eman ta zabal zazu

UPV EHU

Vegetation of the Cantabrian-Atlantic dunes: ecological drivers and biodiversity patterns at multiple scales

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Agradecimientos

Tu gitana que adevinhas
me lo digas pues no lo se
si saldré desta aventura
o si nela moriré.

Cancioneiro de Vila Viçosa
José Afonso

Tales eran los versos que escuché con atención por primera vez en un disco de Luar na Lubre cuando iba a uno de los puntos de muestreo en Galicia. Por aquel entonces me encontraba en los inicios de la tesis y me sentí muy identificada con ellos. Me parecía estar adentrándome en una aventura de final incierto y de la que nadie podía asegurarme cómo acabaría. Si saldría todo bien o si me quedaría por el camino. La ilusión y las ganas de aquellos días se mezclaban con las dudas y los temores.

Ha pasado tiempo desde esos inicios. Ahora resulta que la aventura se acerca a su fin. Quién lo diría. Aquel horizonte lejano casi parece al alcance de la mano, a tan solo un paso. Paso que ni mucho será de los más fáciles. Atrás quedan otros pasos, otros momentos. Y fueran como fueran, casi siempre compartidos. Porque esta aventura, aunque parece que la escribe un único protagonista, no es cierto. Hay otras personas que lo acompañan y a las que es justo reconocer y agradecer.

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Y hasta este 2020 llega la aventura de una tesis sobre dunas costeras. Muestreos mirando al horizonte sin olvidar el suelo, donde estaban las plantas. Ahora vienen otros horizontes, distintos y difusos, a los que acompañarán otras canciones. Otros sones del mar o de la tierra. En cualquier caso, como dice una letra de Mike Oldfield, *Only time, only time will tell.*

Resumen

Introducción

Las dunas costeras se forman por la acumulación de arena que el viento trae desde la playa y que lleva tierra adentro. El origen de esta arena está en la erosión de las rocas de los acantilados o de las montañas. En el caso de las montañas los ríos son los encargados de transportarla hacia el mar. En el norte de la península ibérica los ecosistemas dunares más extensos se ubican junto a estuarios o desembocaduras de ríos que aportan una gran cantidad de sedimentos, parte de los cuales se acaba depositando en las playas y arenales costeros.

Los ecosistemas dunares son muy cambiantes y dinámicos, tanto en el tiempo como en el espacio, debido a la continua acción del viento y las olas. A causa de ello, se produce un marcado gradiente decreciente de exposición a estos elementos desde las zonas más cercanas a la orilla hasta las situadas más hacia el interior, tierra adentro. Como consecuencia se crea un fuerte gradiente ecológico que afecta a la distribución de la vegetación, que da lugar a una zonación vegetal muy característica que se reproduce en todas las costas del mundo. Así, en las costas atlánticas europeas se distinguen diferentes hábitats, que están recogidos en la Directiva Hábitat 92/43/CEE de la Comisión Europea debido a la importancia ecológica que presentan y a su singularidad. En concreto, para este estudio se han considerado los tres hábitats más importantes y más ampliamente distribuidos.

El primero de ellos, que ocupa la primera banda de vegetación vivaz, es la duna embrionaria (código de hábitat 2110 en la Directiva). Es un hábitat muy expuesto al viento y el oleaje, cuya cobertura vegetal se encuentra dominada por especies como *Elytrigia juncea* y otras plantas muy tolerantes a la inundación por las olas. La segunda banda de vegetación la forman las dunas móviles (código 2120), que presentan una mayor acumulación de arena y poca materia orgánica. La especie dominante es *Ammophila arenaria*. La tercera banda de vegetación está formada por las dunas fijas (código 2130). Dada su ubicación tierra adentro, a lo largo del gradiente dunar, este es un hábitat más protegido de la acción del viento y el mar, con una mayor concentración de materia orgánica en el sustrato, en el que no suele haber una especie que se destaque por su abundancia.

Atendiendo a la composición de especies, desde el punto de vista fitosociológico en estos hábitats se reconocen varios sintaxones, todos ellos pertenecientes a la Clase *Ammophiletea*, según el siguiente esquema sintaxonómico:

Clase *Ammophiletea* Br.-Bl et Tx. ex Westhoff et al. 1946
Vegetación costera del Mediterráneo y del mar Negro

Orden *Ammophiletalia* Br.-Bl. et Tx. ex Westhoff et al. 1946

Céspedes de herbáceas altas en dunas costeras móviles y embrionarias de las costas templadas y boreo-atlánticas del Mediterráneo y los mares Negro y Caspio

Alianza *Ammophilion* Br.-Bl. 1921

Céspedes de herbáceas altas en dunas costeras móviles y embrionarias de las costas mediterráneas. Se distinguen cuatro asociaciones en el área estudiada.

—*Euphorbio paraliae-Agropyretum junceiformis* Tüxen in Br.-Bl. & Tüxen 1952 corr. Darimont, Duvigneaud & Lambinon 1962

—*Otantho maritimi-Ammophiletum australis* Géhu & Tüxen 1975 corr. F.Prieto & T.E. Díaz 1991

—*Sileno thorei-Ammophiletum arenariae* (Géhu 1968) Géhu, Géhu-Franck & Bournique 1995

—*Galio arenari-Hieracietum eriophori* Géhu (1968) 1982

Orden *Artemisio-Koelerietalia* Sissingh 1974

Praderas arenosas y arbustivas de dunas grises estabilizadas de las costas templadas del océano Atlántico y costas norte del mar Adriático y mar de Liguria

Alianza *Euphorbio portlandicae-Helichrysion stoechadis* Géhu et R.Tx. in Sissingh 1974

Praderas arenosas de arbustos enanos en dunas grises estabilizadas de las costas franco-atlánticas del Océano Atlántico

—*Helichryso stoechadis-Koelerietum arenariae* Loriente 1974 corr. Rivas-Martínez, Fernández-González & Loidi 1997

Orden *Crucianelletalia maritimae* Sissingh 1974

Praderas mediterráneas y cántabro-franco-atlánticas con arbustos enanos en dunas estabilizadas

Alianza *Helichrysion picardii* (Rivas-Mart., M. Costa et Izco in Rivas-Mart. et al. 1990) Rivas-Mart. et al. 1999

Matorrales enanos ibero-atlánticos en costas dunares.

—-*Iberidetum procumbentis* Bellot 1968

Tabla 1: Resumen de los tipos de diversidad por nivel (alfa, beta) y por componente (taxonómica, funcional y filogenética).

Diversidad	Alfa	Beta
Taxonómica	Lista de especies de un lugar o hábitat	Variación de especies entre hábitats
Funcional	Valor y rango de los atributos funcionales de las especies de un lugar o hábitat	Cambios de grupos taxonómicos entre hábitats con funciones similares o diferentes
Filogenética	Relaciones evolutivas entre los grupos taxonómicos de un lugar o hábitat	Cambios filogenéticos entre hábitats

Además del estudio del ecosistema dunar, otro aspecto importante que desarrolla esta tesis es el concepto de biodiversidad. Esta se puede definir como la diversidad de especies, genética y de ecosistemas en un lugar. La diversidad se puede considerar a varios niveles: alfa, beta y gamma. La diversidad alfa hace referencia a un lugar determinado de estudio, mientras que el conjunto de todas las áreas es la gamma diversidad. La diversidad beta es la variación de especies entre hábitats.

Por otro lado, según el componente de diversidad analizado podemos hablar de diversidad taxonómica, funcional o filogenética. La diversidad taxonómica está relacionada con la composición de especies. La diversidad funcional se define como el valor y rango de diversos atributos funcionales de los organismos en un ecosistema dado. La diversidad filogenética, por su parte, incorpora las relaciones evolutivas entre las especies.

Metodología

El estudio se llevó a cabo a lo largo de la costa norte de España y parte de la costa suroccidental de Francia con una distancia total de 750 km. El área se encuentra en la provincia biogeográfica Europea Atlántica y dentro de ella en la subprovincia Cántabro Atlántica. Dentro de esta subprovincia se reconocen cuatro sectores biogeográficos: Galaico-Portugués Septentrional (GP), Galaico Septentrional-Asturiano (GA), Cántabro-Vascónico (CB) y Aquitano-Landés (AL).

Dentro del área de estudio se seleccionaron 12 localidades (Figura 1) de acuerdo a que presentaran un ecosistema no alterado y condiciones de naturalidad. Asimismo, se buscó que tuvieran suficiente área para poder realizar los muestreos.

En cada localidad se muestrearon 12 cuadrados de 100 m^2, 10 x 10 m, que a su vez contenían cuadrados anidados de menor tamaño. El esquema de distribución de los cuadrados se presenta en la Figura 2 .

De los doce cuadrados de 100 m^2 muestreados en cada playa, cuatro de ellos fueron ubicados en dunas embrionarias, cuatro en dunas móviles y cuatro en dunas fijas. El número total de cuadrados de cada tamaño se indica en la Tabla 2 .

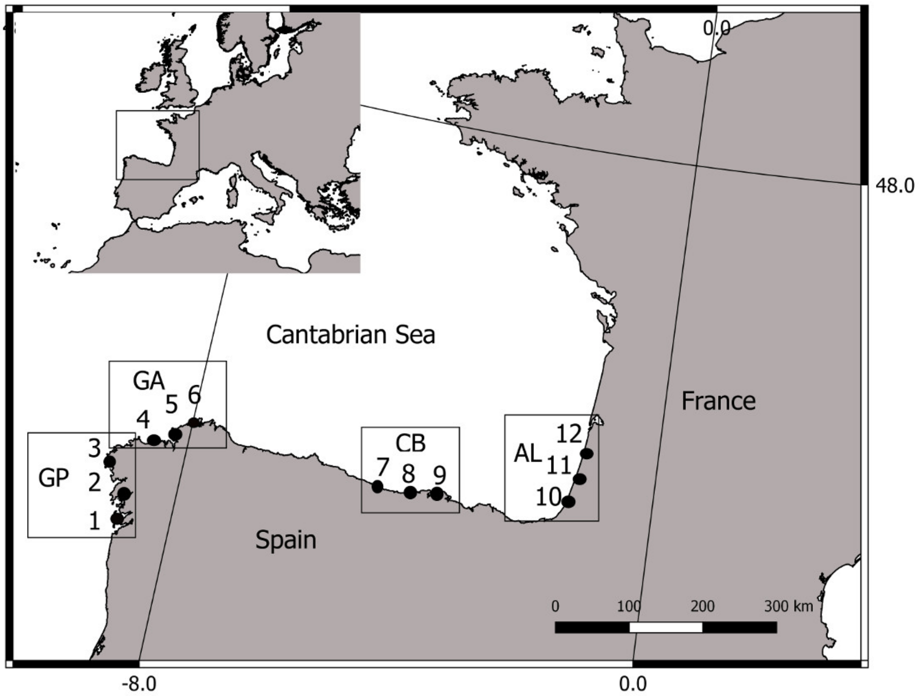

Figura 1: Área de estudio. Doce localidades de Galicia a Francia. 1. La Lanzada 2. As Furnas 3. Carnota 4. Barrañán 5. San Xurxo 6. Valdoviño 7. Oyambre 8. Liencres 9. Noja 10. Tarnos 11. Casernes 12. Messanges. Sectors: AL = Aquitano-Landés, CB = Cántabro-Vascónico, GA = Galaico Septentrional-Asturiano and GP = Galaico-Portugués Septentrional.

Para medir la diversidad funcional, se analizaron un total de diez atributos para medir la diversidad funcional. Estos atributos fueron: la forma vital de Raunkiaer, la distribución geográfica, el inicio y duración de la floración, el tipo de polinización, el tipo de fruto y su mecanismo de dispersión, el área foliar específica, la altura de la planta y el peso de la semilla. En cada cuadrado de 100 m^2 se tomaron muestras del suelo que se analizaron en el laboratorio. Los parámetros analizados fueron: pH, materia orgánica (%), Kjeldahl Nitrogen (%), P (mg/l), Na (mg/l), K (mg/l), Mg (mg/l), Ca (mg/l) and textura (%). Respecto al clima se obtuvieron datos de temperatura media anual, temperatura media diurna, isotermalidad, estacionalidad de la temperatura, rango anual de temperatura, temperatura media del mes más cálido, precipitación anual, precipitación del mes más seco, precipitación del mes más cálido. También se construyó un árbol filogenético con las especies inventariadas a partir del árbol filogenético de referencia R20120829 para plantas, que se corresponde con el APG III (Angiosperm Phylogeny Group).

Los análisis de datos en su mayor parte se realizaron con el programa R destacándose los paquetes *Vegan* y *Picante* con sus funciones. Con Picante se calcularon los índices de diversidad filogenética. Con Vegan se construyeron las ordenaciones espaciales de db-RDA (Distance-Based Redundance Data Analysis) y los CCA (Correspondence Canonical Analysis) y las particiones de la variación. También se utilizó el programa PERMANOVA+ para Primer en algunas comparaciones entre sectores biogeográficos para diversidad alfa.

