt-Römermann M, Gray A, Vanbergen AJ, Bergès L, Bohner A, Brooker RW, De Bruyn L, De Cinti B, Dirnböck T, Grandin U, *et al.* 2011. Functional traits and local environment predict vegetation responses to disturbance: a pan-European multi-site experiment. *Journal of Ecology* 99(3): 777-787.

Bertness MD, Callaway R. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9(5): 191-193.

Biondi E. 2007. Thoughts on the ecology and syntaxonomy of some vegetation typologies of the Mediterranean coast. *Fitosociologia* 44(1): 3-10.

Bird E. 2008. *Coastal Geomorphology: An Introduction*. Chichester: John Wiley & Sons.

Biswas SR, Wagner HH. 2014. A temporal dimension to the stress gradient hypothesis for intraspecific interactions. *Oikos* 123(11): 1323-1330.

Bonsall MB, van der Meijden E, Crawley MJ. 2003. Contrasting dynamics in the same plant-herbivore interaction. *Proceedings of the National Academy of Sciences* 100(25): 14932-14936.

Bonte D, Criel P, Vanhoutte L, Van Thournout I, Maelfait JP. 2004. The importance of habitat productivity, stability and heterogeneity for spider species richness in coastal grey dunes along the North Sea and its implications for conservation. *Biodiversity and Conservation* 13(11): 2119-2134.

Borics G, Várbíró G, Padisák J. 2013. Disturbance and stress: different meanings in ecological dynamics? *Hydrobiologia* 711(1): 1-7.

Bornhofen S, Barot S, Lattaud C. 2011. The evolution of CSR life-history strategies in a plant model with explicit physiology and architecture. *Ecological Modelling* 222(1): 1-10.

Bossuyt B, Cosyns E, Hoffmann M. 2007. The role of soil seed banks in the restoration of dry acidic dune grassland after burning of Ulex europaeus scrub. *Applied Vegetation Science* 10(1): 131.

Bowker MA, Soliveres S, Maestre FT. 2010. Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *Journal of Ecology* 98(3): 551-560.

Brooker R 2010. Plant Communitites, Plant-Plant Interactions, and Climate Change. In: Pugnaire FI ed. *Positive Plant Interactions and Community Dynamics*. Boca Raton, Florida, USA: CRC Press, 99-123.

Brooker RW, Callaghan T V. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81: 196–207.

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, TielbÖRger K, Travis JMJ, Anthelme F, *et al.* 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96(1): 18-34.

Brown AC., McLachlan A. 2010. *The Ecology of Sandy Shores*: Elsevier Science.

Brunbjerg AK, Borchsenius F, Eiserhardt WL, Ejrnaes R, Svenning J-C, Prinzing A. 2012b. Disturbance drives phylogenetic community structure in coastal dune vegetation. *Journal of Vegetation Science* 23(6): 1082-1094.

Brunbjerg AK, Cavender-Bares J, Eiserhardt WL, Ejrnaes R, Aarssen LW, Buckley HL, Forey E, Jansen F, Kattge J, Lane C, *et al.* 2014a. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. *Journal of Plant Ecology* 7(2): 101-114.

Brunbjerg AK, Ejrnæs R, Svenning J-C. 2012a. Species sorting dominates plant metacommunity structure in coastal dunes. *Acta Oecologica* 39: 33-42.

Brunbjerg AK, Svenning J-C, Ejrnæs R. 2014b. Experimental evidence for disturbance as key to the conservation of dune grassland. *Biological Conservation* 174: 101-110.

Bunce RGH, Bogers MMB, Evans D, Halada L, Jongman RHG, Mucher CA, Bauch B, de Blust G, Parr TW, Olsvig-Whittaker L. 2013a. The significance of habitats as indicators of biodiversity and their links to species. *Ecological Indicators* 33: 19-25.

Bunce RGH, Bogers MMB, Evans D, Jongman RHG. 2012. Rule based system for in situ identification of Annex I habitats. Wageningen, The Netherlands: Alterra.

Bunce RGH, Bogers MMB, Evans D, Jongman RHG. 2013b. Field identification of habitats directive Annex I habitats as a major European biodiversity indicator. *Ecological Indicators* 33: 105-110.

Bunce RGH, Metzger MJ, Jongman RHG, Brandt J, de Blust G, Elena-Rossello R, Groom GB, Halada L, Hofer G, Howard DC, *et al.* 2007. A standardized procedure for surveillance and monitoring European habitats and provision of spatial data. *Landscape Ecology* 23(1): 11-25.

Bunce RGH, Roche P, Brgers MMB, Walczak M, de Blust G, Geijzendorffer IR, van den Borre J. 2010. Handbook for Surveillance and Monitoring of Habitats, Vegetation and Selected Species: Wageningen UR.

Bush DM, Neal WJ, Young RS, Pilkey OH. 1999. Utilization of geoindicators for rapid assessment of coastal-hazard risk and mitigation. *Ocean and Coastal Management* 42(8): 647-670.

Caccianiga M, Luzzaro A, Pierce S, Ceriani RM, Cerabolini B. 2006. The functional basis of a primary succession resolved by CSR classification. *Oikos* 112(1): 10-20.

Caldeira MC, Hector A, Loreau M, Pereira JS. 2005. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. *Oikos* 110(1): 115-123.

Callaway RM 2007. Positive Interactions and Community Organization. *Positive Interactions and Interdependence in Plant Communities*: Springer Netherlands, 295-333.

Callaway RM. 1995. Positive interactions among plants. *The Botanical Review* 61(4): 306-349.

Calvino-Cancela M, Mendez-Rial R, Reguera-Salgado J, Martin-Herrero J. 2014. Alien plant monitoring with ultralight airborne imaging spectroscopy. *PLoS One* 9(7): e102381.

Carboni M, Carranza ML, Acosta A. 2009. Assessing conservation status on coastal dunes: A multiscale approach. *Landscape and Urban Planning* 91(1): 17-25.

Carter R, Nordstrom K, Psuty N. 1990. The study of coastal dunes. Nordstrom, K and Psuty, N and Carter, B ed. Coastal dunes: form and process. John Wiley New York, 1–14.

Carvalho GS, Granja HM, Loureiro E, Henriques R. 2006. Late Pleistocene and Holocene environmental changes in the coastal zone of northwestern Portugal. *Journal of Quaternary Science* 21(8): 859-877.

Carvalho JC, Cardoso P, Crespo LC, Henriques S, Carvalho R, Gomes P. 2012. Determinants of spider species richness in coastal dunes along a gradient of mediterraneity. *Insect Conservation and Diversity* 5(2): 127-137.

Castanho C de T, Prado PI. 2014. Benefit of shading by nurse plant does not change along a stress gradient in a coastal dune. *PloS one* 9: e105082.

Castanho CT, Lortie CJ, Zaitchik B, Prado PI. 2015a. A meta-analysis of plant facilitation in coastal dune systems: responses, regions, and research gaps. *PeerJ* 3: e768.

Castanho CT, Oliveira AA, Prado PI, Acosta A. 2012. The importance of plant life form on spatial associations along a subtropical coastal dune gradient. *Journal of Vegetation Science* 23(5): 952-961.

Castanho CT, Oliveira AA, Prado PI. 2015b. Does extreme environmental severity promote plant facilitation? An experimental field test in a subtropical coastal dune. *Oecologia* 178(3): 855-866.

Castroviejo S. 1986-2015. *Flora Iberica 1-8, 10-15, 17-18, 21*. Madrid: Real Jardín Botánico, CSIC.

Cavieres L, Badano E 2010. Consequences of Facilitation of Species Diversity in Terrestrial Plant Communitites. In: Pugnaire FI ed. *Positive Plant Interactions and Community Dynamics*. Boca Raton, Florida, USA: CRC Press, 39-58.

Cavieres LA, Brooker RW, Butterfield BJ, Cook BJ, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Schob C, Xiao S, *et al.* 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters* 17(2): 193-202.

Chikhradze N, Henriques R, Elashvili M, Kirkitadze G, Janelidze Z, Bolashvili N, Lominadze G. 2015. Close Range Photogrammetry in the Survey of the Coastal Area Geoecological Conditions (on the Example of Portugal). *Earth* 4(5-1): 35-40.

Chozas S, Correia O, Porto M, Hortal J. 2015. Local and regional-scale factors drive xerophytic shrub community dynamics on Mediterranean stabilized dunes. *Plant and Soil* 391(1-2): 413-426.

Chytrý M, Otýpková Z. 2003. Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science* 14: 563–570.

Ciccarelli D, Bacaro G, Chiarucci A. 2012. Coastline Dune Vegetation Dynamics: Evidence of No Stability. *Folia Geobotanica* 47(3): 263-275.

Ciccarelli D, Forino LMC, Balestri M, Pagni AM. 2009. Leaf anatomical adaptations of Calystegia soldanella, Euphorbia paralias and Otanthus maritimus to the ecological conditions of coastal sand dune systems. *Caryologia* 62(2): 142-151.

Ciccarelli D. 2014. Mediterranean coastal sand dune vegetation: influence of natural and anthropogenic factors. *Environmental Management* 54(2): 194-204.

Ciccarelli D. 2015. Mediterranean coastal dune vegetation: Are disturbance and stress the key selective forces that drive the psammophilous succession? *Estuarine, Coastal and Shelf Science*. Doi:10.1016/j.ecss.2015.05.023

Clarke B, Stocker L, Coffey B, Leith P, Harvey N, Baldwin C, Baxter T, Bruekers G, Galano CD, Good M, *et al.* 2013. Enhancing the knowledge–governance interface: Coasts, climate and collaboration. *Ocean & Coastal Management* 86: 88-99.

Coomes DA, Rees M, Turnbull L, Ratcliffe S. 2002. On the mechanisms of coexistence among annual-plant species, using neighbourhood techniques and simulation models. *Plant Ecology* 163(1): 23-38.

Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79(1): 109-126.

Cornwell WK, Ackerly DD. 2010. A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology* 98(4): 814-821.

Cornwell WK, Schwilk LD, Ackerly DD. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87(6): 1465-1471.

Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C. 1998. Biogeografia de Portugal Continental. *Quercetea* 0: 5-56.

Costa JC, Arsenio P, Monteiro-Henriques T, Neto C, Pereira E, Almeida T, Izco J. 2009. Finding the Boundary between Eurosiberian and Mediterranean Salt Marshes. *Journal of Coastal Research*: 1340-1344.

Costa JC, Lousã M, Capelo J, Espírito-Santo MD, Izco J, Ladero M. 2000. The coastal vegetation of the Portuguese Divisory Sector: dunes, cliffs and low-scrub communities. *Finisterra* {XXXV}(69): 69-93.

Costa JC, Lousa M, Espírito-Santo MD. 1996. A vegetaçao do Parque Natural da Ria Formosa (Algarve, Portugal). *Studia Botanica* 15(15): 69-157.

Costa JC, Neto C, Martins M, Lousã M. 2011. Annual dune plant communities in the Southwest coast of Europe. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 145(sup1): 91-104.

Costa JC. 2001. Tipos de vegetação e adaptações das plantas do litoral de Portugal continental. *Homenagem (in honorio) Professor Doutor Soares de Carvalho*: 283-299.

Costa JCA, Neto C, Aguiar C, Capelo J, Espirito Santo MD, Honrado JJ, Pinto-Gomes CJ, Monteiro-Henriques T, Sequeira M, Lousã M. 2012. Vascular Plant communities in Portugal (Continental, The Azores and Madeira). *Global Geobotany* 2: 1-180.

Costa JCA. 1991. *Flora e vegetacão do parque natural da Ria Formosa. .*PhD Thesis, Technical University of Lisbon Lisbon, Portugal.

Craig RK, Ruhl JB. 2010. Governing for Sustainable Coasts: Complexity, Climate Change, and Coastal Ecosystem Protection. *Sustainability* 2(5): 1361-1388.

Craine JM, Dybzinski R, Robinson D. 2013. Mechanisms of plant competition for nutrients, water and light. *Functional Ecology* 27(4): 833-840.

Cushman JH, Lortie CJ, Christian CE. 2011. Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *Journal of Ecology* 99(2): 524-531.

Damgaard C. 2005. *Evolutionary ecology of plant–plant interactions*: Aarhus: Aarhus University Press.

Delgado-Fernandez I, Davidson-Arnott R, Bauer BO, Walker IJ, Ollerhead J. 2013. Evaluation of the optimal resolution for characterizing the effect of beach surface moisture derived from remote sensing on aeolian transport Study Site and Remote Sensing System. *Journal of Coastal Research* (65): 1277-1282.

Delgado-Fernandez I. 2011. Meso-scale modelling of aeolian sediment input to coastal dunes. *Geomorphology* 130(3-4): 230-243.

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47(1): 15-25.

Dolman PM, Panter CJ, Mossman HL. 2010. Securing Biodiversity in Breckland: Guidance for Conservation and Research. First Report of the Breckland Biodiversity Audit.

Dormann CF. 2008. On community matrix theory in experimental plant ecology. Web Ecology 8(1): 108-115.

Dornelas M. 2010. Disturbance and change in biodiversity. *Philos Trans R Soc Lond B Biol Sci* 365(1558): 3719-3727.

Douma JC, de Haan MWA, Aerts R, Witte J-PM, van Bodegom PM. 2012a. Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. *Journal of Ecology* 100(2): 366-380.

Douma JC, Shipley B, Witte JP, Aerts R, van Bodegom PM. 2012b. Disturbance and resource availability act differently on the same suite of plant traits: revisiting assembly hypotheses. *Ecology* 93(4): 825-835.

Dullinger S, Kleinbauer I, Pauli H, Gottfried M, Brooker R, Nagy L, Theurillat JP, Holten JI, Abdaladze O, Benito JL, *et al.* 2007. Weak and variable relationships between environmental severity and small-scale co-occurrence in alpine plant communities. *Journal of Ecology* 95(6): 1284-1295.

Duran O, Moore LJ. 2013. Vegetation controls on the maximum size of coastal dunes. *Proceedings of the National Academy of Sciences* 110(43): 17217-17222.

Dwyer JM, Hobbs RJ, Wainwright CE, Mayfield MM. 2015. Climate moderates release from nutrient limitation in natural annual plant communities. *Global Ecology and Biogeography* 24(5): 549-561.

Dyer AR, Goldberg DE, Turkington R, Sayre C. 2001. Effects of growing conditions and source habitat on plant traits and functional group definition. *Functional Ecology* 15(1): 85-95.

Dytham C. 2011. *Choosing and using statistics: a biologist's guide*. Oxford, United Kingdom: Wiley-Blackwell.

EC. 2013. Interpretation Manual of European union habitats EUR 28, Nature ENV B.3. Brussels, EU: DG Environment, EC - European Commission.

EEA. 2013. Balancing the future of Europe's coasts- knowledge base for integrated management. Copenhagen, Denmark: EEA - European Environment Agency.

Favennec J. 2002. The foredune-backshore system, an indicator of costal dynamics. *The example of the Aquitance coast observatory. Littoral 2002 Proceedings book*: 345-353.

Feagin RA, Ben Wu X. 2005. An experimental approach for quantifying the spatial interactions of plants under different treatment conditions. *Ecoscience* 12(1): 44-52.

Feagin RA, Ben Wu X. 2007. The Spatial Patterns of Functional Groups and Successional Direction in a Coastal Dune Community. *Rangeland Ecology & Management* 60(4): 417-425.

Feagin RA, Figlus J, Zinnert JC, Sigren J, Martínez ML, Silva R, Smith WK, Cox D, Young DR, Carter G. 2015. Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Frontiers in Ecology and the Environment* 13(4): 203-210.

Fenu G, Carboni M, Acosta ATR, Bacchetta G. 2013a. Environmental Factors Influencing Coastal Vegetation Pattern: New Insights from the Mediterranean Basin. *Folia Geobotanica* 48(4): 493-508.

Fenu G, Cogoni D, Ferrara C, Pinna MS, Bacchetta G. 2012. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*: 1-17.

Fenu G, Cogoni D, Ulian T, Bacchetta G. 2013b. The impact of human trampling on a threatened coastal Mediterranean plant: The case of Anchusa littorea Moris (Boraginaceae). *Flora - Morphology, Distribution, Functional Ecology of Plants* 208(2): 104-110.

Feola S, Carranza ML, Schaminée JHJ, Janssen JAM, Acosta ATR. 2011. EU habitats of interest: an insight into Atlantic and Mediterranean beach and foredunes. *Biodiversity and Conservation* 20(7): 1457-1468.

Fernández Montoni MV, Fernández Honaine M, del Río JL. 2014. An Assessment of Spontaneous Vegetation Recovery in Aggregate Quarries in Coastal Sand Dunes in Buenos Aires Province, Argentina. *Environmental Management* 54: 180–193.

Fidalgo F, Santos A, Pimenta S, Marques J, Honrado J. 2014. Regional Environmental Gradients Influence Ecophysiological Responses of Dominant Coastal Dune Plants to Changes in Local Conditions. *Journal of Coastal Research* 297(4): 893-903.

Forey E, Chapelet B, Vitasse Y, Tilquin M, Touzard B, Michalet R. 2008. The relative importance of disturbance and environmental stress at local and regional scales in French coastal sand dunes. *Journal of Vegetation Science* 19(4): 493-502.

Forey E, Lortie CJ, Michalet R. 2009. Spatial patterns of association at local and regional scales in coastal sand dune communities. *Journal of Vegetation Science* 20(5): 916-925.

Forey E, Touzard B, Michalet R. 2010. Does disturbance drive the collapse of biotic interactions at the severe end of a diversity–biomass gradient? *Plant ecology* 206(2): 287-295.

Fortunato AB, Clímaco M, Oliveira F, Oliveira A, Sancho F, Freire P. 2008. Dinâmica Fisiográfica da Orla Costeira: Estudos de Reabilitação e Protecção. *Revista de Gestão Costeira Integrada* 8(1): 45-63.

Foster BL, Questad EJ, Collins CD, Murphy CA, Dickson TL, Smith VH. 2011. Seed availability constrains plant species sorting along a soil fertility gradient. *Journal of Ecology* 99(2): 473-481.

Franco JA, Afonso MLR. 1998. *Nova Flora de Portugal (Continente e Açores). Gramineae.* Lisboa: Escolar Editora.

Franco JA, Rocha-Afonso ML. 2003. *Nova Flora de Portugal (Continente e Acores). Alismataceae-Iridaceae, Gramineae e Juncaceae-Orchidaceae*. Lisboa: Escolar Editora.

Franco JA. 1971. *Nova Flora de Portugal (Continente e Acores). Lycopodiaceae-Umbelllferae*. Lisboa: Escolar Editora.

Franco JA. 1984. *Nova Flora de Portugal (Continente e Açores). Clethraceae - Compositae*. Lisboa: Edição do autor.