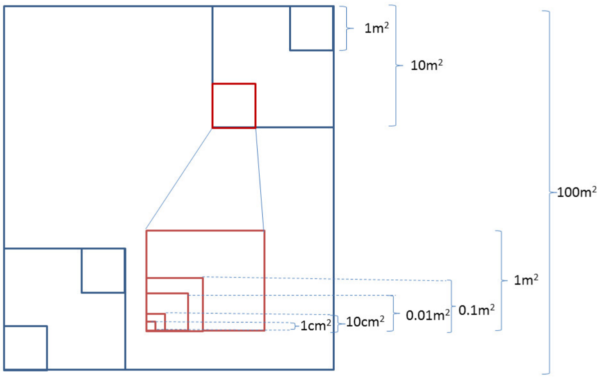

Figura 2: Esquema de cuadrados anidados de muestreo de 100 m^2 a 1 cm^2.

Tabla 2: Número de cuadrados de muestreo a diferentes escalas por tipo de vegetación, localidad y total de localidades.

	Total por tipo de vegetación	Total por localidad	Total por conjunto de 12 localidades
100 m^2	48	12	144
10 m^2	96	24	288
1 m^2	192	48	576
0.1 m^2	192	48	576
0.01 m^2	192	48	576
0.001 m^2	192	48	576
0.0001 m^2	192	48	576
Total	1104	276	3312

Resultados

Análisis de diversidad alfa

En este capítulo se analiza la diversidad taxonómica, funcional y filogenética a nivel alfa de los cuadrados de 10 m^2. Para la diversidad taxonómica se usa el índice de Shannon; para la diversidad funcional el CWM (Community Weighted Mean) y el índice de Rao; para la diversidad filogenética el NRI (Net Relatedness Index) y el NTI (Nearest Taxon Index). Con el fin de ver una distribución inicial de los cambios de composición en el gradiente ecológico se llevó a cabo un NMDS (non-Metric Multidimensional Scaling) usando la distancia de Bray-Curtis. Los índices fueron comparados mediante PERMANOVA y modelos lineares mixtos. Los resultados mostraron mayores valores de diversidad taxonómica y funcional según nos desplazamos en el gradiente ecológico desde la playa hacia el interior, mientras que la diversidad filogenética disminuyó.

Análisis de diversidad beta

En este capítulo se estudió la diversidad taxonómica, funcional y filogenética de los cuadrados de 10 m^2 a nivel de diversidad beta. Se analizaron mediante db-RDA (Distance-based Redundance Data Analysis) según diferentes índices. Para la diversidad taxonómica se usó el de Bray-Curtis, para la diversidad filogenética los equivalentes en diversidad beta de NRI y NTI que son el Dpw y el D_{nn} y para la diversidad funcional una versión del D_{pw} basado en una matriz de distancias. Por otra parte, se descompuso la diversidad beta en dos componentes: riqueza y reemplazamiento. Los resultados indicaron una falta de relación con el gradiente biogeográfico en duna embrionaria para la diversidad funcional y filogenética. Las dunas móviles y fijas sí mostraron una relación entre la distancia a lo largo de la costa y la distribución de los cuadrados en la ordenación espacial excepto para el D_{pw} de las dunas móviles. Respecto a la descomposición de la beta diversidad se encontró una mayor contribución del componente de riqueza en duna embrionaria y de reemplazamiento en duna fija.

Componentes de diversidad a diferentes escalas

En este apartado se abordan los cambios que se producen en la diversidad taxonómica, funcional y filogenética según la escala en la que sean medidas. Aquí se tuvieron en cuenta las series de cuadrados anidados desde 1 cm^2 hasta 100 m^2. Para cada uno de los tres componentes de la diversidad se usaron diferentes índices. Para la diversidad taxonómica se usó la riqueza, obteniéndose las clásicas curvas SAR (Species Area Relationship). Para la diversidad filogenética se usó el índice de Faith y para diversidad funcional uno equivalente basado en un dendrograma derivado de los datos de atributos. Los cálculos se realizaron tanto para el total de especies como para una división entre especies generalistas y especialistas propias de los hábitats dunares. Referido a los resultados se obtuvo un incremento de las pendientes de las curvas desde la duna embrionaria a la duna fija para los tres tipos de diversidad. Las especies especialistas reflejaron patrones de distribución por áreas similares al de total de especies, lo que indica que las especialistas tienen mayor influencia en los patrones de biodiversidad del ecosistema. Se vio una correlación entre especialistas y generalistas en áreas de 100 m^2. A escalas pequeñas no se observó relación en las dunas embrionarias y móviles, siendo negativa en el caso de la duna fija, indicando una competencia significativa entre los dos grupos de especies.

Factores abióticos

Este capítulo incluye el análisis de factores abióticos como las variables edáficas, climáticas y las coordenadas espaciales. Se han estudiado diferentes variables del suelo como son la granulometría, el pH, la materia orgánica y la abundancia de algunos elementos químicos (N, P, Na, K, Mg, Ca). Entre las variables climáticas se seleccionaron algunas relacionadas con la temperatura y la precipitación, con mayor significancia biológica. Para ver la relación entre la vegetación y los factores abióticos se realizaron tres grupos de CCA (Canonical Correspondence Analysis): uno para la granulometría y el resto de variables del suelo, otro con las variables climáticas y un tercer grupo de CCA con todas las variables analizadas en conjunto. Por otra parte, se estudió el porcentaje de variación explicada por las variables edáficas, climáticas y espaciales para el total de especies y para las especialistas y generalistas. Entre los resultados obtenidos se observó una disminución del pH y un incremento de la materia orgánica desde la orilla hacia el interior. En el sector Aquitano-Landés las concentraciones de minerales fueron inferiores al resto de sectores. El porcentaje de variación explicado para la composición de especies por las variables de espacio, clima y suelo fue diferente según el tipo de duna, siendo mayor en dunas fijas. Asimismo también fue mayor para especies especialistas.

Integración

Integrando los resultados obtenidos se ha observado que el gradiente ambiental desde el mar hacia tierra adentro es el que más influye en la zonación de las comunidades y en la composición de sus especies. En duna embrionaria, la comunidad más expuesta al viento y al mar, se da una selección de especies muy concretas y bien adaptadas. Aquí las especies generalistas están casi ausentes y predominan las especialistas. Esta especialización se traduce en una homogeneidad en los atributos funcionales que lleva a bajos valores de diversidad funcional en comparación con otras comunidades. Esta selección de atributos se da en diferentes géneros y familias, lo que conlleva mayores valores de diversidad filogenética que en dunas fijas.

La selección de especies junto a sus atributos se da a lo largo de la costa estudiada. Sin embargo, la presencia de algunas especies particulares en algunas localidades, sobre todo en los extremos del área de estudio hizo que se encontrara una relación entre la diversidad taxonómica y la distancia a lo largo de la costa. Esto no influyó en la diversidad funcional y filogenética que se mantuvo homogénea.

La duna móvil es una comunidad de transición entre la duna embrionaria y la duna fija. Se aprecia más diversidad en número de especies, además de en funcionalidad y relación de familias y géneros. Esta comunidad está dominada principalmente por *Ammophila arenaria* subsp. *australis* que puede imponer sus atributos a la comunidad debido a su abundancia, como en el caso de la altura. Esta comunidad fue la más variable en representación a lo largo del área de estudio. En Francia la presencia de *Ammophila* era escasa llegando a la completa ausencia en alguna playa. En el resto de localidades se encontraba fragmentada y en manchas aisladas.

La duna fija es la comunidad situada más al interior estudiada. Esto hace que el efecto de las olas y el viento sea menor. Como consecuencia aparecen más especies generalistas provenientes de ambientes humanizados o ruderalizados que se encontraban detrás de las dunas costeras. Estos podían ser aparcamientos o paseos marítimos. Debido a la protección de este hábitat pueden crecer más especies, lo que hace que la riqueza de especies sea mayor. Este aumento de la riqueza va seguido de un incremento de la diversidad funcional. La diversidad filogenética es menor que en duna embrionaria, aunque algún índice más relacionado con la riqueza dio valores mayores de diversidad filogenética. Asimismo se observa que hay un incremento de géneros y especies dentro de las familias más abundantes como gramíneas y compuestas.

Esta diversificación en duna fija dentro del gradiente ecológico también se traduce en cambios a lo largo de la costa. La composición de especies se divide en dos grandes grupos, por un lado los sectores occidentales Galaico-Asturiano y Galaico-Portugués, por otro lado los sectores orientales Cántabro-Vascónico y Aquitano-Landés. Esta división territorial también se refleja en la diversidad funcional y en la filogenética, aunque se observó que en varios casos géneros de la misma familia o incluso especies del mismo género se reemplazaban de una zona a otra. Un ejemplo es el cambio de *Helichrysum stoechas* por *Helicrysum picardii*. Este reemplazamiento de especies podría estar motivado por la transición climática que se da a lo largo del área de estudio.

La zona oriental con Cantabria y Francia presentan temperaturas más bajas y una mayor precipitación a lo largo del año. En la zona occidental, en Galicia, las temperaturas se hacen más templadas y los veranos son relativamente más secos. Esto hace que se den unas condiciones más propicias para el crecimiento de especies de óptimo mediterráneo. La aparición de especies mediterráneas conlleva un importante cambio a nivel taxonómico y funcional. Las variables edáficas indicaron que, por ejemplo, la granulometría se mantenía constante dentro de las localidades, lo que es congruente con la corta distancia, cientos de metros tierra adentro, en la que se encontraban distribuidas las comunidades vegetales en cada sistema dunar, no dando lugar a una disminución significativa del tamaño de grano de arena hacia el interior. Sin embargo, se observó la presencia de una arena más fina en las playas cántabras, lo que estaría ligado a la dominancia de sustratos calizos de esta zona frente a los sustratos graníticos de las áreas gallegas.

Asimismo, se observó un incremento en el número de especies con el tamaño de área muestreada, que fue seguido por un aumento de la diversidad funcional y la filogenética. La pendiente de este incremento fue más acusada en duna fija que en la duna embrionaria, lo que coincide con el aumento observado de la riqueza específica a lo largo del gradiente ecológico. Referido al incremento de los distintos componentes de la diversidad, se vio que el patrón está dominado por las especies especialistas de hábitats dunares. Esto es congruente con la escasa de presencia de especies generalistas en la duna embrionaria y la escasa cobertura en el resto de comunidades vegetales estudiadas.

En resumen se puede concluir que las condiciones ecológicas a nivel local contribuyen con mayor importancia a la distribución de las especies en las dunas costeras, siendo más selectivas en las comunidades cercanas al mar, más influidas por el viento y el oleaje. Esta situación da lugar a una duna embrionaria más homogénea a lo largo del área de estudio y a una diversificación en dos zonas en la duna fija. Este fenómeno de homogeinidad en la duna embrionaria se cumple para la composición de especies y se da también en la diversidad

funcional y filogenética. La diferenciación biogeográfica se podría atribuir en parte a la transición climática de condiciones más atlánticas en el este a más mediterráneas en el oeste.

Este trabajo resalta la singularidad de cada tipo de vegetación en las dunas costeras y cómo se comportan los diferentes componentes de la diversidad en cada uno de ellos. Puede ser especialmente útil para ver qué especies son más comunes a lo largo del área de estudio y cuáles son más infrecuentes, así como para subrayar la importancia de la diversidad funcional y filogenética. Finalmente, el trabajo aporta valiosa información para fijar futuras estrategias de gestión en estos hábitats de interés para la conservación, compaginando su funciones ecológicas, educativas o recreativas.

Chapter 1

General introduction

1.1. Coastal dune formation

Coastal dunes are ecosystems found on all continents and under a wide range of climatic and geologic conditions (Maun, 2009). They are eolian land forms that develop in coastal situations where a sand-sized sediment is available to be transported inland by the ambient winds (Martínez et al., 2004). Sand can come from many sources. Mountains are eroded and that sand is transported by the rivers to the sea. Another source of sand can be the erosion of the cliffs. Then, with the action of the waves and wind that sand is transported inland.

In first place, beaches are formed. Beaches depend on wave energy, sand quantity, beach orientation and rate of sea level all in a dynamic equilibrium (Pilkey et al., 1998). Beaches and dunes are tightly related and have a great impact in the evolution and development of the coasts (Packham and Willis, 1997). When sand is dried by the action of wind it goes inland. The mean grain size decrease with increasing distance from the coastline (Ishikawa et al., 1995). When sand finds an obstacle, a stone or a plant, it begins to accumulate. However, sand dunes are more than sand piles. They are stratified and alternate layers of sand when the wind blows and other films of silt and clay when the wind is not blowing (Loidi and Campos, 2008).