Franks SJ, Peterson CJ. 2003. Burial disturbance leads to facilitation among coastal dune plants. *Plant Ecology* 168(1): 13-21.

Frosini S, Lardicci C, Balestri E. 2012. Global change and response of coastal dune plants to the combined effects of increased sand accretion (burial) and nutrient availability. *PLoS One* 7(10): e47561.

Gallego-Fernández JB, Martínez ML. 2011. Environmental Filtering and Plant Functional Types on Mexican Foredunes along the Gulf of Mexico. *Ecoscience* 18(1): 52-62.

Garcia Novo F, Diaz Barradas MC, Zunzunegui M, Garcia Mora R, Gallego Fernandez JB 2008. Plant Functional Types in Coastal Dune Habitats. *Coastal Dunes*: Springer, 155-167.

García-Mora MR, Gallego-Fernández JB, García-Novo F. 1999. Plant functional types in coastal foredunes in relation to environmental stress and disturbance. *Journal of Vegetation Science* 10(1): 27-34.

García-Mora MR, Gallego-Fernández JB, García-Novo F. 2000. Plant diversity as a suitable tool for coastal dune vulnerability assessment. *Journal of Coastal Research*: 990-995.

García-Mora MR, Gallego-Fernández JB, Williams AT, Garcia-Novo F. 2001. A coastal dune vulnerability classification. A case study of the SW Iberian Peninsula. *Journal of Coastal Research*: 802-811.

Gilbert ME, Ripley BS. 2008. Biomass reallocation and the mobilization of leaf resources support dune plant growth after sand burial. *Physiologia Plantarum* 134(3): 464-472.

Gomes JFA. 2012. *The use of digital aerial photography as support for restoration, management and habitat monitoring programmes.* Master thesis presented to the University of Porto.

Gonçalves JA, Henriques R. 2015. UAV photogrammetry for topographic monitoring of coastal areas. *ISPRS Journal of Photogrammetry and Remote Sensing* 104: 101-111.

Gotelli NJ, Entsminger GL. 2001. EcoSim: Null models software for ecology. Version 7.0. *Acquired Intelligence Inc. & Kesey-Bear*: http://homepages.together.net/~gentsmin/ecosim.htm.

Gotelli NJ, McCabe DJ. 2002. Species Co-Occurrence: A Meta-Analysis of J. M. Diamond's Assembly Rules Model. *Ecology* 83(8): 2091-2096.

Gotelli NJ. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81(9): 2606-2621.

Gotzenberger L, de Bello F, Brathen KA, Davison J, Dubuis A, Guisan A, Leps J, Lindborg R, Moora M, Partel M, *et al.* 2012. Ecological assembly rules in plant communities--approaches, patterns and prospects. *Biological reviews of the Cambridge Philosophical Society* 87(1): 111-127.

Gracia Prieto FJ, Sanjaume E, Hernández L, Hernández AI, Flor G, Gómez-Serrano M 2009. Dunas marítimas y continentales. In: AA. V ed. *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España*. Madrid: Ministerio de Medio Ambiente, y Medio Rural y Marino.

Granja H. 1997. Bad practice in the coastal zone of Portugal–coastal dynamics and management. *Journal of Coastal Conservation* 2: 16-17.

Granja HM 2002. Reconstituição Paleoambiental da Zona Costeira, a Norte da Laguna de Aveiro, desde a Idade Média até à Actualidade.In Moderna IdH. *Actas do Seminário "O Litoral em Perspectiva Histórica (sécs. XVI a XVII), Um Ponto da Situação Historiográfica"*. Porto: Instituto de História Moderna, Universidade do Porto. 93-109.

Granja HM, Bastos L, Pinho JLS, Gon\ccalves J, Henriques RF, Mendes J, Bio A, Magalhães A, Gonçalves J, Henriques RF, *et al.* Programa multidisciplinar de monitoriza\ccão de curto termo para apoio ao planeamento e gestão da zona costeira.

Granja HM, Bastos L, Pinho JLS, Gonçalves J, Henriques RF, Mendes J, Bio A, Magalhães A, Gonçalves J, Henriques RF, *et al.* 2011. Programa multidisciplinar de monitorização a o de curto termo para apoio ao planeamento

e gestão da zona costeira. VI Congresso sobre Planeamento e Gestão das Zonas Costeiras dos Países de Expressão Portuguesa, APRH.

Granja HM, Carvalho GS. 1992. Dunes and Holocene deposits of the coastal zone north of Mondego Cape, Portugal, in: Carter, R.W.G. *et al.* (Ed.) (1992). Coastal dunes: geomorphology, ecology and management for conservation: *Proceedings of the 3rd European Dune Congress* Galway, Ireland, 17-21 June 1992. pp. 43-50.

Gratani L, Crescente MF, Varone L, Gini E, Ricotta C, Bonito A. 2013. Sand Dune Species Distribution and Size Variations in Two Areas Inside a Natural Protected Area Subjected to Different Human Disturbance. *American Journal of Plant Sciences* 04(09): 1899-1910.

Gray AJ. 1985. Adaptation in perennial coastal plants-with particular reference to heritable variation in Puccinellia maritima and Ammophila arenaria. *Vegetatio* 61(1-3): 179-188.

Gray SRJ, Gagnon AS, Gray SA, O'Dwyer B, O'Mahony C, Muir D, Devoy RJN, Falaleeva M, Gault J. 2014. Are coastal managers detecting the problem? Assessing stakeholder perception of climate vulnerability using Fuzzy Cognitive Mapping. *Ocean & Coastal Management* 94: 74-89.

Grime JP. 1973. Competitive Exclusion in Herbaceous Vegetation. *Nature* 242(5396): 344-347.

Grime JP. 1974. Vegetation classification by reference to strategies. *Nature* 250(5461): 26-31.

Grime JP. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* 111(982): 1169.

Grime JP. 1984. The Ecology of Species, Families and Communities of the Contemporary British Flora. *New Phytologist* 98(1): 15-33.

Grime JP. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Chichester, United Kingdom: Wiley.

Grime JP. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17(2): 255-260.

Gross N, Börger L, Soriano-Morales SI, Le Bagousse-Pinguet Y, Quero JL, García-Gómez M, Valencia-Gómez E, Maestre FT, Schwinning S. 2013. Uncovering

multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology* 101(3): 637-649.

Gross N, Suding KN, Lavorel S, Roumet C. 2007. Complementarity as a mechanism of coexistence between functional groups of grasses. *Journal of Ecology* 95(6): 1296-1305.

Grunewald R. 2006. Assessment of Damages from Recreational Activities on Coastal Dunes of the Southern Baltic Sea. *Journal of Coastal Research* 225: 1145-1157.

Guerin GR, Martín-Forés I, Biffin E, Baruch Z, Breed MF, Christmas MJ, Cross HB, Lowe AJ. 2014. Global change community ecology beyond species-sorting: a quantitative framework based on mediterranean-biome examples. *Global Ecology and Biogeography* 23(10): 1062-1072.

Gwenzi W, Veneklaas EJ, Bleby TM, Yunusa IAM, Hinz C. 2012. Transpiration and plant water relations of evergreen woody vegetation on a recently constructed artificial ecosystem under seasonally dry conditions in Western Australia. *Hydrological Processes* 26(21): 3281-3292.

Hammer Ø 2013. PAST: Paleontological Statistics, Version 3.0 Reference Manual. Oslo, Norway: Natural History Museum, University of Oslo.

Hanley ME, Hoggart SPG, Simmonds DJ, Bichot A, Colangelo MA, Bozzeda F, Heurtefeux H, Ondiviela B, Ostrowski R, Recio M, *et al.* 2014. Shifting sands? Coastal protection by sand banks, beaches and dunes. *Coastal Engineering* 87: 136-146.

Harpole WS, Tilman D. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446(7137): 791-793.

Hautier Y, Seabloom EW, Borer ET, Adler PB, Harpole WS, Hillebrand H, Lind EM, MacDougall AS, Stevens CJ, Bakker JD, *et al.* 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508(7497): 521-525.

He Q, Bertness MD. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology* 95(6): 1437-1443.

Henriques MV, Neto C. 2002. Caracterização geo-ecológica dos sistemas de cordões dunares da estremadura TL - 37. *Finisterra* 37 VN - r(74): 5-31.

Henriques RFF. 2007. *Monitorização da zona costeira tendo em vista a sua vulnerabilidade – aplicação à zona costeira noroeste de Portugal.* PhD Thesis, University of Minho Braga, Portugal

Hernández-Cordero AI, Pérez-Chacón Espino E, Hernández-Calvento L. 2015. Vegetation, distance to the coast, and aeolian geomorphic processes and landforms in a transgressive arid coastal dune system. *Physical Geography* 36(1): 60-83.

Hesp P. 1989. A review of biological and geomorphological processes involved in the initiation and development of incipient foredunes. *Proceedings of the Royal Society of Edinburgh* 96B: 181-201.

Hesp P. 1991. Ecological processes and plant adaptations on coastal dunes. *Journal of Arid Environments* 21: 165-191.

Hesp P. 2002. Foredunes and blowouts: initiation, geomorphology and dynamics. *Geomorphology* 48(1-3): 245-268.

Hillebrand H, Bennett DM, Cadotte MW. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89(6): 1510-1520.

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics* 43(1): 227-248.

Hodgson JG, Wilson PJ, Hunt R, Grime JP, Thompson K. 1999. Allocating C-S-R Plant Functional Types: A Soft Approach to a Hard Problem. *Oikos* 85(2): 282.