Storms cause rapid rates of sediment movement. Winds move sand grains onshore where vegetation helps to trap them, creating large sand dunes in areas with abundant sediment (Doody, 2013). Sediment budget is an important concept related to the amount of sediment that enters and leaves a system. Sand dunes have some crucial factors such as material input, sediment size, wind speed and the presence of obstacles (Martínez, 2009).

In Spain we find the most important dune fields next to estuaries or river mouths. In the northern Spanish coasts there are many short but mighty rivers so that sand provision is abundant. When these sediments reach the sea they are transported through littoral drift along the Atlantic and Cantabrian coasts. This sedimentary deposition is often increased by the high degree of soil erosion present in many parts of the northern coast, in many areas as a consequence of logging or withdrawal of *Eucalyptus* or *Pinus* plantations (Doody, 2015). In France, South of Arcachon and Les Landes in the Gascony coast, behind the foredune there is a fringe of formerly transgressive dune ridges 60-70 m high and up to 6 km wide. The ridges have been stabilised by pine plantations of *Pinus pinaster* introduced from 1801 onwards by Nicolas Brémontier (Doody, 2010).

1.2. Ecology

Sandy seashores hold one of the most dynamic landscapes on earth due to the action of wind, waves and tides (van der Meulen and Udo de Haes, 1996; Maun, 2008). Moreover, coastal dunes include an outstanding ecological diversity in terms of environmental heterogeneity and species composition (Van Der Maarel, 2003). Coastal dune landscapes are harsh environments embedded in constraining ecotones (Acosta et al., 2006; Bazzichetto et al., 2016). In addition, the species inhabiting coastal dune landscapes are usually well adapted to drastic landscape changes (Malavasi et al., 2018).

Gradients have been successfully used to understand many aspects of plant ecology. Gradients provide an ideal opportunity to study natural variation in abiotic factors that may drive community change (Grime, 1977, 1979; Tilman, 1988; Goldberg, 1990; Bertness and Callaway, 1994; Callaway, 1995, 1997). Coastal dunes are characterized by strong ecological gradients due to differences in the abiotic conditions. These differences allow for the establishment of a typical spatial arrangement of the plant community along a sea-inland gradient, typically described as «zonation» (Tordoni et al., 2018). Thus, along a coast-to-inland gradient with changing environmental conditions (soil, nutrients, microclimate) the establishment of various species is favoured.

Different habitats form the sea-inland gradient: beach, embryo or white dune, mobile or yellow dunes and finally fixed or grey dunes. In our study we did not sampled beaches due to the scarce vegetation that grows there and the human pressure that makes it even less present. Coastal dunes are valuable places and are recognised in the Habitats Directive 92/43/EEC (European Commission, 1992) with the following codes: «Annual vegetation of drift lines» (habitat code 1210), including both the Atlantic and Mediterranean seashores, and two foredune habitats: the «Embryonic shifting dunes» (habitat code 2110) and the «Shifting dunes along the shoreline with Ammophila arenaria» (habitat code 2120). «Fixed coastal dunes with herbaceous vegetation» (habitat code 2130) are the grey dunes.

About the functioning of the ecosystem we can talk about environmental filters. Coastal dunes are exposed to harsh environmental conditions such as strong winds and waves. This could lead to environmental filtering species, in particular those next to sea. The current use of the environmental filtering concept has its roots in the study of plant community assembly and dynamics in the late 1970's and early 1980's (Bazzaz, 1991; Nobel and Slatyer, 1977; Van der Valk, 1981; Woodward and Diament, 1991). These foundational studies described the environment as a metaphorical «sieve» or «filter» that only permits species with particular traits or phenotypes to establish and persist (Kraft et al., 2015). Environmental filtering is predicted to promote the establishment of new species that possess optimal traits for underlying abiotic conditions, causing traits to converge towards a single optima (Weiher et al., 1998). Strong abiotic filters are expected to constrain the range of species trait values and to lead to convergent or «underdispersed» local trait distributions (Weiher et al., 1998; Cornwell et al., 2006; Grime, 2006). Following the sea-inland gradient environmental forces tend to be lower. Then, instead of trait convergence we find trait divergence in communities under low environmental stress compared to communities in stressful environments (Conti et al., 2017). Competition is expected to create a divergent or «overdispersed» distribution of trait values among locally co-occurring species (MacArthur and Levins, 1967).

1.3. Species adaptations

There are a number of factors controlling plant distribution and productivity and adaptations to stress or disturbance are likely to be very important (Barbour, 1992). Constantly blowing winds, moving sand, salt, and heavy storms have an impact, so only specialized plants are able to survive within the beach and embryo and mobile dune habitats (Hesp, 1991). Specialization is based on particular adaptations, which we will summarize following Loidi and Campos (2008) and Martínez, (2009). One of the biggest challenges of coastal species is sand burial by the wind, as the surrounding conditions change when the plant is covered by sand. For example, temperature decreases and there is less oxygen around the roots, while humidity and nutrients increase. To overcome this situation, the plant can extend their stems or create new ones to reach the surface. Burial is not always a problem and in some cases can also promote plant growth up to the point that some plants have become so specialized, that they actually require regular burial of sand to maintain high vigor (Eldred and Maun, 1982). But burial not only affects a plant as an adult, it also has an influence when it is a seed. When a seed is buried it can die, grow or remain as a seed. Some dune species have an annual life cycle, so they pass the most unfavorable season as a seed. Seeds can be dispersed in most cases by wind or animals.

Droughts and floods are other important factors affecting coastal dune habitats. Soil does not store too much water, so species tend to grow and develop in the seasons were resources are available. Species can also accumulate water in the roots, leaves and stems. In case of floods, in particular in dune slacks, there is low oxygen in the roots. In this situation plants can create small roots and take surface oxygen (Martínez, 2009).

Salinity is one of the characteristics of coastal dune ecosystems. Salinity comes from the sea and it is brought by the wind as salt spray. Plants have different strategies to overcome salinity. They can exclude the salt by well adapted leaves with thick cuticle. Plants can secrete the salt using specialized glands. They can store water in the leaves and that succulence counteracts the salinity. Dune species can store salt in some parts such as the leaves, which they later drop.

1.4. Coastal dune importance

Coastal habitats support high levels of biodiversity, much of which is restricted to coastal areas (Pakeman et al., 2017). They host a great number of habitats considered to be relevant to international conservation goals (Janssen et al., 2016) in terms of environmental heterogeneity and variability of species composition (Van Der Maarel, 2003; Martínez and Psuty, 2004; Carranza et al., 2008; Acosta et al., 2009; Peyrat and Fichtner, 2011). Coastal dunes are very valuable and offer a lot of services. The economic benefits that society receive from the natural functioning of the beach and coastal dunes are very high, especially from the point of view of protection, recreation, and aesthetic factors (Ciccarelli, 2015).

Coastal dunes serve as a resilient barrier to the destructive forces of waves and wind (Tordoni et al., 2018). Dunes absorb the impact of high-energy storms preventing or delaying intrusion of waters into inland areas (Gómez-Pina et al., 2002). Dunes act as a protection from sea storms (Everard et al., 2010; Barbier et al., 2011). Beaches with a depleted sediment supply have implications, especially for hotels and other infrastructure established near frontal dunes. As the beach losses sediment it becomes susceptible to erosion (Doody, 2013). Coastal dunes act as a sand reservoir during periods of sediment drought, limiting the erosion processes, or at least delaying their effects (Bertoni et al., 2014). The rich resource potential of the ecological structure of coastal areas and coastal settlements and the ease of transportation have made these regions attractive for relaxation for centuries (Praveena and Aris, 2010; Needham and Szuster, 2011).

Coastal dunes are unique transitional ecosystems and as such they are characterized by a highly specialized fauna and flora (Carter et al., 1992; Martínez and Psuty, 2004; McLachlan and Brown, 2006). They support a rich and varied fauna and flora with many species especially adapted to the habitat (Doody, 2013). For example, they provide nesting, foraging and stop-over areas for many species of vertebrates and invertebrates and harbour unique biological assemblages of plants (McLachlan and Brown, 2006). Dune vegetation also provides an essential habitat for several animal taxa, like insects, gastropods, reptiles and birds (Verstrael, 1996; McLachlan and Brown, 2006). Dune grasslands harbour a high number of plant species, many of which are endemic or highly specialized to this habitat (Prisco et al., 2012).

1.5. Threats

The unique ecological characteristics of coastal dunes make these systems also particularly fragile environments, which are considered among the most endangered in Europe (Van der Meulen and de Haes, 1996; Carboni et al., 2009; Feola et al., 2011). It has been estimated that in Europe roughly 85% of the present area is under threat (European Environmental Agency, 1999). Coastal areas in general, and sand dunes in particular, are considered to be land types with the highest levels of development and human impact (Drees, 1997; Holdgate, 1993; Van der Meulen and Salman, 1996). European coastal dune ecosystems are threatened by anthropogenic disturbance resulting in a substantial loss of regional biodiversity (Piotrowska, 1988; Łabuz, 2004).

Human disturbance can be defined as the human activities that imply the alteration of the physical environment, which causes changes in community and ecosystem structure and composition (Drake et al., 1989; Pyle, 1995). Habitat loss is a great threat for this ecosystem. Erosion is the most important factor of disturbance that causes structural alterations of the typical spatial pattern of dune plant communities (Ciccarelli, 2015). Several potential hazards threaten these coastal ecosystems, but coastal erosion and tourism are predominant (Iannantuono et al., 2004). Trampling and presence of paths, connected with human recreational activities, appear to have a detrimental impact on sand dunes (Ciccarelli, 2015). In particular, several studies have highlighted that moderate to high human trampling intensity can decrease plant diversity, cover, and productivity especially regarding rare and threatened coastal plants (Andersen, 1995; Kutiel et al., 1999; Lemauviel and Rozé, 2003; Kerbiriou et al., 2008; Santoro et al., 2012; Farris et al., 2013; Fenu et al., 2013).

Furthermore, we can include urbanization. Human activities in littoral areas are widespread and have been intensifying in the course of the 20th century, since historically urban zones have developed in coastal areas in most parts of the world (Cori, 1999). The 44% of the world's population lives within 150 km of the coast (UN Atlas of the Oceans, 2014), and by 2025 it is estimated that circa 75% of the world's population will live within 60 km of the sea (Small and Nicholls, 2003). Most of the world's megacities are situated in the coastal zone where a very particular combination of geographic, economic, and historical conditions are still attracting people and stimulating different migration processes (Brown et al., 2009; Seto et al., 2011; Barragán and de Andrés, 2015). 80% of major cities with over 10 million inhabitants are coastal (Martínez, 2008).

Human disturbance impact species richness and the number of generalists and alien species (Rodgers, 2002). Generalists species are those species that grow in many different habitats apart from coastal dunes (Castillo and Moreno-Casasola, 1996), while specialists species are those well adapted to the dune ecosystem and only live there (Hesp, 1991). Next to holiday resorts, which is urbanization next to the coast, dune species composition changes toward more common ruderal generalists. This could be related to the neighbouring effects from the nearby holiday resort and the different species planted (Grunewald, 2006). Disturbed dunes have lower cover of native dune-building grasses, which we could consider specialists, and have higher cover of alien and generalists (Rodgers, 2002).

Looking at the biological side we can speak about plant invasions. The ability of invasive species to spread and become locally dominant represents a threat to the integrity of the invaded habitats (Richardson et al., 2000; Kolar and Lodge, 2001; Chytrý et al., 2009; Moravcová et al., 2010; Herrera et al., 2017). We can find several alien and invasive species in the Atlantic coast such as *Carpobrotus* sp., *Arctotheca calendula*, *Arundo donax*, *Conyza* sp., *Cortaderia selloana*, *Cynodon dactylon*, *Euphorbia polygonifolia*, *Oenothera* sp. *Yucca* sp. to mention the most frequent ones (Mapama, 2011). If we include trees and shrubs next to coastal dunes we could list: *Acacia* sp., *Baccharis halimifolia*, *Eucalyptus globulus* and *Pinus radiata*. About mosses we could highlight the presence of *Campylopus introflexus*, which was not found in our study although mosses and lichens were taken into account. In particular, the iceplant (*Carpobrotus* sp.) was studied and in Mediterranean coasts was found to correlate negatively with taxonomic diversity in some studied sites (Jucker et al., 2013). This invasive species may affect not only patterns of species richness, but could also change ecosystem functioning and reduce evolutionary potential.

The conservation of coastal dune ecosystems is of major international concern (Martínez and Psuty, 2004) and specific programs designed to preserve natural dune habitats require the ability to predict the nature and extent of losses of biodiversity in response to land cover transformations (Gargano et al., 2012). For effective decision-making concerning coastal conservation, an understanding of which drivers are the most important in shaping changes in the vegetation is necessary (Pakeman et al., 2017). This understanding is essential to propose decisions for coastal protection using rigorous scientific criteria (Tordoni et al., 2018).

1.6. Syntaxonomy

Three different habitats embryo, mobile and fixed dunes can be considered due to the inland environmental gradient, which results in a turnover of species. However, along the coast not the same taxonomic units at the level of association are present, so we expect a change of species along the biogeographical gradient, in particular between the most separated beaches of biogeographical sectors. A syntaxonomic scheme, based on several sources (Rivas-Martínez et al., 2011; Demartini, 2016; Mucina et al., 2016; Marcenò et al., 2018), would be the following one:

Class *Ammophiletea* Br.-Bl et Tx. ex Westhoff et al. 1946

Mediterranean and Black Sea coastal dune vegetation

Order *Ammophiletalia* Br.-Bl. et Tx. ex Westhoff et al. 1946

Tall-grass perennial swards on mobile white and embryonic coastal dunes of the warm-temperate to boreo-atlantic coasts of the Mediterranean and the Black and Caspian Seas

Alliance *Ammophilion* Br.-Bl. 1921

Tall-grass perennial swards on mobile white and embryonic coastal sand dunes of the Mediterranean

—*Euphorbio paraliae-Agropyretum junceiformis* Tüxen in Br.-Bl. & Tüxen 1952 corr. Darimont, Duvigneaud & Lambinon 1962

—*Otantho maritimi-Ammophiletum australis* Géhu & Tüxen 1975 corr. F.Prieto & T.E. Díaz 1991

—*Sileno thorei-Ammophiletum arenariae* (Géhu 1968) Géhu, Géhu-Franck & Bournique 1995

—*Galio arenari-Hieracetum eriophori* Géhu (1968) 1982

Order *Artemisio-Koelerietalia* Sissingh 1974

Sandy grasslands and scrub on base-rich stabilized grey hind dunes of the shores of the cool-temperate Atlantic Ocean and the northern seaboards of the Ligurian and Adriatic Seas

Alliance *Euphorbio portlandicae-Helichrysion stoechadis* Géhu et R.Tx. in Sissingh 1974

Sandy grasslands and dwarf scrub on base-rich stabilized grey hind dunes of the francoatlantic shores of the Atlantic Ocean

—*Helichryso stoechadis-Koelerietum arenariae* Loriente 1974 corr. Rivas-Martínez, Fernández-González & Loidi 1997

Order *Crucianelletalia maritimae* Sissingh 1974

Mediterranean and Cantabro-Francoatlantic dwarf scrub and grasslands on stabilized coastal hind dunes

Alliance *Helichrysion picardii* (Rivas-Mart., M. Costa et Izco in Rivas-Mart. et al. 1990) Rivas-Mart. et al. 1999

Iberoatlantic dwarf scrub on stabilized coastal hind dunes

—*Iberidetum procumbentis* Bellot 1968

1.7. Taxonomic, functional and phylogenetic diversity

Biodiversity or biological diversity was first used by Lovejoy (1980). It can be defined as «species, genetic, and ecosystem diversity in an area» (Swingland, 2001). It can be assessed at different levels. Alpha diversity includes the base sampling unit of a particular site related to the spatial grain of the study, while the area that aggregate of all sampling units (and the diversity inside) is the gamma diversity (Barton et al., 2013). Between alpha and gamma diversity we have beta diversity. Beta diversity is generally defined as the variation in the identities of species among sites and it provides a direct link between biodiversity at local scales and the broader regional species pool (Whittaker, 1960, 1972). Decomposing beta diversity from alpha diversity provides a better understanding of the drivers of community assemblage across latitudinal and altitudinal gradients (Chase et al., 2011; Kraft et al., 2011).

Two types of beta diversity can be recognized. On the one hand, beta diversity as turnover or species replacement. In this case beta diversity is focused on measuring change in community structure from one sampling unit to another along a spatial, temporal or environmental gradient. It involves gain and loss of species due to environmental filtering, competition and historical events (Leprieur et al., 2011). On the other hand, beta diversity can be studied as the variation in community structure among a set of sample units within a

Table 1.1: Summary of types of diversity by level (alpha, beta) and by component (taxonomic, functional and phylogenetic).

Diversity	Alpha	Beta
Taxonomic	List of species of a site	Variation of species among communities
Functional	Value and range of the functional traits in a site	Changes between communities of taxa with either similar or different functions
Phylogenetic	Evolutionary relationships between taxa of a site	Phylogenetically changes between communities

given spatial or temporal extent, or within a given category of a factor, such as a habitat type or experimental treatment (Anderson et al., 2010).

Biodiversity is not only species diversity, taxonomic diversity (TD). Two sites can have the same exact species diversity but wildly different levels of phylogenetic and functional diversity (Faith, 1992; Petchey and Gaston, 2006). Therefore, focusing only on species diversity is limited and ecologists attempt to quantify the evolutionary and functional dissimilarity between communities (Swenson et al., 2012). Functional diversity (FD) could be defined as «the value and range of the functional traits of the organisms in a given ecosystem» (Tilman et al., 2001), which is a broadly used definition (Mason et al., 2005). Plant traits are morphological, anatomical, biochemical, physiological or phenological features measurable at the individual level (Violle et al., 2007) and reflect the outcome of evolutionary and community assembly processes responding to abiotic and biotic environmental constraints (Valladares et al., 2007). Phylogenetic diversity (PD) takes the evolutionary relationships between taxa into account (Faith, 1992).

Using TD, PD, and FD in tandem is useful since it allows us to explicitly test predictions about the differential effects of competition and environmental filtering on PD and FD (Arnan et al., 2016). It also provides a broader view in the ecosystem diversity (Malavasi et al., 2016). These diversity components can be explored not only at the alpha level, but also at the beta level. Functional beta diversity tries to discriminate changes between communities of taxa with either similar or different functions in the system, while phylogenetic beta diversity looks for disentangling phylogenetically terminal and basal changes between communities (Cardoso et al., 2014).

1.8. Summary of objectives and dissertation structure

This study was set on the coastal dunes of south Atlantic Europe and it consisted of a survey on three vegetation types at different scales, where traits values and soil variables were measured. Then, this work may represent a valuable set of community composition samples on coastal dunes in Atlantic coasts. Indeed, this dataset is included in a collaborative database of nested-plots measures named GrassPlot (Dengler et al., 2018). The thesis explores how taxonomic, functional and phylogenetic diversity change across the ecological gradient, the geographical distance and considering scale. Then abiotic variables, as environmental factors and climate, were taken into account to explain community assemblage.

The specific objectives are as follows:

1. To study the changes of TD, FD and PD at alpha diversity level across the ecological gradient.
2. To assess the variation of TD, FD and PD at beta diversity level considering the distance along the coast.
3. To compare the diversity area relationships for TD, FD and PD between all species and generalist and specialists.
4. To explore the relationship between species composition and three groups of variables: soil, climate and spatial distribution of plots including biogeographical comparisons.

About thesis structure, chapter 1 provides a general overview of the ecosystem studied, describes the study area and states the specific aims of the study. Chapter 2 includes the description of the methodology, which is common to all the following chapters of the thesis. Chapter 3 explains how TD, FD and PD change along the ecological gradient at alpha diversity. This chapter corresponds to two published articles, one in *Estuarine, Coastal and Shelf Science* and the other in *Data in Brief*. Chapter 4 focuses on the changes on beta diversity. This chapter is ready to be submitted to *Journal of Vegetation Science*. Chapter 5 considers changes of TD, FD and PD at different scales in the three vegetation types. Finally, chapter 6 explores the abiotic variables of soil and climate in relation to the community composition.

1.9. References

Acosta, A., Carranza, M.L., Izzi, C.F., 2009. Are there habitats that contribute best to plant species diversity in coastal dunes? Biodivers. Conserv. 18, 1087–1098. https://doi.org/10.1007/s10531-008-9454-9

Acosta, A., Izzi, C.F., Stanisci, A., 2006. Comparison of native and alien plant traits in Mediterranean coastal dunes. Community Ecol. 7, 35–41. https://doi.org/10.1556/ComEc.7.2006.1.4

Andersen, U.V., 1995. Resistance of Danish coastal vegetation types to human trampling. Biol. Conserv. 71, 223–230. https://doi.org/10.1016/0006-3207(94)00031-K

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2010. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist: Roadmap for beta diversity. Ecol. Lett. 14, 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Arnan, X., Cerdá, X., Retana, J., 2016. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40, 448–457. https://doi.org/10.1111/ecog.01938

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81, 169–193. https://doi.org/10.1890/10-1510.1

Barbour, M.G., 1992. Life at the leading edge: The beach plant syndrome., in: Seeliger, V. (Ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, pp. 291–306.

Barragán, J.M., de Andrés, M., 2015. Analysis and trends of the world's coastal cities and agglomerations. Ocean Coast. Manag. 114, 11–20. https://doi.org/10.1016/j.ocecoaman.2015.06.004

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B., Didham, R.K., 2013. The spatial scaling of beta diversity. Glob. Ecol. Biogeogr. 22, 639–647. https://doi.org/10.1111/geb.12031

Bazzaz, F.A., 1991. Habitat selection in plants. Am. Nat. 137, S116–S130.

Bazzichetto, M., Malavasi, M., Acosta, A., Carranza, M., 2016. How does dune morphology shape coastal EC habitats occurrence? A remote sensing approach using airborne LiDAR on the Mediterranean coast. Ecol. Indic. 71, 618–626. https://doi.org/10.1016/j.ecolind.2016.07.044

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bertoni, D., Biagioni, C., Sarti, G., Ciccarelli, D., Ruocco, M., 2014. The role of sediment grain-size, mineralogy, and beach morphology on plant communities of two Mediterranean coastal dune systems. Ital. J. Geosci. 133, 271–281. https://doi.org/10.3301/IJG.2014.09

Brown, R.R., Keath, N., Wong, T.H.F., 2009. Urban water management in cities: historical, current and future regimes. Water Sci. Technol. 59, 847–855. https://doi.org/10.2166/wst.2009.029

Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112, 143–149. https://doi.org/10.1007/s004420050293

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349. https://doi.org/10.1007/BF02912621

Carboni, M., Carranza, M.L., Acosta, A., 2009. Assessing conservation status on coastal dunes: A multiscale approach. Landsc. Urban Plan. 91, 17–25. https://doi.org/10.1016/j.landurbplan.2008.11.004

Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius, M., Borges, P.A.V., Podani, J., Schmera, D., 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. J. Biogeogr. 41, 749–761. https://doi.org/10.1111/jbi.12239

Carranza, M.L., Acosta, A.T.R., Stanisci, A., Pirone, G., Ciaschetti, G., 2008. Ecosystem classification for EU habitat distribution assessment in sandy coastal environments: An application in central Italy. Environ. Monit. Assess. 140, 99–107. https://doi.org/10.1007/s10661-007-9851-7

Carter, R.W.G., Curtis, T.G.F., Sheehy-Skeffington, M.J. (Eds.), 1992. Coastal Dunes: Geomorphology, Ecology and Management for Conservation, 1 edition. ed. CRC Press, Rotterdam.

Castillo, S.A., Moreno-Casasola, P., 1996. Coastal sand dune vegetation: An extreme case of species invasion. J. Coast. Conserv. 2, 13–22. https://doi.org/10.1007/BF02743033

Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M., Inouye, B.D., 2011. Using null models to disentangle variation in community dissimilarity from variation in alpha-diversity. Ecosphere 2, art24. https://doi.org/10.1890/ES10-00117.1

Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C., Vilà, M., 2009. European map of alien plant invasions based on the quantitative assessment across habitats. Divers. Distrib. 15, 98–107. https://doi.org/10.1111/j.1472-4642.2008.00515.x

Ciccarelli, D., 2015. Mediterranean coastal dune vegetation: Are disturbance and stress the key selective forces that drive the psammophilous succession? Estuar. Coast. Shelf Sci. 165, 247–253. https://doi.org/10.1016/j.ecss.2015.05.023

Conti, L., Bello, F. de, Lepš, J., Acosta, A.T.R., Carboni, M., 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. J. Veg. Sci. 28, 762–773. https://doi.org/10.1111/jvs.12533 Cori, B., 1999. Spatial dynamics of Mediterranean coastal regions. J. Coast. Conserv. 5, 105–112. https://doi.org/10.1007/BF02802747

Cornwell, W.K., Schwilk, D.W., Ackerly, D.D., 2006. A Trait-Based Test for Habitat Filtering: Convex Hull Volume. Ecology 87, 1465–1471. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Demartini, C., 2016. Les végétations des côtes Manche-Atlantique françaises: essai de typologie et de cartographie dynamic-caténales. Université de Bretagne Occidentale.