Hofer G, Wagner HH, Herzog F, Edwards PJ. 2008. Effects of topographic variability on the scaling of plant species richness in gradient dominated landscapes. *Ecography* 31(1): 131-139.

Holmgren M, Scheffer M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology* 98(6): 1269-1275.

Honrado J, Alves P, Lomba A, Vicente J, Silva G, Nepomuceno H, Barreto Caldas F. 2006. Perennial vegetation of coastal sand dunes in northern Portugal. *Silva Lusitana* 14(2): 269-275.

Honrado J, Vicente J, Lomba A, Alves P, Macedo JA, Henriques R, Granja H, Caldas FB. 2010. Fine-scale patterns of vegetation assembly in the monitoring of changes in coastal sand-dune landscapes. *Web Ecology* 10(1): 1-14.

Houle G. 2002. Trade-off between growth ability and stress tolerance in Leymus mollis (Poaceae) along a subarctic coastal dune sequence in northern Quebec. *Canadian Journal of Botany* 80(8): 869-874.

Houser C, Hobbs C, Saari B. 2008. Posthurricane Airflow and Sediment Transport over a Recovering Dune. *Journal of Coastal Research* 244: 944-953.

Houston J. 2008. Management of Natura 2000 habitats: Fixed coastal dunes with herbaceous vegetation (" grey dunes ") 2130. *Ecosystems*: 34-34.

Hubbell SP. 2001. *The unified neutral theory of biodiversity and biogeography (MPB-32)*: Princeton University Press.

Hunt R, Hodgson JG, Thompson K, Bungener P, Dunnett NP, Askew aP. 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science* 7(2): 163-170.

ICNF 2015a. ICNF - Rede Nacional de Áreas Protegidas. http://www.icnf.pt/portal/ap/rnap: ICNF - Instituto da Conservação da Natureza e das Florestas, Lisboa, Portugal.

ICNF 2015b. ICNF - Rede Natura 2000. http://www.icnf.pt/portal/naturaclas/rn2000: ICNF - Instituto da Conservação da Natureza e das Florestas, Lisboa, Portugal.

Ievinsh G. 2006. Biological basis of biological diversity: physiological adaptations of plants to heterogeneous habitats along a sea coast. *Acta Universitatis Latviensis* 710: 53-79.

IPCC. 2014. IPCC Fifth Assessment Synthesis Report-Climate Change 2014: Synthesis Report: Intergovernmental Panel on Climate Change (IPCC).

Isermann M, Rooney P. 2014. Biological Flora of the British Isles: Eryngium maritimum. *Journal of Ecology* 102(3): 789-821.

Isermann M. 2009. *Phytodiversity in relation to scale.*PhD Thesis, University of Bremen.

Izco J. 1989. El Río Miño: barrera y camino en la migración de las plantas. *El río Miño*: 87-97.

Izco J. 1992. Diversidad y originalidad ecológica y florística del litoral cántabro-atlántico español. *Anales de la Real Academia de Farmacia* 58(4): 483-508.

Jeffers ES, Bonsall MB, Brooks SJ, Willis KJ. 2011. Abrupt environmental changes drive shifts in tree-grass interaction outcomes. *Journal of Ecology* 99(4): 1063-1070.

Jentsch A, Beyschlag W. 2003. Vegetation ecology of dry acidic grasslands in the lowland area of Central Europe. *Flora - Morphology, Distribution, Functional Ecology of Plants* 198(1): 3-25.

Jiménez-Alfaro B, Marcenò C, Guarino R, Chytrý M, Ladle R. 2015. Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages. *Journal of Biogeography* 42(3): 452-462.

JNCC. 2006. Common Standards Monitoring guidance for upland habitats. Peterborough, United Kingdom: JNCC - Joint Nature Conservation Committee.

Joesting HM, Sprague MO, Smith WK. 2012. Seasonal and diurnal leaf orientation, bifacial sunlight incidence, and leaf structure in the sand dune herb Hydrocotyle bonariensis. *Environmental and Experimental Botany* 75: 195-203.

Jost L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88(10): 2427-2439.

Kazakou E, Vile D, Shipley B, Gallet C, Garnier E. 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology* 20(1): 21-30.

Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3(2): 157-164.

Kent M, Coker P. 1994. *Vegetation description and analysis: a practical approach*. Chichester, New York: John Wiley & Sons.

Kent M, Owen NW, Dale P, Newnham RM, Giles TM. 2001. Studies of vegetation burial: a focus for biogeography and biogeomorphology? *Progress in Physical Geography* 25(4): 455-482.

Kikvidze Z, Armas C. 2010. Plant Interaction Indices Based on Experimental Plant Performance Data. *Positive Plant Interactions and Community Dynamics*: 17-38.

Kim D, Yu KB. 2009. A conceptual model of coastal dune ecology synthesizing spatial gradients of vegetation, soil, and geomorphology. *Plant Ecology* 202(1): 135-148.

Kim JY, Kim G-Y, Do Y, Joo G-J. 2014b. Effects of Monsoon on Topography, Soil Variables, and Coastal Plants. *Estuaries and Coasts* 38(2): 494-505.

Kim Y, Choi KH, Jung PM. 2014a. Changes in foredune vegetation caused by coastal forests. *Ocean & Coastal Management* 102: 103-113.

Kirkpatrick JB, Harris S 1999. Coastal, heath and wetland vegetation. In: Reid JB, Hill RS, Brown MJ, Hovenden MJ eds. *Vegetation of Tasmania, Flora of Australia* Hobart, Tasmania, Australia: Australian Biological Resources Study, 304-332.

Kosmidou V, Petrou Z, Bunce RGH, Mücher CA, Jongman RHG, Bogers MMB, Lucas RM, Tomaselli V, Blonda P, Padoa-Schioppa E, *et al.* 2014. Harmonization of the Land Cover Classification System (LCCS) with the General Habitat Categories (GHC) classification system. *Ecological Indicators* 36: 290-300.

Kraft NJB, Valencia R, Ackerly DD. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science* 322: 580–582.

Kuiters AT, Kramer K, Van der Hagen HGJM, Schaminée JHJ. 2009. Plant diversity, species turnover and shifts in functional traits in coastal dune vegetation: Results from permanent plots over a 52-year period. *Journal of Vegetation Science* 20(6): 1053-1063.

Kumordzi BB, Wardle DA, Freschet GT, Prinzing A. 2015. Plant assemblages do not respond homogenously to local variation in environmental conditions: functional responses differ with species identity and abundance. *Journal of Vegetation Science* 26(1): 32-45.

Łabuz T. 2013. Polish coastal dunes – affecting factors and morphology. *Landform Analysis* 22: 33-59.

Łabuz TA, Grunewald R. 2007. Studies on Vegetation Cover of the Youngest Dunes of the świna Gate Barrier (Western Polish Coast). *Journal of Coastal Research* 231(1): 160-172.

Laliberte E, Zemunik G, Turner BL. 2014. Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345(6204): 1602-1605.

Lang M, Vain A, Bunce RG, Jongman RH, Raet J, Sepp K, Kuusemets V, Kikas T, Liba N. 2015. Extrapolation of in situ data from 1-km squares to adjacent squares using remote sensed imagery and airborne lidar data for the assessment of habitat diversity and extent. *Environmental Monitoring and Assessment* 187(3): 76.

Laughlin DC, Joshi C, Richardson SJ, Peltzer DA, Mason NWH, Wardle DA, Kühn I. 2015. Quantifying multimodal trait distributions improves trait-based predictions of species abundances and functional diversity. *Journal of Vegetation Science* 26(1): 46-57.

Laughlin DC, Laughlin DE. 2013. Advances in modeling trait-based plant community assembly. *Trends in Plant Science* 18(10): 584-593.

Lavalle C, Gomes CR, Baranzelli C, Silva FBE. 2011. JRC Technical Notes: Coastal Zones Policy alternatives impacts on European Coastal Zones 2000 – 2050. Luxembourg: Joint Research Centre - Institute for Environment and Sustainability.

Le Bagousse-Pinguet Y, Forey E, Touzard B, Michalet R, de Bello F. 2013. Disentangling the effects of water and nutrients for studying the outcome of

plant interactions in sand dune ecosystems. *Journal of Vegetation Science* 24(2): 375-383.

Le Bagousse-Pinguet Y, Maalouf J-P, Touzard B, Michalet R. 2014. Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. *Oikos* 123(7): 777-785.

Lemauviel S, Gallet S, Rozé F. 2003. Sustainable management of fixed dunes: example of a pilot site in Brittany (France). *Comptes rendus biologies* 326: 183-191.

Lemauviel S, Roze F. 2003. Response of three plant communities to trampling in a sand dune system in Brittany (France). *Environmental Management* 31(2): 227-235.

Lepš J, Šmilauer P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge, United Kingdom: Cambridge University Press.

Levin N, Kidron GJ, Ben-Dor E. 2008. A field quantification of coastal dune perennial plants as indicators of surface stability, erosion or deposition. *Sedimentology* 55(4): 751-772.

Lewis RJ, Marrs RH, Pakeman RJ. 2014b. Inferring temporal shifts in landuse intensity from functional response traits and functional diversity patterns: a study of Scotland's machair grassland. *Oikos* 123(3): 334-344.

Lewis RJ, Pakeman RJ, Angus S, Marrs RH. 2014a. Using compositional and functional indicators for biodiversity conservation monitoring of semi-natural grasslands in Scotland. *Biological Conservation* 175: 82-93.