Dengler, J., Wagner, V., Dembicz, I., García-Mijangos, I., Naqinezhad, A., Boch, S., Chiarucci, A., Conradi, T., Filibeck, G., Guarino, R., Janišová, M., Steinbauer, M., Aćić, S., Acosta, A., Akasaka, M., Allers, M.-A., Apostolova, I., Axmanová, I., Bakan, B., Biurrun, I., 2018. GrassPlot - A database of multi-scale plant diversity in Palaearctic grasslands. Phytocoenologia 48, 331–347. https://doi.org/10.1127/phyto/2018/0267

Doody, J.P., 2015. Sand dune - Country Report, Spain. Available from: http://www.coastalwiki.org/wiki/Sand_dune_-_Country_Report,_Spain (accessed on 2-09-2016).

Doody, J.P., 2013. Sand Dune Conservation, Management and Restoration, Coastal Research Library. Springer Netherlands, Dordrecht.

Doody, J.P., 2010. Sand dune - Country Report, France. Available from `http://www.coastalwiki.org/wiki/Sand_dune_-_Country_Report,_France` (accessed on 2-09-2016)

Drake, J., Mooney, H., Castri, D., Groves, F., Kruger, F., Williamson, M., 1989. Biological Invasions: A Global Perspective (SCOPE 37). Biometrics 47. `https://doi.org/10.2307/2532533`

Drees, J.M., 1997. Coastal dunes, recreation and planning, Proceedings of European Seminar, Castricum, November 1995 Publication EUUC Service. ed. the Netherland

Eldred, R.A., Maun, M.A., 1982. A multivariate approach to the problem of decline in vigour of *Ammophila*. Can. J. Bot. 60, 1371–1380. `https://doi.org/10.1139/b82-174`

European Commission, 1992. Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. Off. J. L.

European Environmental Agency, 1999. Coastal and marine zones: environment at the turn of the century, Chapter 3/14. Copenhagen.

Everard, M., Jones, L., Watts, B., 2010. Have we neglected the societal importance of sand dunes? An ecosystem services perspective. Aquat. Conserv. Mar. Freshw. Ecosyst. 20, 476–487. `https://doi.org/10.1002/aqc.1114`

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10. `https://doi.org/10.1016/0006-3207(92)91201-3`

Farris, E., Pisanu, S., Ceccherelli, G., Filigheddu, R., 2013. Human trampling effects on Mediterranean coastal dune plants. Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 147, 1043–1051. `https://doi.org/10.1080/11263504.2013.861540`

Fenu, G., Cogoni, D., Ulian, T., Bacchetta, G., 2013. The impact of human trampling on a threatened coastal Mediterranean plant: The case of Anchusa littorea Moris (*Boraginaceae*). Flora - Morphol. Distrib. Funct. Ecol. Plants 208, 104–110. `https://doi.org/10.1016/j.flora.2013.02.003`

Feola, S., Carranza, M.L., Schaminée, J.H.J., Janssen, J.A.M., Acosta, A.T.R., 2011. EU habitats of interest: an insight into Atlantic and Mediterranean beach and foredunes. Biodivers. Conserv. 20, 1457–1468. `https://doi.org/10.1007/s10531-011-0037-9`

Gargano, D., Mingozzi, A., Massolo, A., Rinaldo, S., Bernardo, L., 2012. Patterns of vegetation cover/dynamics in a protected Mediterranean mountain area: Influence of the ecological context and protection policy. Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 146, 9–18. `https://doi.org/10.1080/11263504.2011.641689`

Goldberg, D.E., 1990. Components of resource competition in plant communities., in: Grace, J., Tilman, D. (Eds.), Perspectives on Plant Competition. New York, pp. 27–49

Gómez-Pina, G., Muñoz-Pérez, J.J., Ramírez, J.L., Ley, C., 2002. Sand dune management problems and techniques, Spain. J. Coast. Res. 36, 325–332. https://doi.org/10.2112/1551-5036-36.sp1.325

Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. J. Veg. Sci. 17, 255–260.

Grime, J.P., 1979. Plant strategies and vegetation processes. John Wiley & Sons, Toronto.

Grime, J.P., 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. Am. Nat. 111, 1169–1194.

Grunewald, R., 2006. Assessment of damages from recreational activities on coastal dunes of the Southern Baltic Sea. J. Coast. Res. 1145–1157. https://doi.org/10.2112/05-0464.1

Herrera, M., Campos, J.A., Dana, E.D., 2017. Alien plants and their influence on vegetation, in: Loidi, J. (Ed.), The vegetation of the Iberian Peninsula: Volume 2, Plant and Vegetation. Springer International Publishing, Cham, pp. 499–531. https://doi.org/10.1007/978-3-319-54867-8_11

Hesp, P.A., 1991. Ecological processes and plant adaptations on coastal dunes. J. Arid Environ.

Holdgate, M.W., 1993. The sustainable use of tourism—a key conservation issue. Ambio 481–482.

Iannantuono, E., Rosskopf, C.M., Stanisci, A., Acosta, A.T.R., Aucelli, P.P.C., 2004. Effetti della dinamica costierasull'evoluzione dei sistemi dunali presenti lungo la costamolisana (Italia meridionale). Atti. Accad. Naz. Lincei 205, 321–331.

Ishikawa, S., Furukawa, A., Oikawa, T., 1995. Zonal plant distribution and edaphic and micrometeorological conditions on a coastal sand dune. Ecol. Res. 10, 259–266. https://doi.org/10.1007/BF02347851

Janssen, J.A.M., Rodwell, J.S., García Criado, M., Gubbay, S., Haynes, T., Nieto, A., Sanders, N., Calix, M., 2016. European Red list of habitats. Part 2. Terrestrial and freshwater habitats. European Union.

Jucker, T., Carboni, M., Acosta, A.T.R., 2013. Going beyond taxonomic diversity: deconstructing biodiversity patterns reveals the true cost of iceplant invasion. Divers. Distrib. 19, 1566–1577. https://doi.org/10.1111/ddi.12124

Kerbiriou, C., Leviol, I., Jiguet, F., Julliard, R., 2008. The impact of human frequentation on coastal vegetation in a biosphere reserve. J. Environ. Manage. 88, 715–728. https://doi.org/10.1016/j.jenvman.2007.03.034

Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16, 199–204. https://doi.org/10.1016/S0169-5347(01)02101-2

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599. https://doi.org/10.1111/1365-2435.12345

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P., Myers, J.A., 2011. Disentangling the drivers of beta Diversity along latitudinal and elevational gradients. Science 333, 1755–1758. https://doi.org/10.1126/science.1208584

Kutiel, P., Zhevelev, H., Harrison, R., 1999. The effect of recreational impacts on soil and vegetation of stabilised Coastal Dunes in the Sharon Park, Israel. Ocean Coast. Manag. 42, 1041–1060. https://doi.org/10.1016/S0964-5691(99)00060-5

Łabuz, T.A., 2004. Coastal dune development under natural and human influence on Swina Gate Barrier (Polish coast of Pomeranian Bay). Coastline Rep. 2, 129–138.

Lemauviel, S., Rozé, F., 2003. Response of three plant communities to trampling in a sand dune system in brittany (france). Environ. Manage. 31, 227–235. https://doi.org/10.1007/s00267-002-2813-5

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S., Oberdorff, T., 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecol. Lett. 14, 325–334. https://doi.org/10.1111/j.1461-0248.2011.01589.x

Loidi, J., Campos, J.A., 2008. Guía visual de la flora dunar de Gorliz. Diputación Foral de Bizkaia, Bilbao, pp. 195.

Lovejoy, T.E., 1980. The Global 2000 Report to the President, in: Barney, G.O. (Ed.), The Technical Report. Penguin, New York, pp. 327–332

MacArthur, R., Levins, R., 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am. Nat. 101, 377–385.

Malavasi, M., Bartak, V., Carranza, M.L., Simova, P., Acosta, A.T.R., 2018. Landscape pattern and plant biodiversity in Mediterranean coastal dune ecosystems: Do habitat loss and fragmentation really matter? J. Biogeogr. 45, 1367–1377. https://doi.org/10.1111/jbi.13215

Malavasi, M., Conti, L., Carboni, M., Cutini, M., Acosta, A.T.R., 2016. Multifaceted analysis of patch-level plan diversity in response to landscape spatial pattern and history on Mediterranean dunes. Ecosystems. 19, 850-864. https://doi.org/10.1007/s10021-016-9971-4

Mapama, 2011. Plan de control y eliminación de especies vegetales invasoras de sistemas dunares. http://www.mapama.gob.es/es/costas/temas/proteccion-costa/TODO_tcm7-338467.pdf (accessed on 08-08-2017).

Marcenò, C., Guarino, R., Loidi, J., Herrera, M., Isermann, M., Knollová, I., Tichý, L., Tzonev, R.T., Acosta, A.T.R., FitzPatrick, Ú., Iakushenko, D., Janssen, J.A.M., Jiménez-Alfaro, B., Kącki, Z., Keizer-Sedláková, I., Kolomiychuk, V., Rodwell, J.S., Schaminée, J.H.J., Šilc, U., Chytrý, M., 2018. Classification of European and Mediterranean coastal dune vegetation. Appl. Veg. Sci. 21(3), 533-559. https://doi.org/10.1111/avsc.12379

Martínez, M.L., 2009. Las playas y las dunas costeras: un hogar en movimiento, La ciencia para todos. Fondo de Cultura Económica.

Martínez, M.L., 2008. Dunas costeras. Investig. Cienc. 26–35.

Martínez, M.L., Psuty, N.P. (Eds.), 2004. Coastal dunes: ecology and conservation, ecological studies. Springer-Verlag, Berlin Heidelberg.

Martínez, M.L., Psuty, N.P., Lubke, R.A., 2004. A perspective on coastal dunes, in: M.L. Martínez, N.P. Psuty (Eds.), Coastal Dunes. Springer, Heidelberg, pp. 3–10.

Mason, N.W., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118.

Maun, M.A., 2009. The biology of coastal sand dunes. Oxford University Press, New York.

Maun, M.A., 2008. Burial of plants as a selective force in sand dunes, in: coastal Dunes, ecological studies. Springer, Berlin, Heidelberg, pp. 119–135. https://doi.org/10.1007/978-3-540-74002-5_8

McLachlan, A., Brown, A., 2006. The ecology of sandy shores, 2nd Edition. Academic Press, Burlington.

Moravcová, L., Pyšek, P., Jarošík, V., Havlíčková, V., Zákravský, P., 2010. Reproductive characteristics of neo-phytes in the Czech Republic: traits of invasive and non-invasive species. Preslia 82, 869–878.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., García, R.G., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., Tichý, L., 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl. Veg. Sci. 19, 3–264. https://doi.org/10.1111/avsc.12257

Needham, M.D., Szuster, B.W., 2011. Situational influences on normative evaluations of coastal tourism and recreation management strategies in Hawai'i. Tour. Manag. 32, 732–740. https://doi.org/10.1016/j.tourman.2010.06.005

Nobel, I.R., Slatyer, R.O., 1977. Post-fire succession of plants in Mediterranean ecosystems., in: Mooney, H.A., Conrad, C.E. (Eds.), Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. United States Forest Service, Palo Alto, California, USA, pp. 27–36.

Packham, J.R., Willis, A.J., 1997. Ecology of dunes, salt narsh and shingle. Springer US.

Pakeman, R.J., Hewison, R.L., Lewis, R.J., 2017. Drivers of species richness and compositional change in Scottish coastal vegetation. Appl. Veg. Sci. 20, 183–193. https://doi.org/10.1111/avsc.12283

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Peyrat, S., Fichtner, A., 2011. Plant species diversity in dry coastal dunes of the southern Baltic coast. Community Ecol. 12, 220–226. https://doi.org/10.1556/ComEc.12.2011.2.10

Pilkey, O.H., Neal, W.J., Riggs, S.R., Webb, C.A., Bush, D.M., Bullock, J., Pilkey, D.F., Cowan, B.A., 1998. The North Carolina shore and its barrier islands: restless ribbons of sand. Duke University Press Books, Durham.

Piotrowska, H., 1988. The dynamics of the dune vegetation on the Polish Baltic coast. Vegetatio 77, 169–175. https://doi.org/10.1007/BF00045762

Praveena, S.M., Aris, A.Z., 2010. Groundwater resources assessment using numerical model: A case study in low-lying coastal area. Int. J. Environ. Sci. Technol. 7, 135–146. https://doi.org/10.1007/BF03326125

Prisco, I., Acosta, A.T.R., Ercole, S., 2012. An overview of the Italian coastal dune EU habitats. Ann. Bot. 2, 39–48.

Pyle, L.L., 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac river. Am. Midl. Nat. 134, 244–253. https://doi.org/10.2307/2426295

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Rivas-Martínez, S., Díaz, T.E., Penas, A., Fernández (Eds.), 2011. Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. Itinera Geobotánica 18, 5–424.

Rodgers, J.C., 2002. Effects of Human Disturbance on the Dune Vegetation of the Georgia Sea Islands. Phys. Geogr. 23, 79–94. https://doi.org/10.2747/0272-3646.23.1.79

Santoro, R., Jucker, T., Prisco, I., Carboni, M., Battisti, C., Acosta, A.T.R., 2012. Effects of trampling limitation on coastal dune plant communities. Environ. Manage. 49, 534–542. https://doi.org/10.1007/s00267-012-9809-6

Seto, K.C., Fragkias, M., Güneralp, B., Reilly, M.K., 2011. A meta-analysis of global urban land expansion. PLOS ONE 6, e23777. https://doi.org/10.1371/journal.pone.0023777

Small, C., Nicholls, R.J., 2003. A gobal analysis of human settlement in coastal zones. J. Coast. Res. 19, 584–599. Swenson, N.G., Erickson, D.L., Mi, X., Bourg, N.A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J.K., Liu, X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S.J., Ye, W., Zhang, J., Zimmerman, J.K., Kress, W.J., 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. Ecology 93, S112–S125. https://doi.org/10.1890/11-0402.1

Swingland, I., 2001. Biodiversity, Definition of. Encycl. Biodivers. 1, 377–391. https://doi.org/10.1016/B0-12-226865-2/00027-4

Tilman, D., 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press. Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294, 843–845. https://doi.org/10.1126/science.1060391

Tordoni, E., Napolitano, R., Maccherini, S., Re, D.D., Bacaro, G., 2018. Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline. Ecol. Res. 1–12. https://doi.org/10.1007/s11284-018-1629-6

UN Atlas of the Oceans, 2014. Human settlements on the coast. http://www.oceansatlas.org/servlet/CDSServlet?status=ND0xODc3JjY9ZW4mMzM9KiYzNz1rb3M

Valladares, F., Gianoli, E., Gómez, J.M., 2007. Ecological limits to plant phenotypic plasticity. New Phytol. 176, 749–763. https://doi.org/10.1111/j.1469-8137.2007.02275.x

Van Der Maarel, E., 2003. Some remarks on the functions of European coastal ecosystems. Phytocoenologia 33, 187–202. https://doi.org/10.1127/0340-269X/2003/0033-0187

Van der Meulen, F., de Haes, H.U., 1996. Nature conservation and integrated coastal zone management in Europe: present and future. Landsc. Urban Plan. 34, 401–410.

Van der Meulen, F., Salman, A.H.P.M., 1996. Management of Mediterranean coastal dunes. Ocean Coast. Manag., Coastal Zone Management in the Mediterranean 30, 177–195. https://doi.org/10.1016/0964-5691(95)00060-7

Van der Meulen, F., Udo de Haes, H.A., 1996. Nature conservation and integrated coastal zone management in Europe: present and future. Landsc. Urban Plan. 34, 401–410. https://doi.org/10.1016/0169-2046(95)00234-0

Van der Valk, A.G., 1981. Succession in wetlands: a gleasonian approach. Ecology 62, 688–696. https://doi.org/10.2307/1937737

Verstrael, T.J., 1996. Research on breeding birds in Dutch dune areas. Landsc. Urban Plan. 34, 301–313. https://doi.org/10.1016/0169-2046(95)00238-3

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Weiher, E., D. Paul Clarke, G., A. Keddy, P., 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos 81, 309–322. https://doi.org/10.2307/3547051

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251. https://doi.org/10.2307/1218190

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338. https://doi.org/10.2307/1943563

Woodward, F.I., Diament, A.D., 1991. Functional approaches to predicting the ecological effects of global change. Funct. Ecol. 5, 202–212. https://doi.org/10.2307/2389258

Chapter 2

Methodology

2.1. Study area

The present study was conducted along 750 km of the Atlantic coast of north Spain and southwest France. The area is included in the Atlantic European Province, Cantabrian Atlantic Subprovince from a biogeographical point of view. The French area belongs to the Aquitaine-Landes (AL) sector, while the Spanish area includes three different sectors: Cantabrian and Basque (CB), North Galicia and Asturias (GA) and Galicia and North Portugal (GP) (Rivas-Martínez, 1982; Rivas-Martínez et al., 2017b).

Twelve sites were selected according to some criteria such as having a good representation of the three main dune habitats and enough extension to place the plots. Deeply disturbed locations were avoided. In each one of the four biogeographical sectors three locations were sampled (Figure. 2.1).

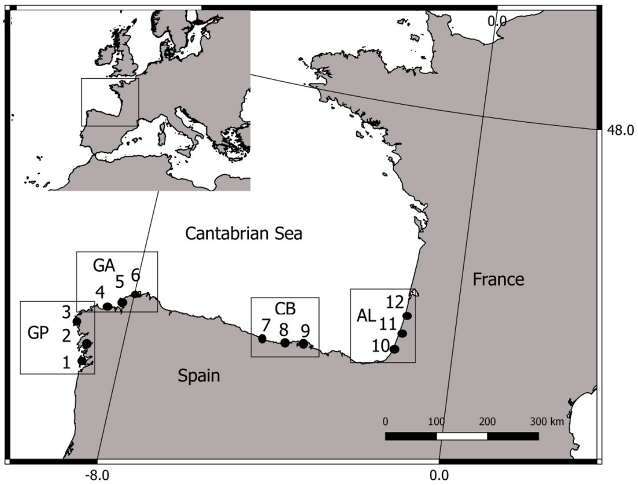

Figure 2.1: Study area. Twelve locations sampled from Galicia (Spain) to France grouped by biogeographic sectors. Galicia and North Portugal: 1. La Lanzada 2. As Furnas 3. Carnota North Galicia and Asturias: 4. Barrañán 5. San Xurxo 6. Valdoviño Cantabrian and Basque: 7. Oyambre 8. Liencres 9. Noja Aquitaine-Landes 10. Tarnos 11. Casernes 12. Messanges.

In the western face of the Galician coast, in the Galicia and North Portugal sector, three beaches could be mentioned. La Lanzada is included in the Complexo intermareal Umia - O Grove, A Lanzada, punta Carreirón e lagoa Bodeira (Mapama, 2016a). It has a special plan for bird care Chorlitejo Patinegro (*Charadrius alexandrinus*). An airport was planned to be constructed in the past, which finally did not take place. However, some of the buildings such as roads had to be removed in order to protect the place. As Furnas is in Porto do Son and it is a small beach 790 m long (Turismo Galicia, 2017). Carnota is included in the SAC (Special Area of Conservation) Carnota - Monte Pindo (Mapama, 2016b). Again is important for the *Charandrius alexandrinus* bird. It is the biggest beach in Galicia with 7 km long (Turismo Galicia, 2015).

In the north coast of Galicia, in the North Galicia and Asturias sector, we find three beaches. San Xurxo and Valdoviño are included in the Ártabra

Coast SAC (Mapama, 2016c). Valdoviño has also a lagoon behind the beach. Barrañán is included in the Costa da Morte SAC.

In Cantabria the coast follows an E-W orientation, which gives importance to the NW-SE winds. Wind is the major factor in sand mobilization in this area. Then waves, have a predominant component from NW (Saumell and Gracia, 2011). Looking at the beaches in the Cantabrian and Basque sector and following a line from west to east we sampled El Rosal beach next to Oyambre, San Vicente de la Barquera. Oyambre is included in the SAC Rías Occidentales y Duna. Liencres is in the SAC Dunas de Liencres y Estuario del Pas (Naturaspain, 2017a). Liencres dune field is a Natural Park since 1986 (CantabriaRural, 2017). Noja beach is also in a Natural Park since 2006 (CantabriaRural, 2017).

The French area is set along a N-S axis in the coast in the Aquitaine-Landes sector. Three different beaches were sampled: Tarnos, Casernes and Messanges, all of them in Les Landes, southwestern France. Tarnos is included in the Zone naturelle d'intérêt écologique, faunistique et floristique (Natural zone of ecological interest, fauna and flora), abbreviated as ZNIEFF, which is a type of natural environment recognized by France. It presents 192.36 ha and in the past it was a military field for training. Casernes beach is proposed as a SCI (Site of Community Importance) included in the Dunes modernes du littoral landais de Vieux-Boucau à Hossegor located in Seignoise (INPN.MNHN, 2007). Messanges is the northeast beach sampled.

The Cantabrian coast is exposed in E-W position with a dominant north face (Saumell and Gracia, 2011). Galicia and Cantabria show high sedimentary deposition, while in Asturias cliffs are abundant (Doody, 2015). In Galicia and Cantabria estuaries open and there sand dune fields occur in numerous localities (Saumell and Gracia, 2011). In the southwestern France cliffs are less common and a continuous dune field is present. Along the western areas of the study area temperate hyperoceanic submediterranean conditions predominate, while in the eastern areas a temperate oceanic bioclimate is dominant (Rivas-Martínez et al., 2004, 2017a). A detailed bioclimatic characterization of each sector is presented on Table 2.2.

2.2. Sampling

In each beach a total of twelve 100 m^2 plots were sampled, four 100 m^2 for each dune habitat: embryo, mobile and fixed dunes. Corners of the plots were set in NW-SE axis. Each 100 m^2 plot was then subsampled and two 10 m^2 subplots were set in the corners following Dengler (2009) (Figure 2.2). Then in each 10 m^2 subplot two 1 m^2 squares were set. From 0.1 m^2 to 0.0001 m^2 (1 cm^2) only one series per 1 m^2 was applied. It is important to replicate samples at small areas and take the mean to avoid biases. For example, if there are several replicates floristic, structural, and environmental heterogeneity on the larger spatial scale can be assessed (Dengler, 2009). Moreover, models perform worse when in nested-plot series without replication and average (Dengler et al., 2019). Coastal dunes present high heterogeneity even in the same 100 m^2

Table 2.1: Summary of the sites sampled including location, longitude and conservation status. SPA = Special Protection Areas, SAC = Special Areas of Conservation, SCI = Sites of Community Importance

Site	Biogeographical sector	Location	Longitude	Conservation status
La Lanzada	Galicia and North Portugal	O Grove, Pontevedra, Galicia, Spain	2 km	SPA Complexo intermareal Umia - O Grove, A Lanzada, punta Carreirón e lagoa Bodeira
As Furnas	Galicia and North Portugal	Porto do Son, A Coruña, Galicia, Spain	0.79 km	Unknown
Carnota	Galicia and North Portugal	Santa Comba de Carnota, A Coruña, Galicia, Spain	7 km	SAC Carnota - Monte Pindo
Barrañán	North Galicia and Asturias	Arteixo, A Coruña, Galicia, Spain	1.1 km	SAC Costa da Morte
San Xurxo	North Galicia and Asturias	Ferrol, A Coruña, Galicia, Spain	1.8 km	SAC Costa Ártabra
Valdoviño	North Galicia and Asturias	Valdoviño, A Coruña, Galicia, Spain	3.5 km	SAC Costa Ártabra
Oyambre	Cantabrian and Basque	San Vicente de la Barquera, Cantabria, Spain	2.5 km	SAC Rías Occidentales y duna de Oyambre
Liencres	Cantabrian and Basque	Piélagos, Cantabria, Spain	1.5 km	SAC Dunas de Liencres y Estuario del Pas
Noja	Cantabrian and Basque	Noja, Cantabria, Spain	0.5 km	SAC Marismas de Santoña, Victoria, Joyel y Ría de Ajo
Tarnos	Aquitaine-Landes	Tarnos, Landes, France	Continuous beach	ZNIEFF - Zone naturelle d'intérêt écologique, faunistique et floristique
Casernes	Aquitaine-Landes	Seignoisse, Landes, France	Continuous beach	SCI Dunes modernes du littoral landais de Vieux-Boucau à Hossegor
Messanges	Aquitaine-Landes	Messanges, Landes, France	Continuous beach	Unknown

Table 2.2: Climatic data for sectors. Galicia and North Portugal (GP), North Galicia and Asturis (GA), Cantabrian and Basque (CB) and Aquitaine-Landes sector (AL). Longitude (Long), latitude (Lat), elevation (Ele, m.a.s.l.), annual mean temperature (T, in ºC), positive annual rainfall (Pp, in mm), continentality index (Ic), ombrotermic indices of summer months (Ios_1, Ios_2, Ios_3 and Ios_4, for June, June+July, June+July+August and June+July+August+September, respectively), thermicity index (It) , Mediterraneity index of July (Im_1). For more information about used bioclimatic indices see (Rivas-Martínez et al., 2011, 2017a).