Li J, Qu H, Zhao H, Zhou R, Yun J, Pan C. 2015. Growth and physiological responses of Agriophyllum squarrosum to sand burial stress. *Journal of Arid Land* 7: 94–100.

Liancourt P, Callaway RM, Michalet R. 2005. Stress Tolerance and Competitive-Response Ability Determine the Outcome of Biotic Interactions. *Ecology* 86(6): 1611-1618.

Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B. 2013. Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS One* 8(7): e67737.

Liu B, Liu Z, Lü X, Maestre FT, Wang L. 2013. Sand burial compensates for the negative effects of erosion on the dune-building shrub Artemisia wudanica. *Plant and Soil* 374(1-2): 263-273.

Liu X, Lu Y, Xue Y, Zhang X. 2014. Testing the importance of native plants in facilitation the restoration of coastal plant communities dominated by exotics. *Forest Ecology and Management* 322: 19-26.

Loidi J, Biurrun I, Campos JA, García-Mijangos I, Herrera M. 2007. A survey of health vegetation of the Iberian Peninsula and Northern Morocco: A biogeographic and bioclimatic approach. *Phytocoenologia* 37(3-4): 341-370.

Lomba A, Alves P, Honrado J. 2008. Endemic Sand Dune Vegetation of the Northwest Iberian Peninsula: Diversity, Dynamics, and Significance for Bioindication and Monitoring of Coastal Landscapes. *Journal of Coastal Research* 2(sp2): 113-121.

Loreau M, de Mazancourt C. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist* 172(2): E48-66.

Loreau M, de Mazancourt C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* 16: 106-115.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, *et al.* 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294(5543): 804-808.

Lortie CJ, Turkington R. 2008. Species-specific positive effects in an annual plant community. *Oikos* 117(10): 1511-1521.

Lozoya JP, Sardá R, Jiménez JA. 2011. A methodological framework for multi-hazard risk assessment in beaches. *Environmental Science & Policy* 14(6): 685-696.

Lucrezi S, Saayman M, van der Merwe P. 2014. Influence of infrastructure development on the vegetation community structure of coastal dunes: Jeffreys Bay, South Africa. *Journal of Coastal Conservation* 18(3): 193-211.

Luna MCMdM, Parteli EJR, Herrmann HJ. 2012. Model for a dune field with an exposed water table. *Geomorphology* 159-160: 169-177.

Luzuriaga AL, Sanchez AM, Maestre FT, Escudero A. 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PLoS One* 7(7): e41270.

Macarthur R, Levins R. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* 101(921): 377.

Macedo JA, Alves P, Lomba Â, Vicente J, Henriques R, Granja H, Honrado J. 2010. On the interest of plant functional classifications to study community—level

effects of increased disturbance on coastal dune vegetation. *Acta Botanica Gallica* 157(2): 305-315.

Macedo JAM. 2008. *A Functional Approach to Modelling Vegetation-Environment Relations in Coastal Sand Dunes* MSc Thesis, University of Porto Porto.

Maestre FT, Bowker MA, Escolar C, Puche MD, Soliveres S, Maltez-Mouro S, Garcia-Palacios P, Castillo-Monroy AP, Martinez I, Escudero A. 2010. Do biotic interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and biological soil crust communities. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1549): 2057-2070.

Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97(2): 199-205.

Maestre FT, Cortina J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society B: Biological Sciences* 271(Suppl 5): S331-333.

Maire V, Gross N, Borger L, Proulx R, Wirth C, da Silveira Pontes L, Soussana JF, Louault F. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* 196(2): 497-509.

Maire V, Gross N, da Silveira Pontes L, Picon-Cochard C, Soussana J-Fo. 2009. Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology* 23(4): 668-679.

Malkinson D, Jeltsch F. 2007. Intraspecific facilitation: a missing process along increasing stress gradients? Insights from simulated shrub populations. *Ecography* 30(3): 339-348.

Maltez-Mouro S, Maestre FT, Freitas H. 2009. Weak effects of the exotic invasive Carpobrotus edulis on the structure and composition of Portuguese sand-dune communities. *Biological Invasions* 12(7): 2117-2130.

Maltez-Mouro S, Maestre FT, Freitas H. 2010. Co-occurrence patterns and abiotic stress in sand-dune communities: Their relationship varies with spatial scale and the stress estimator. *Acta Oecologica* 36(1): 80-84.

Mancini F, Dubbini M, Gattelli M, Stecchi F, Fabbri S, Gabbianelli G. 2013. Using Unmanned Aerial Vehicles (UAV) for High-Resolution Reconstruction of

Topography: The Structure from Motion Approach on Coastal Environments. *Remote Sensing* 5(12): 6880-6898.

Marini L, Battisti A, Bona E, Federici G, Martini F, Pautasso M, Hulme PE. 2012. Alien and native plant life-forms respond differently to human and climate pressures. *Global Ecology and Biogeography* 21(5): 534-544.

Martínez ML, Gallego-Fernández JB, García-Franco JG, Moctezuma C, Jiménez CD. 2006. Assessment of coastal dune vulnerability to natural and anthropogenic disturbances along the Gulf of Mexico. *Environmental Conservation* 33(02): 1.

Martins MC, Neto CS, Costa JC. 2013. The meaning of mainland Portugal beaches and dunes' psammophilic plant communities: a contribution to tourism management and nature conservation. *Journal of Coastal Conservation* 17(3): 279-299.

Masetti R, Fagherazzi S, Montanari A. 2008. Application of a barrier island translation model to the millennial-scale evolution of Sand Key, Florida. *Continental Shelf Research* 28(9): 1116-1126.

Mateus J. 1992. *Holocene and present-day ecosystems of the Carvalhal Region, Southwest Portugal.* PhD Thesis, University of Utrecht Utrecht, The Netherlands.

Maun MA, Perumal J. 1999. Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecology Letters* 2(1): 14-18.

Maun MA. 1998. Adaptations of plants to burial in coastal sand dunes. *Canadian Journal of Botany* 76(5): 713-738.

Maun. 2009. *The biology of coastal sand dunes*. Oxford, United Kingdom: Oxford University Press.

McGill BJ. 2010. Towards a unification of unified theories of biodiversity. *Ecology Letters*13(5): 627-642.

McIntyre S, Lavorel S, Landsberg J, Forbes TDA. 1999. Disturbance response in vegetation - towards a global perspective on functional traits. *Journal of Vegetation Science* 10(5): 621-630.

McIntyre S, Lavorel S, Tremont RM. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*: 31-44.

Medina J, Meier S, Rubio R, Curaqueo G, Borie F, Aguilera P, Oehl F, Cornejo P. 2015. Arbuscular mycorrhizal status of pioneer plants from the mouth of lake Budi, Araucanía Region, Chile. Journal of soil science and plant nutrition 15.

Medrano H, Flexas J, Galmés J. 2008. Variability in water use efficiency at the leaf level among Mediterranean plants with different growth forms. *Plant and Soil* 317(1-2): 17-29.

Metzger MJ, Brus DJ, Bunce RGH, Carey PD, Gonçalves J, Honrado JP, Jongman RHG, Trabucco A, Zomer R. 2013. Environmental stratifications as the basis for national, European and global ecological monitoring. *Ecological Indicators* 33: 26-35.

Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9(7): 767-773.

Michalet R, Brooker RW, Lortie CJ, Maalouf J-P, Pugnaire FI. 2015a. Disentangling direct and indirect effects of a legume shrub on its understorey community. *Oikos.* Doi: 10.1111/oik.01819

Michalet R, Le Bagousse-Pinguet Y, Maalouf J-P, Lortie CJ, Palmer M. 2014. Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science* 25(2): 609-613.

Michalet R, Maalouf J-P, Choler P, Clément B, Rosebery D, Royer J-M, Schöb C, Lortie CJ. 2015b. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography* 38(4): 335-345.

Michalet R, Touzard B. 2010. Biotic Interactions, Biodiversity, and Community Productivity. *Positive Plant Interactions and Community Dynamics* 59-78.

Miller TE, Gornish ES, Buckley HL. 2009. Climate and coastal dune vegetation: disturbance, recovery, and succession. *Plant Ecology* 206(1): 97-104.

Mod HK, le Roux PC, Luoto M, Michalet R. 2014. Outcomes of biotic interactions are dependent on multiple environmental variables. *Journal of Vegetation Science* 25(4): 1024-1032.

Monge JA, Gornish ES. 2015. Positive Species Interactions as Drivers of Vegetation Change on a Barrier Island. *Journal of Coastal Research* 299(1): 17-24.

Mori AS, Fujii S, Kurokawa H. 2014. Ecological consequences through responses of plant and soil communities to changing winter climate. *Ecological Research* 29(4): 547-559.

Mouchet MA, Villéger S, Mason NWH, Mouillot D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24(4): 867-876.

Mouillot D, Mason NW, Wilson JB. 2007. Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia* 152(4): 729-737.

Mücher CA, Hennekens SM, Bunce RGH, Schaminée JHJ, Schaepman ME. 2009. Modelling the spatial distribution of Natura 2000 habitats across Europe. *Landscape and Urban Planning* 92(2): 148-159.

Murrell DJ. 2010. When does local spatial structure hinder competitive coexistence and reverse competitive hierarchies? *Ecology* 91(6): 1605-1616.

Neto C, Costa JC, Honrado J, Capelo J. 2007. Phytosociological associations and Natura 2000 habitats of Portuguese coastal sand dunes. *Fitosociologia* 44(2): 29-35.