Station	Sector	Long	Lat	Ele	T	Pp	Ic	Ios_1	Ios_2	Ios_3	Ios_4	It	Im_1
Noia	GP	8º 53’W	42º 47’N	104	13.8	1833	11.4	2.6	2.61	3.13	4.16	311	2.23
Padrón	GP	8º 38’W	42º 44’N	58	14.8	1692	11.8	1.24	1.88	2.42	3.34	334	4.71
La Coruña	GA	8º 22’W	43º 23’N	57	13.7	963	8.6	1.83	2.08	2.14	2.52	332	3.69
Porto do Baqueiro	GA	7º 41’W	43º 47’N	80	13.1	2080	8.6	2.36	3.08	4.21	5.66	317	2.41
Comillas	CB	4º 17’W	43º 23’N	24	13.5	1242	10.1	2.49	3.99	4.06	4.52	309	2.32
Oriñón	CB	3º 19’W	43º 24’N	63	13.9	1400	10.7	2.9	3.87	3.94	4.39	320	1.99
Hondarribia	AL	1º 47’W	43º 21’N	8	14.1	1720	12	4.34	5.08	5.16	5.9	310	1.35
Bordeaux	AL	0º 42’W	44 º49’N	49	12.8	1539	15.3	2.38	2.43	2.27	2.99	234	2.49

Table 2.3: Number of samplings at different scales by vegetation type, site and total sites.

	Total by vegetation type	Total by site	Total by 12 sites
100 m^2	48	12	144
10 m^2	96	24	288
1 m^2	192	48	576
0.1 m^2	192	48	576
0.01 m^2	192	48	576
0.001 m^2	192	48	576
0.0001 m^2	192	48	576
Total	1104	276	3312

plot, in particular in embryo dunes were patches with bare sand alternate with patches with two or more species.

In each 10 m^2 subplot, plant species abundance was recorded with the extended Braun-Blanquet scale (Van Der Maarel, 1979), in which value + = 0.1, 1 = 1-4%, 2 is divided in 2m = 5%, 2a = 5-12% y 2b = 12-25%, 3 = 25-49%, 4 = 50-74%, 5 = 75-100%. Then, in the two corners of 10 m^2 subplots 1 m^2 squares were surveyed. In 1 m^2 squares abundance was sampled directly as percentage. Finally, for each 1 m^2 square a series of subsquares from 1 cm^2 to 1 m^2 were sampled. In this series and in the 100m^2 species were recorded as presence/absence. We applied shoot presence sampling method instead of root presence as shoot method performs better than root method in SARs models (Dengler et al., 2019). Sampling took place during the months of June and July of 2014 and 2015.

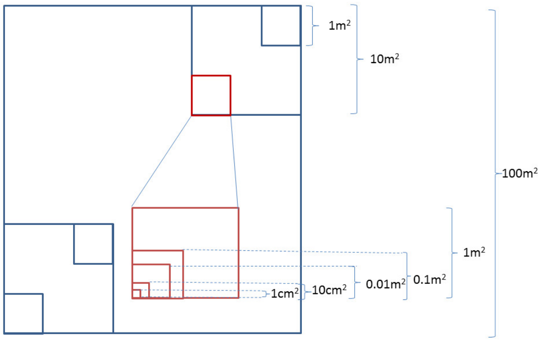

Figure 2.2: Sampling scheme of nested plots of subplots from 100 m^2 to 1 cm^2.

Due to the sampling scheme there were different number of replicates depending on the plot size. A summary of the number of plots by plot size is in Table 2.3.

2.3. Traits

Ten different traits were analysed both together or separately (Table 2.4). We included life form as it reflects the general growth pattern of the species. We expect a change of life forms in the community from embryo to fixed dunes. Geographical distribution is the geographical range where the species is recorded. As the study area is located in southwest Europe, near the Mediterranean region, we could find more Mediterranean species in the western sites. Flowering onset and span are related to reproduction strategies. We think that Mediterranean species could have a retarded flowering onset in comparison with Atlantic species. Pollination, fruit type and seed dispersal are also reproductive characteristics. We wonder if there is a replacement on pollination strategies from embryo to fixed dunes, due to the less exposure to wind and waves and if it is also linked to fruit types. Seed dispersal can be diverse and we ask if different mechanisms characterise each vegetation type.

The LHS scheme (leaf-height-seed) includes specific leaf area, plant height and seed mass. It is a plant ecology strategy scheme that requires the measurement of only three easy-to-measure traits (Laughlin et al., 2010). SLA, Specific Leaf Area, is related to the leaf economics spectrum and how the plant responds to chances of rapid growth (Reich et al., 1997). Plant height involves the competition for light (Keddy and Shipley, 1989; Aarssen and Jordan, 2001). Seed mass has a link with dispersal capabilities and cotyledon-stage seedling survivorship (Westoby et al., 1996; Jakobsson and Eriksson, 2000).

For the LHS framework (Westoby, 1998) SLA, height and seed mass of the most abundant species were measured. Height was directly recorded in the field, while SLA and seed mass were measured a posteriori in the laboratory following Pérez-Harguindeguy et al. (2013). From ten to twenty individuals were selected. They were adults without any sign of disturbance. Height was measured with a rule from soil to the tallest part of the plant including inflorescence. For SLA, a number of leaves, depending on the species, were collected. Then, leaves were pressed and scanned with the program ImageJ (Schneider et al., 2012) to know the area. After that leaves were dried in a laboratory oven for 24 h at 60°C and weighted in a scale. The final result was the division of the total area by the dry weight. Seeds needed to be gathered together due to the small weight in some cases. If they were heavy enough, they were set in groups in order to have some replicates. Seeds were dried in a laboratory oven for 24 h at 60°C and then weighted. Finally, the weight was divided by the number of seeds gathered.

For less abundant species and other traits data were collected from online databases and regional and national floras (Castroviejo, 1986; Aizpuru et al., 2007). The online databases where the data were retrieved from:

- Biolflor (Kühn et al., 2004)
- Kew Garden (Royal Botanic Gardens Kew, 2008)
- LEDA (Kleyer et al., 2008)
- Seed Dispersal (Hintze et al., 2013)
- Try (Kattge et al., 2011)

Table 2.4: List of traits analysed with decomposition in categories for discrete ones.

Trait	Description	Data Type	Attribute	Source
Life form	Raunkiaer life form	Nominal	Chamaephyte, geophyte, hemicryptophyte, phanerophyte, therophyte	Bibliography
Geographical distribution	Geographical range	Nominal	Alien, Eurosiberian, Mediterranean, Pluriregional	Bibliography
Flowering onset	Beginning of flowering	Quantitative	1-12	Bibliography
Flowering span	Flowering duration	Quantitative	1-12	Bibliography
Pollination	Pollination vector	Nominal	Selfing, wind, animals	Bibliography
Fruit type	Fruit type	Nominal	Capsule, caryopsis, follicle, legume, nut, schizocarp, siliqua	Bibliography
Seed dispersal	Seed dispersal vector	Nominal	Anemochorous, autochorous, barochorous, hydrochorous, without adaptations, zoochorous	Bibliography
SLA	Specific Leaf Area (Leaf area / dry weight)	Quantitative	cm^2/g	Bibliography and measured
Plant height	Plant height at maturity	Quantitative	m	Bibliography and measured
Seed mass	Weight of dried dispersules	Quantitative	g	Bibliography and measured

When several values of the same trait were recorded, we took the mean in order to balance extreme values.

In the case of non-vascular plants, no traits were measured or searched. For the identification the advice of experts was asked. Patxi Heras helped with mosses identifications and Javier Etayo with the lichens.

2.4. Environmental variables

Soil samples were collected to explore environmental variables. For these samples we took sand, approximately 0.5 kg, from the middle of each 100 m^2 plot at 10-15 cm depth. Then, samples were air dried and sent to the Laboratorio Agroambiental Fraisoro in Gipuzkoa (Basque Country, Spain). There eight soil parameters and soil texture, in percentage of grain size, were measured. Soil parameters assessed included pH, organic matter (%), Kjeldahl Nitrogen (%), P (mg/l), Na (mg/l), K (mg/l), Mg (mg/l), Ca (mg/l) and soil texture (%) (Table 2.5).

Climate variables (Table 2.5) were also studied and data were obtained from WorldClim (Fick and Hijmans, 2017). Finally, we included the spatial coordinates of each 100 m^2 plot to see if spatial location of the plots along the coast and in each site played a significant role.

Climate and soil variables have been used in coastal dune studies. Lee et al., (2007) studied the relationship between soil particle size and plant communities in coasts of south Korea. In south Korea Ihm et al., (2007) analyzed soil variables such as pH, Cl, Na, organic matter and soil texture. Angiolini et al., (2013) studied pH, $CaCO_3$, organic matter or field capacity in Mediterranean coastal dunes. Also in Mediterranean coasts climatic variables as annual mean temperature or annual precipitation were analyzed by D'Antraccoli et al., (2019).

2.5. Phylogenetic diversity

A phylogenetic tree was used to calculate distance between the branches to obtain measures of phylogenetic diversity. The reference tree selected was Phylomatic tree R20120829 for plants (Bermer et al., 2009), which is the APG III (Angiosperm Phylogeny Group), because it was the tree that included most of the species in our study. One species, *Cynodon dactylon*, was not included and it was manually added. Polytomies were randomly resolved, as trees containing polytomies have less resolution and statistical power (Swenson, 2009). Branch length was estimated using BLADJ (Branch Length Adjustment) and an age file according to (Wikström et al., 2001) in Phylocom (Webb et al., 2008). If we use few dated nodes, then, the resulting phylogenetic distance is better than using only the number of intervening nodes as phylogenetic distance (Webb, 2000).

Table 2.5: Summary of the soil, bioclimatic and spatial variables included.

Variable type	Variable name	Unit	Variable type
Soil	pH	-	Lab measure
	Organic matter	%	Lab measure
	Kjeldahl Nitrogen	%	Lab measure
	pH	mg/l	Lab measure
	Na	mg/l	Lab measure
	K	mg/l	Lab measure
	Ca	mg/l	Lab measure
	Soil texture		
	-Silt and clay (0.063 mm)	%	Lab measure
	-Fine sand (0.063-0.25 mm)	%	Lab measure
	-Coarse sand (0.25-2 mm)	%	Lab measure
	-Gravel(2-4mm)	%	Lab measure
Bioclimatic	BIO1 Annual Mean Temperature	°C	Wordclim
	BIO2 Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C	Wordclim
	BIO3 Isothermality (BIO2/BIO7) (* 100)	-	Wordclim
	BIO4 Temperature Seasonality (standard deviation *100)	-	Wordclim
	BIO7 Temperature Annual Range (BIO5-BIO6)	°C	Wordclim
	BIO10 Mean Temperature of Warmest Quarter	°C	Wordclim
	BIO12 Annual Precipitation	mm	Wordclim
	BIO14 Precipitation of Driest Month	mm	Wordclim
	BIO18 Precipitation of Warmest Quarter	mm	Wordclim
Geographical	Spatial coordinates	Decimal degrees	Field measure

2.6. Data analysis

We applied different analyses to explore data and obtain results. In some cases, we took into account the nested design. 10 m^2 subplots were nested in 100 m^2 plots, which were nested sites nested in biogeographical sectors. Most of the analyses were performed with R (R Core Team, 2015) and different packages, which we will detail.

First, to construct the phylogenetic tree we used the *Brranching* package (Chamberlain, 2015). In order to calculate phylogenetic indices such NTI (Nearest Taxon Index) and NRI (Net Relatedness Index) *Picante* (Kembel et al., 2010) package was applied. For alpha diversity analysis we first explored data with an NMDS (non-multidimensional scaling) with Vegan package (Oksanen et al., 2016). The differences in floristic composition of biogeographic sectors were tested by nested permutational multivariate analyses of variance (PERMANOVA) (Anderson, 2001) using PERMANOVA+ for Primer software (Clarke and Gorley, 2006). To compare the diversity indices we applied linear mixed models (Zuur et al., 2009) to include the nested design. Models were calculated with *lme4* R package (Bates et al., 2015) and pairwise comparisons were conducted using R package *lmeans* (Lenth, 2016).

For beta diversity analyses we applied a Distance-Based Redundance Data Analysis (db-RDA) (Legendre and Anderson, 1999) to conduct the constrained ordination. db-RDA is a useful tool for modelling communities through environmental predictors (Peres-Neto et al., 2006). The ordination was calculated with capscale function of *Vegan* package. Then, to disentangle variation partitioning varpart function in the *Vegan* package was applied. Total beta diversity and replacement and richness components were calculated following (Legendre, 2014) with *adespatial* R package (Dray et al., 2016).

Spatial scale analyses for the different diversity indices were accomplished through linear regressions using a power law, which is the function recommended for constructing or establishing species-area relationships (SAR) with nested plots (Dengler et al., 2019). ANOVA was performed to test whether the local z-values changes across these grain-size transitions. Analyses were replicated for all species and generalist and dune specialist species separately. Specialists are those species that are constrained to particular habitats and they are well adapted to them. Generalist species appear in more diverse habitats, as they present higher environmental tolerances (Büchi and Vuilleumier, 2014). We calculated the correlation between the number of specialist and generalist. We looked if the correlation was significant and in that case if it was positive or negative.