Neto C, Pereira E, Reis E, Costa JC. 2008. Carta da Vegetação Natural Potencial de Caldas da Rainha. *Finisterra* XLIII: 31-51.

Neto CS. 1993. A flora e a vegetação das dunas de S.Jacinto. *Finisterra* XXVIII(55-56): 101-148.

Nielsen KE, Degn HJ, Damgaard C, Bruus M, Nygaard B. 2011. A native species with invasive behaviour in coastal dunes: evidence for progressing decay and homogenization of habitat types. *AMBIO* 40(7): 819-823.

Nylén T, le Roux PC, Luoto M. 2013. Biotic interactions drive species occurrence and richness in dynamic beach environments. *Plant ecology* 214(12): 1455-1466.

Olden JD, Rooney TP. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* 15(2): 113-120.

Olff H, Huisman J, Tooren BFV. 1993. Species Dynamics and Nutrient Accumulation During Early Primary Succession in Coastal Sand Dunes. *The Journal of Ecology* 81(4): 693.

Ortega M, Guerra C, Honrado JP, Metzger MJ, Bunce RGH, Jongman RHG. 2013. Surveillance of habitats and plant diversity indicators across a regional gradient in the Iberian Peninsula. *Ecological Indicators* 33: 36-44.

Otto R, Krüsi BO, Kienast F. 2007. Degradation of an arid coastal landscape in relation to land use changes in Southern Tenerife (Canary Islands). *Journal of Arid Environments* 70: 527–539.

Page L, Thorp V. 2010. Tasmanian Coastal Works Manual: A best practice management guide for changing coastlines. Hobart, Tasmania, Australia: Department of Primary Industries, Parks, Water and Environment of Tasmania.

Pausas JG, Austin MP. 2001. Patterns of plant species richness in relation to different environments: An appraisal. *Journal of Vegetation Science* 12(2): 153-166.

Perrone R, Salmeri C, Brullo S, Colombo P, De Castro O. 2015. What do leaf anatomy and micro-morphology tell us about the psammophilous Pancratium maritimum L. (Amaryllidaceae) in response to sand dune conditions? *Flora - Morphology, Distribution, Functional Ecology of Plants* 213: 20-31.

Peyrat J, Fichtner A. 2011. Plant species diversity in dry coastal dunes of the southern Baltic coast. *Community Ecology* 12(2): 220-226.

Peyrat J. 2011. *Landscape and vegetation of southern Baltic dune systems: diversity, landuse changes and threats.*PhD Thesis, University of Kiel Kiel, Germany.

Pianka ER. 1994. *Evolutionary Ecology*. New York, USA: Harper Collins.

Pierce S. 2014. Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass production. *Functional Ecology* 28(1): 253-257.

Pintó J, Martí C, Fraguell RM. 2014. Assessing Current Conditions of Coastal Dune Systems of Mediterranean Developed Shores. *Journal of Coastal Research* 296: 832-842.

Pistón N, Armas C, Schöb C, Macek P, Pugnaire FI. 2015. Phylogenetic distance among beneficiary species in a cushion plant species explain interaction outcome. *Oikos*. DOI: 10.1111/oik.01979.

Prisco I, Acosta ATR, Ercole S. 2012. An Overview of the Italian Coastal Dune EU Habitats. *Annali di Botanica* 2: 39-48.

Provoost S, Jones MLM, Edmondson SE. 2011. Changes in landscape and vegetation of coastal dunes in northwest Europe: a review. *Journal of Coastal Conservation* 15(1): 207-226.

Psuty NP 2008. The Coastal Foredune: A Morphological Basis for Regional Coastal Dune Development. In: Martínez ML, Psuty N eds. *Coastal Dunes*: Springer Berlin Heidelberg, 11-27.

Pugnaire FI, Armas C, Maestre FT. 2011. Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function. *Journal of Arid Environments* 75(12): 1310-1320.

Pugnaire FI, Zhang L, Li R, Luo T, Foster B. 2015. No evidence of facilitation collapse in the Tibetan plateau. *Journal of Vegetation Science* 26(2): 233-242.

Pugnaire FI. 2010. *Positive Plant Interactions and Community Dynamics*. Boca Raton, London, New York: CRC Press.

Questad EJ, Foster BL. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* 11(7): 717-726.

Rajaniemi TK, Goldberg DE, Turkington R, Dyer AR. 2012. Local filters limit species diversity, but species pools determine composition. *Perspectives in Plant Ecology, Evolution and Systematics* 14(6): 373-380.

Raunkiaer C. 1937. *Plant Life Forms*. Oxford, United Kingdom: The Clarendon Press.

Redon M, Bergès L, Cordonnier T, Luque S. 2014. Effects of increasing landscape heterogeneity on local plant species richness: how much is enough? *Landscape Ecology* 29(5): 773-787.

Reice SR. 1994. Nonequilibrium determinants of biological community structure. American Scientist 82: 424–435.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. 2003. The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *International Journal of Plant Sciences* 164(S3): S143-S164.

Ren J, Tao L, Liu XM. 2002. Effect of sand burial depth on seed germination and seedling emergence of Calligonum L. species. Journal of Arid Environments 51: 603–611.

Reynolds J, Maestre F, Kemp PR, Stafford-Smith DM, Lambin E 2007. Natural and human dimensions of land degradation in drylands: causes and consequences. Springer, 247-257.

Ricalde MF, Andrade JL, Durán R, Dupuy JM, Simá JL, Us-Santamaría R, Santiago LS. 2010. Environmental regulation of carbon isotope composition and crassulacean acid metabolism in three plant communities along a water availability gradient. *Oecologia* 164: 871–80.

Ripley BS, Pammenter NW 2008. 9 Physiological Characteristics of Coastal Dune Pioneer Species from the Eastern Cape, South Africa. In: Martínez ML, Psuty NP eds. *Coastal Dunes*. Berlin: Springer, 137-154.

Ripley BS, Pammenter NW, Smith VR. 1999. Function of Leaf Hairs Revisited: The Hair Layer on Leaves Arctotheca populifolia Reduces Photoinhibition, but

Leads to Higher Leaf Temperatures Caused by Lower Transpiration Rates. *Journal of Plant Physiology* 155(1): 78-85.

Ripley BS. 2001. *The ecophysiology of selected coastal dune pioneer plants of the Eastern Cape.*PhD Thesis, Rhodes University Grahamstown, South Africa.

Rivas-Martínez S, Díaz TE, Fernández-González F, Izco J, Loidi J, Lousa M, Penas A. 2002b. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. 2. *Itinera Geobotanica*.

Rivas-Martínez S, González FF, Arregui JJL, Lousã MF, Merino ÁP. 2001. Sintaxonomical checklist of vascular plant communities of Spain and Portugal to association level. *Itinera Geobotanica* (14): 5-341.

Rivas-Martínez S, González TED, González FF, Sevillano JI, Arregui JJL, Lousã MF, Merino ÁP. 2002a. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklis of 2001. Part 1. *Itinera Geobotanica* (15): 5-432.

Roxburgh SH, Shea K, Wilson JB. 2004. The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence. *Ecology* 85(2): 359-371.

Rozema J, Bijwaard P, Prast G, Broekman R. 1985. Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio* 62(1-3): 499-521.

Rubinstein Y, Groner E, Yizhaq H, Svoray T, Bar P. 2013. An eco-spatial index for evaluating stabilization state of sand dunes. *Aeolian Research* 9: 75-87.

Rykiel EJ. 1985. Towards a definition of ecological disturbance. *Austral ecology* 10(3): 361-365.

Ryu W, Sherman DJ. 2014. Foredune Texture: Landscape Metrics and Climate. *Annals of the Association of American Geographers* 104(5): 903-921.

Salman A, Lombardo S, Doody P. 2004. Living with coastal erosion in Europe: sediment and space for sustainability: EUCC.

Santoro R, Jucker T, Carboni M, Acosta ATR, Adler P. 2012. Patterns of plant community assembly in invaded and non-invaded communities along a natural environmental gradient. *Journal of Vegetation Science* 23(3): 483-494.

Sanyal A, Decocq G. 2015. Biological Flora of the British Isles: Crambe maritima. *Journal of Ecology* 103(3): 769-788.

Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, van de Koppel J, van de Leemput IA, Levin SA, van Nes EH, *et al.* 2012. Anticipating critical transitions. *Science* 338(6105): 344-348.

Schellberg J, Pontes LdS. 2012. Plant functional traits and nutrient gradients on grassland. *Grass and Forage Science* 67(3): 305-319.

Schmidtlein S, Feilhauer H, Bruelheide H, Rocchini D. 2012. Mapping plant strategy types using remote sensing. *Journal of Vegetation Science* 23(3): 395-405.

Schöb C, Armas C, Guler M, Prieto I, Pugnaire FI, Brooker R. 2013a. Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology* 101(3): 753-762.

Schöb C, Armas C, Pugnaire FI. 2013b. Direct and indirect interactions co-determine species composition in nurse plant systems. *Oikos* 122(9): 1371-1379.

Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122(3): 297-305.

Seiferling I, Proulx R, Wirth C. 2014. Disentangling the environmental-heterogeneity–species-diversity relationship along a gradient of human footprint. *Ecology* 95(8): 2084-2095.

Sherman D, Hotta S. 1990. Aeolian sediment transport: theory and measurement. *Coastal Dunes: Form and Process* 17: 37-37.

Silva GM, Hesp P, Peixoto J, Dillenburg SR. 2008. Foredune vegetation patterns and alongshore environmental gradients: Moçambique Beach, Santa Catarina Island, Brazil. *Earth Surface Processes and Landforms* 33(10): 1557-1573.

Silva GM. 2006. *Padrões Fitogeográficos em Sistemas Dunares do Noroeste de Portugal Continental.* MSc Thesis, University of Porto Porto, Portugal.

Silva P, Pinho P, Correia AI, Branquinho C, Correia O 2004. Estudo de Indicadores de Vulnerabilidade de sistemas dunares: um contributo para a gestão integrada de zonas costeiras. *8ª Conferência Nacional de Ambiente, Livro de Actas*. Lisboa.

Smyth TAG, Hesp PA. 2015. Aeolian dynamics of beach scraped ridge and dyke structures. *Coastal Engineering* 99: 38-45.

Spanò C, Balestri M, Bottega S, Grilli I, Forino LMC, Ciccarelli D. 2013a. Anthemis maritima L. in different coastal habitats: A tool to explore plant plasticity. *Estuarine, Coastal and Shelf Science* 129: 105-111.

Spanò C, Bruno M, Bottega S. 2013b. Calystegia soldanella: dune versus laboratory plants to highlight key adaptive physiological traits. *Acta Physiologiae Plantarum* 35(4): 1329-1336.

Stallins JA, Parker AJ. 2003. The Influence of Complex Systems Interactions on Barrier Island Dune Vegetation Pattern and Process. *Annals of the Association of American Geographers* 93(1): 13-29.

Stallins JA. 2003. Dune plant species diversity and function in two barrier island biogeomorphic systems. *Plant ecology* 165(2): 183-196.

Stankevièiûtë J. 2001. Correlation between species number and homogeneity in plant communities of the Lithuanian seacoast. *Biologija* 2.

Statsoft I 2010. Statistica (data analysis software system). Version 8.0. 2007.

Stein A, Kreft H. 2014. Terminology and quantification of environmental heterogeneity in species-richness research. *Biological reviews of the Cambridge Philosophical Society* 90(3): 815-836.

Sterk M, Gort G, Klimkowska A, van Ruijven J, van Teeffelen AJA, Wamelink GWW. 2013. Assess ecosystem resilience: Linking response and effect traits to environmental variability. *Ecological Indicators* 30: 21-27.

Stokes CJ, Archer SR. 2010. Niche differentiation and neutral theory: an integrated perspective on shrub assemblages in a parkland savanna. *Ecology* 91(4): 1152-1162.

Suding KN, Lavorel S, Chapin FS, Cornelissen JHC, DÍAz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas M-L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14(5): 1125-1140.

Tarhouni M, Belgacem AO, Neffati M, Henchi B. 2007. Qualification of rangeland degradation using plant life history strategies around watering points in southern Tunisia. *Pakistan Journal of Biological Sciences* 10(8): 1229-1235.

ter Braak CJF, Šmilauer P. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). *Section on Permutation Methods. Microcomputer Power, Ithaca, New York*: 10-10.

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277(5330): 1300-1302.

Tilman D, Pacala S. 1993. The maintenance of species richness in plant communities.

Tilman D. 1982. *Resource Competition and Community Structure*. Princeton, New Jersey, USA: Princeton University Press

Timmermann A, Damgaard C, Strandberg MT, Svenning J-C, Bennett J. 2015. Pervasive early 21st-century vegetation changes across Danish semi-natural ecosystems: more losers than winners and a shift towards competitive, tall-growing species. *Journal of Applied Ecology* 52(1): 21-30.

Tirado R, Pugnaire FI. 2003. Shrub spatial aggregation and consequences for reproductive success. *Oecologia* 136(2): 296-301.

Tissier EJ, McLoughlin PD, Sheard JW, Johnstone JF. 2013. Distribution of Vegetation along Environmental Gradients on Sable Island, Nova Scotia. *Ecoscience* 20(4): 361-372.

Tobias M. 2015. California foredune plant biogeomorphology. *Physical Geography* 36: 19-33.

Tsoar H. 2000. Geomorphology and paleogeography of sand dunes that have formed thekurkar ridges in the coastal plain of Israel. *Israel Journal of Earth Sciences* 49(3): 189-196.

Turnbull LA, Coomes D, Hector A, Rees M. 2004. Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology* 92(1): 97-109.

Turner MG, Collins SL, Lugo AL, Magnuson JJ, Rupp TS, Swanson FJ. 2003. Disturbance Dynamics and Ecological Response: The Contribution of Long-Term Ecological Research. BioScience 53(1): 46-56.

Ulrich W, Gotelli NJ. 2010. Null model analysis of species associations using abundance data. *Ecology* 91(11): 3384-3397.

UNEP. 2006. Marine and coastal ecosystems and human wellbeing: a synthesis report based on the findings of the Millennium Ecosystem Assessment: UNEP - United Nations Environment Programme.

van der Valk AG. 1975. The floristic composition and structure of foredune plant communities of cape hatteras national seashore. *Chesapeake Science* 16(2): 115-126.

Vaz AS, Macedo JA, Alves P, Honrado JP, Lomba A. 2015. Plant species segregation in dune ecosystems emphasises competition and species sorting over facilitation. *Plant Ecology and Diversity* 8(1): 113-125.

Vaz AS, Marques JF, Honrado J. 2014. Patterns of lichen diversity in coastal sand-dunes of northern Portugal. *Botanica Complutensis* 38: 89-96.

Veloso-Gomes F, Taveira-Pinto F, das Neves L, Pais Barbosa J, Coelho C. 2004. Erosion risk levels at the NW Portuguese coast: The Douro mouth - Cape Mondego stretch. *Journal of Coastal Conservation* 10(1): 43.

Vick JK, Young DR. 2011. Spatial Variation in Environment and Physiological Strategies for Forb Distribution on Coastal Dunes. *Journal of Coastal Research* 277(6): 1113-1121.

Wang S, Chen A, Pacala SW, Fang J. 2015. Density-dependent speciation alters the structure and dynamics of neutral communities. *Journal of Theoretical Biology* 372: 128-134.

Wang S, Loreau M. 2014. Ecosystem stability in space: alpha, beta and gamma variability. *Ecology Letters* 17(8): 891-901.

Waugh JM, Aarssen LW. 2011. Spatial indicators of plant community assembly from a 453-year sand-dune chronosequence. *Plant Ecology and Diversity* 4(2-3): 153-165.

Weltzin JF, McPherson GR. 2000. Implications of precipitation redistribution for shifts in temperate savanna ecotones. *Ecology* 81: 1902–1913.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199(2): 213-227.

Williams AT, Alveirinho-Dias J, Garcia Novo F, García-Mora MR, Curr R, Pereira A. 2001. Integrated coastal dune management: checklists. *Continental Shelf Research* 21(18-19): 1937-1960.

Williams BM, Houseman GR. 2013. Experimental evidence that soil heterogeneity enhances plant diversity during community assembly. *Journal of Plant Ecology* 7(5): 461-469.

Wilson JB, Gitay H. 1995. Limitations to species coexistence: evidence for competition from field observations, using a patch model. *Journal of Vegetation Science* 6(3): 369-376.

Wilson JB, Lee WG. 2000. C-S-R triangle theory: community-level predictions, tests, evaluation of criticisms, and relation to other theories. *Oikos* 91(1): 77-96.

Wilson JB. 1994. The Intermediate Disturbance Hypothesis of Species Coexistence Is Based on Patch Dynamics. *New Zealand Journal of Ecology* 18(2): 176-181.

Wilson, JB, Sykes MT. 1999. Is zonation on coastal sand dunes determined primarily by sand burial or by salt spray? A test in New Zealand dunes. *Ecology Letters* 2(4): 233-236.

Yan N, Baas ACW. 2015. Parabolic dunes and their transformations under environmental and climatic changes: Towards a conceptual framework for understanding and prediction. *Global and Planetary Change* 124: 123-148.

Zelený D, Li C-F, Chytrý M. 2010. Pattern of local plant species richness along a gradient of landscape topographical heterogeneity: result of spatial mass effect or environmental shift? *Ecography* 33(3): 578-589.

Zhang L, Baas ACW. 2012. Mapping functional vegetation abundance in a coastal dune environment using a combination of LSMA and MLC: a case study at Kenfig NNR, Wales. *International Journal of Remote Sensing* 33(16): 5043-5071.

Zorina SO. 2014. The sediment accommodation space and sedimentary successions in platformal basins: Mechanisms of formation. *Doklady Earth Sciences* 455(2): 399-402.

Zuo X, Wang S, Zhao X, Lian J. 2014. Scale dependence of plant species richness and vegetation-environment relationship along a gradient of dune stabilization in Horqin Sandy Land, Northern China. *Journal of Arid Land* 6(3): 334-342.

Appendices

Appendix 1 - List of species recorded during field surveys.

Species names	Family
Aetheorhiza bulbosa ssp. *bulbosa* (L.) Cass.	*Compositae*
*Agrostis stolonifera*L. var. *pseudopungens* (Lange) Kérguélen	*Gramineae*
Aira praecox L.	*Gramineae*
Ammophila arenaria (L.) Link ssp. *arundinacea* H. Lindb.	*Gramineae*
Anagallis monelli L. var. *macrophylla* (Ball) Vasc.	*Primulaceae*
Andryala integrifolia L.	*Compositae*
Anthyllis vulneraria L. ssp. *iberica* (W. Becker) Jalas ex Cullen	*Leguminosae*
Antirrhinum cirrhigerum Welw. ex Ficalho	*Scrophulariaceae*
Artemisia crithmifolia L.	*Compositae*
Briza maxima L.	*Gramineae*
Bromus diandrus Roth	*Gramineae*
Bromus rigidus Roth	*Gramineae*
Cakile maritima Scop. ssp. *integrifolia* (Hornem.) Greuter et Burdet	*Cruciferae*
Cakile maritima ssp. *maritima* Scop.	*Cruciferae*
Calystegia soldanella (L.) R. Br.	*Convolvulaceae*
Carex arenaria L.	*Cyperaceae*
Centaurium chloodes (Brot.) Samp.	*Gentianaceae*
*Cerastium diffusum*ssp. *diffusum* Pers.	*Caryophyllaceae*
Cistus salviifolius L.	*Cistaceae*
Corema album (L.) D. Don	*Empetraceae*
Corrigiola littoralis ssp. *littoralis* L.	*Caryophyllaceae*
Corynephorus canescens (L.) P. Beauv.	*Gramineae*
Crataegus monogyna Jacq.	*Rosaceae*
Crucianella maritima L.	*Rubiaceae*

Species names	Family
Cyperus capitatus Vand.	*Cyperaceae*
Cytisus grandiflorus (Brot.) DC.	*Leguminosae*
Daphne gnidium L.	*Thymelaeaceae*
Elymus farctus (Viv.) Runemark ex Melderis ssp. *boreali-atlanticus* (Simonet et Guin.) Melderis	*Gramineae*
Erodium cicutarium (L.) L'Hér.	*Geraniaceae*
Eryngium maritimum L.	*Umbelliferae*
Euphorbia paralias L.	*Euphorbiaceae*
Euphorbia portlandica L.	*Euphorbiaceae*
Evax pygmaea (L.) Brot. ssp. *ramosissima* (Mariz) R. Fernandes et I. Nogueira	*Compositae*
Filago minima (Sm.) Pers.	*Compositae*
Halimium calycinum (L.) K. Koch	*Cistaceae*
Helichrysum italicum (Roth) G.Don ssp. *picardi* (Boiss. et Reut.) Franco	*Compositae*
Herniaria ciliolata Melderis ssp. *robusta* Chaudhri	*Caryophyllaceae*
Hypochaeris glabra L.	*Compositae*
Hypochaeris radicata L.	*Compositae*
Iberis procumbens ssp. *procumbens* Lange	*Cruciferae*
Jasione maritima (Duby) Merino var. *sabularia* (P. Cout.) Sales et Hedge	*Campanulaceae*
Juniperus phoenicea ssp. *phoenicea* L.	*Cupressaceae*
Lagurus ovatus L.	*Gramineae*
Leontodon taraxacoides ssp. *taraxacoides* (Vill.) Mérat	*Compositae*
Linaria polygalifolia Hoffmanns. et Link	*Scrophulariaceae*
Lotus creticus L.	*Leguminosae*
Lupinus angustifolius L.	*Leguminosae*

Species names	Family
Malcolmia littorea (L.) R.Br.	*Cruciferae*
Medicago marina L.	*Leguminosae*
Myrtus communis L.	*Myrtaceae*
Orobanche purpurea Jacq.	*Orobanchaceae*
Otanthus maritimus (L.) Hoffmanns. et Link	*Compositae*
Pancratium maritimum L.	*Amaryllidacea*
Paronychia argentea var. *argentea* Lam.	*Caryophyllaceae*
Plantago coronopus L.	*Plantaginaceae*
Polycarpon tetraphyllum ssp. *tetraphyllum* (L.) L.	*Caryophyllaceae*
Polygonum maritimum L.	*Polygonaceae*
Polypodium interjectum Shivas	*Polypodiaceae*
Quercus suber L.	*Fagaceae*
Reichardia gaditana (Willk.) Samp.	*Compositae*
Rubia peregrina L.	*Rubiaceae*
Rubus ulmifolius Schott	*Rosaceae*
Rumex acetosella L. ssp. *angiocarpus* (Murb.) Murb.	*Polygonaceae*
Scirpoides holoschoenus (L.) Soják	*Cyperaceae*
Scrophularia frutescens L.	*Scrophulariaceae*
Sedum acre L.	*Crassulaceae*
Sedum album L.	*Crassulaceae*
Sedum sediforme (Jacq.) Pau	*Crassulaceae*
Senecio gallicus Vill. in Chaix	*Compositae*
Sesamoides purpurascens (L.) G. López	*Resedaceae*
Seseli tortuosum L.	*Umbelliferae*
Silene littorea ssp. *littorea* Brot.	*Caryophyllaceae*

Species names	Family
Silene niceensis All.	*Caryophyllaceae*
Silene portensis ssp. *portensis* L.	*Caryophyllaceae*
Stauracanthus genistoides (Brot.) Samp.	*Leguminosae*
Trifolium arvense L.	*Leguminosae*
Ulex europaeus L. ssp. *latebracteatus* (Mariz) Rothm.	*Leguminosae*
Verbascum litigiosum Samp.	*Scrophulariaceae*
Vulpia alopecuros (Schousb.) Dumort.	*Gramineae*
Xolantha guttata (L.) Raf.	*Cistaceae*

Appendix 2 - List of species classified according to the CSR scheme of Grime (1974) and to the dune plant functional types (PFT) of García-Mora *et al.* (1999).

Species	CSR	PFT
Aetheorhiza bulbosa	SR	III
Agrostis stolonifera var. *pseudopungens*	CS	II
Aira praecox	SR	I
Ammophila arenaria ssp. arundinacea	CS	III
Anagallis monelli	S	II
Andryala integrifolia	CR	II
Anthyllis vulnerari ssp. iberica	CS	II
Antirrhinum majus ssp. cirrhigerum	S	II
Artemisia campestris ssp. maritima	CS	II
Briza maxima	R	I
Bromus diandrus	R	I
Bromus rigidus	R	I
Cakile maritima ssp. integrifolia	SR	III
Cakile maritima ssp. maritima	SR	III
Calystegia soldanella	CS	III
Carex arenaria	SR	III
Centaurium chloodes	SR	II
Cerastium diffusum	R	I
Cistus salvifolius	CR	II
Corema album	CS	III
Corrigiola littoralis	SR	II
Corynephorus canescens	CS	II
Crataegus monogyna	C	II

Species	CSR	PFT
Crucianella maritima	S	III
Cyperus capitatus	SR	III
Cytisus grandiflorus	CS	II
Daphne gnidium	SR	II
Elytrigia juncea ssp. boreali-atlantica	CS	III
Erodium cicutarium ssp. bipinnatum	SR	I
Eryngium maritimum	S	III
Euphorbia paralias	S	III
Euphorbia portlandica	SR	II
Evax pygmaea ssp. ramosissima	SR	I
Filago minima	SR	I
Halimium calycinum	CS	II
Helichrysum italicum	CS	III
Herniaria ciliolata	CS	II
Hypochoeris glabra	R	II
Hypochoeris radicata	CR	II
Iberis procumbens	SR	III
Jasione maritima var. sabularia	CS	III
Juniperus phoenicea	CS	III
Lagurus ovatus	SR	I
Leontodon taraxacoides ssp. taraxacoides	CSR	II
Linaria polygalifolia ssp. polygalifolia	SR	II
Lotus creticus	CS	III
Lupinus angustifolius	R	I
Malcolmia littorea	SR	II

Species	CSR	PFT
Medicago marina	S	III
Myrtus communis	C	II
Orobanche purpurea	SR	II
Otanthus maritimus	S	III
Pancratium maritimum	S	III
Paronychia argentea	SR	II
Plantago coronopus	SR	II
Polycarpon tetraphyllum	R	I
Polygonum maritimum	CS	III
Polypodium interjectum	CR	II
Quercus suber	C	II
Reichardia gaditana	CSR	II
Rubia peregrina	CR	II
Rubus ulmifolius	CSR	II
Rumex acetosella ssp. angicarpos	SR	II
Scirpoides holoschoenus	CS	II
Scrophularia frutescens	CS	II
Sedum acre	CS	II
Sedum album	CS	II
Sedum sediforme	CS	II
Senecio gallicus	CR	I
Sesamoides purpurascens	CS	II
Seseli tortuosum	CS	II
Silene littorea	SR	I
Silene niceensis	SR	I

Species	CSR	PFT
Silene portensis	SR	I
Stauracanthus genistoides	CS	II
Trifolium arvense	R	I
Ulex europaeus ssp. latebracteus	CR	II
Verbascum litigiosum	CS	II
Vulpia alopecuros	R	I
Xolantha guttata	R	I

Appendix 3 – Spearman correlation test results (R) between the species richness of each class of CSR and functional type classifications (n = 92). Statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Species classification	I	II	III	C	CR	CS	CSR	R	S	SR
I		0.487***	-0.147	-0.057	0.147	0.401***	-0.084	0.835***	-0.223*	0.774***
II			-0.172	0.366***	0.558***	0.725***	-0.035	0.515***	-0.077	0.518***
III				0.229*	-0.232*	0.241*	0.214*	-0.256*	0.729***	-0.035
C					0.161	0.252*	0.378***	-0.106	0.297*	-0.125
CR						0.283**	-0.077	0.226*	-0.261*	0.130
CS							-0.279**	0.351**	0.080	0.324**
CSR								-0.133	0.150	-0.011
R									-0.246*	0.545***
S										-0.252*