Soil and climate variables were also assessed. Climate data were retrieved from WordClim (Fick and Hijmans, 2017). First, data of soil chemical variables were reduced to a common scale following the method proposed by Sneath and Sokal, (1973). Canonical Correspondence Analysis (CCA; (ter Braak, 1986)), was used to study the relationship between vegetation and environment (Fenu et al., 2013). This was done with the *cca* function of the *Vegan* package. *Vegan* package with the function *varpart* was also used to calculate the variation partitioning between three group of variables: space, climate and soil.

2.7. References

Aarssen, L.W., Jordan, C., 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. Écoscience 8, 471–477. https://doi.org/10.1080/11956860.2001.11682677

Aizpuru, I., Aseginolaza, C., Uribe-Echebarría, P.M., Urrutia, P., Zorrakin, I., Garín, P., Hermosilla, C.E., Lizaur, X., Patino, S., Pérez Dacosta, J.M., Renobales, G., Valencia, J., 2007. Claves ilustradas de la flora del País Vasco y territorios limítrofes. Publication Service of The Basque Country Government, Vitoria-Gasteiz.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Angiolini, C., Landi, M., Pieroni, G., Frignani, F., Finoia, M.G., Gaggi, C., 2013. Soil chemical features as key predictors of plant community occurrence in a Mediterranean coastal ecosystem. Estuar. Coast. Shelf Sci. 119, 91–100. https://doi.org/10.1016/j.ecss.2012.12.019

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Bermer, B., Bremer, K., Chase, M.W., Fay, M.M., Reveal, J.L., Soltis, D.E., Soltis, P.S., Stevens, P.F., Anderberg, A.A., Moore, M.J., Olmstead, R.G., Rudall, P.J., Sytsma, K.J., Tank, D.C., Wurdack, K., Xiang, J.Q., Zmarzty, S., 2009. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161, 105–121. https://doi.org/10.1111/j.1095-8339.2009.00996.x

Büchi, L., Vuilleumier, S., 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. Am. Nat. 183, 612–624. https://doi.org/10.1086/675756

CantabriaRural, 2017. Parque natural de las dunas de Liencres, parques naturales de Cantabria. https://www.cantabriarural.com/lugares-de-interes/parque-natural-de-las-dunas-de-liencres.html (accessed on 08-08-2017).

Castroviejo, S. (coord. gen.). 1986-2012. Flora iberica 1-8, 10-15, 17-18, 21. Real Jardín Botánico, CSIC, Madrid.

Chamberlain, S., 2015. brranching: Fetch “Phylogenies” from Many Sources. HttpsCRANR-Proj. R package version 0.1.0. Clarke, K., Gorley, R., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E. Plymouth 192.

D’Antraccoli, M., Roma-Marzio, F., Carta, A., Landi, S., Bedini, G., Chiarucci, A., Peruzzi, L., 2019. Drivers of floristic richness in the Mediterranean:

a case study from Tuscany. Biodivers. Conserv. 28, 1411–1429. https://doi.org/10.1007/s10531-019-01730-x

Dengler, J., 2009. A flexible multi-scale approach for standardised recording of plant species richness patterns. Ecol. Indic. 9, 1169–1178. https://doi.org/10.1016/j.ecolind.2009.02.002

Dengler, J., Matthews, T.J., Steinbauer, M.J., Wolfrum, S., Boch, S., Chiarucci, A., Conradi, T., Dembicz, I., Marcenò, C., García-Mijangos, I., Nowak, A., Storch, D., Ulrich, W., Campos, J.A., Cancellieri, L., Carboni, M., Ciaschetti, G., Frenne, P.D., Dolezal, J., Dolnik, C., Essl, F., Fantinato, E., Filibeck, G., Grytnes, J.-A., Guarino, R., Güler, B., Janišová, M., Klichowska, E., Kozub, Ł., Kuzemko, A., Manthey, M., Mimet, A., Naqinezhad, A., Pedersen, C., Peet, R.K., Pellissier, V., Pielech, R., Potenza, G., Rosati, L., Terzi, M., Valkó, O., Vynokurov, D., White, H., Winkler, M., Biurrun, I., 2019. Species–area relationships in continuous vegetation: evidence from Palaearctic grasslands. J. Biogeogr. 0, 1–15. https://doi.org/10.1111/jbi.13697

Doody, J.P., 2015. Sand dune - Country Report, Spain. Available from: http://www.coastalwiki.org/wiki/Sand_dune_-_Country_Report,_Spain (accessed on 2-09-2016).

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Legendre, P., Wagner, H., 2016. adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.0-3. http://CRAN.R-project.org/package=adespatial

Fenu, G., Carboni, M., Acosta, A.T.R., Bacchetta, G., 2013. Environmental factors influencing coastal vegetation pattern: new insights from the Mediterranean Basin. Folia Geobot. 48, 493–508. https://doi.org/10.1007/s12224-012-9141-1

Fick, S., Hijmans, R., 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. https://doi.org/10.1002/joc.5086

Hintze, C., Heydel, F., Hoppe, C., Cunze, S., König, A., Tackenberg, O., 2013. D3: The dispersal and diaspore database – baseline data and statistics on seed dispersal. Perspect. Plant Ecol. Evol. Syst. 15, 180–192. https://doi.org/10.1016/j.ppees.2013.02.001

Ihm, B.-S., Lee, J.-S., Kim, J.-W., Kim, J.-H., 2007. Coastal plant and soil relationships along the southwestern coast of South Korea. J. Plant Biol. 50, 331–335. https://doi.org/10.1007/BF03030663

INPN.MNHN, 2007. Natura 2000 - Formulaire Standard de Donnees - Vieux-Boucau à Hossegor.

Jakobsson, A., Eriksson, O., 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88, 494–502. https://doi.org/10.1034/j.1600-0706.2000.880304.x

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin Iii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY – a global database of plant traits. Glob. Change Biol. 17, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Keddy, P.A., Shipley, B., 1989. Competitive hierarchies in herbaceous plant communities. Oikos 54, 234–241. https://doi.org/10.2307/3565272

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J. Ecol. 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Kühn, I., Durka, W., Klotz, S., 2004. BiolFlor: a new plant-trait database as a tool for plant invasion ecology. Divers. Distrib. 10, 363–365.

Laughlin, D.C., Leppert, J.J., Moore, M.M., Sieg, C.H., 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. Funct. Ecol. 24, 493–501. https://doi.org/10.1111/j.1365-2435.2009.01672.x

Lee, J.-S., Ihm, B.-S., Cho, D.S., Son, D.-Y., Kim, J.-W., 2007. Soil particle sizes and plant communities on coastal dunes. J. Plant Biol. 50, 475. https://doi.org/10.1007/BF03030685

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity: Replacement and richness difference components. Glob. Ecol. Biogeogr. 23, 1324–1334. https://doi.org/10.1111/geb.12207

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1. https://doi.org/10.2307/2657192

Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software 69, 1–33. https://doi.org/10.18637/jss.v069.i01

Mapama, 2016a. Natura 2000 - La Lanzada. http://www.mapama.gob.es/es/biodiversidad/temas/espacios-protegidos/ES0000087_tcm7-154883.pdf (accessed on 08-08-2017).

Mapama, 2016b. Natura 2000 - Carnota - Monte Pindo. http://www.mapama.gob.es/es/biodiversidad/temas/espacios-protegidos/ES1110008_tcm7-153460.pdf (accessed on 08-08-2017).

Mapama, 2016c. Natura 2000 - Costa Ártabra. http://www.mapama.gob.es/es/biodiversidad/temas/espacios-protegidos/ES1110002_tcm7-153454.pdf (accessed on 08-08-2017).

Naturaspain, 2017a. LIC de dunas de Liencres y estuario del Pas. http://www.naturaspain.com/zona-lic-dunas-de-liencres-y-estuario-del-pas.html (accessed 08-08-2017).

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2.3-5.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614–2625.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. https://doi.org/10.1071/BT12225

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/, Vienna, Austria.

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: Global convergence in plant functioning. Proc. Natl. Acad. Sci. 94, 13730–13734.

Rivas-Martínez, S., 1982. Series de vegetación de la región Eurosiberiana de la Península Ibérica. Lazaroa 4, 155–166. Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T.E., Rivas-Sáenz, S., 2017a. Bioclimatology of the Iberian Peninsula and the Balearic Islands, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 29–80. https://doi.org/10.1007/978-3-319-54784-8_2

Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Cantó, P., del Río, S., Costa, J.C., Herrero, L., Molero, J., 2017b. Biogeographic Units of the Iberian Peninsula and Balearic Islands to District Level. A Concise Synopsis, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 131–188. https://doi.org/10.1007/978-3-319-54784-8_5

Rivas-Martínez, S., Penas, A., Días, T.E., 2004. Bioclimatic map of Europe: Bioclimates.

Rivas-Martínez, S., Rivas-Sáenz, S., Merino, S.P., 2011. Worldwide Bioclimatic Classification System. Glob. Geobot. 1, 1–634.

Royal Botanic Gardens Kew, 2008. Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (accesed on 01-07-2015).

Saumell, E.S., Gracia, F.J. (Eds.), 2011. Las dunas en España. Sociedad Española de Geomorfología, Zaragoza.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675. https://doi.org/10.1038/nmeth.2089

Sneath, P.H.A., Sokal, R.R., 1973. Numerical taxonomy. The principles and practice of numerical classification. Numer. Taxon. Princ. Pract. Numer. Classif.

Swenson, N.G., 2009. Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. PLoS ONE 4, e4390. https://doi.org/10.1371/journal.pone.0004390

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179. https://doi.org/10.2307/1938672

Turismo Galicia, 2017. Turismo Galicia - As Furnas. http://www.turismo.gal/recurso/-/detalle/11476/as-furnas?langId=es_ES .

Turismo Galicia, 2015. Turismo Galicia - Carnota. http://www.turismo.gal/recurso/-/detalle/16858/carnota-monte-pindo?langId=es_ES (accessed on 08-08-2017).

Van Der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Am. Nat. 156, 145–155.

Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution.

Bioinformatics 24, 2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729

Westoby, M., Leishman, M., Lord, J., 1996. Comparative ecology of seed size and dispersal. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 351, 1309–1318. https://doi.org/10.1098/rstb.1996.0114

Wikström, N., Savolainen, V., Chase, M.W., 2001. Evolution of the angiosperms: calibrating the family tree. Proc. R. Soc. B Biol. Sci. 268, 2211–2220. https://doi.org/10.1098/rspb.2001.1782

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, Statistics for Biology and Health. Springer New York, New York, NY.

Chapter 3

Changes in plant diversity patterns along dune zonation in south Atlantic European coasts

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Torca, M., Campos, J.A., Herrera, M., 2019b. Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. Estuarine, Coastal and Shelf Science 218, 39–47. https://doi.org/10.1016/j.ecss.2018.11.016

3.1. Introduction

Coastal dunes are present all over the world under a wide range of climatic and geologic conditions (Maun, 2009). They make up 20% of the world's coastlines and they are transitional ecosystems between land and sea (Van Der Maarel, 2003). Moreover, these azonal ecosystems present unique characteristics with a highly specialized fauna and flora (McLachlan and Brown, 2006). With regard to humans, coastal dunes offer protection against winds and tides as well as being used as places for recreation and landscape aesthetics (Ciccarelli, 2014; Del Vecchio et al., 2017; Martínez et al., 2017). However, coastal dune systems are also particularly fragile environments and threatened by several potential dangers (Carboni et al., 2009; Drius et al, 2013), for example, loss of habitat by urbanization (Malavasi et al., 2018). About conservation status of coastal habitats, more than 75% of the habitats reported had an unfavourable assessment (EEA, 2015). By the mid-1980s Europe had already lost almost three-quarters of its coastal sand dunes and heaths because of land-use change, infrastructure development, pollution and urban expansion (The European Commission, 2015). Due to increasing urbanization about the 70% of the dune systems in European coasts has disappeared (Brown and McLachlan, 2002), and as a consequence of the loss of vegetation, dunes and beaches are more prone to wind and water erosion (Gómez-Pina et al., 2002).

Looking at environmental changes conditions, coastal dunes are characterized by a sea-to-inland gradient responsible for the coexistence of different plant communities (Wiedemann and Pickart, 2004; Frederiksen et al., 2006). Coastal dunes present environmental heterogeneity and spatial variability along the sea inland transect gradient which result in a high ecological diversity (Acosta et al., 2009). Biotic and abiotic factors interact, thus leading to a characteristic zonation that represents the succession from embryo to fixed dunes (Ruocco et al., 2014). As a consequence, environmental conditions of coastal plant communities are very specific and the position of plant communities in the sequence tends to be fixed (Carboni et al., 2009; Bazzichetto et al., 2016). In this sense, we speak about vegetation zones with different plant communities: beach, embryo, mobile, fixed or grey dunes. Upper beach and embryo dune vegetation are closer to the sea and more exposed to salt spray, winds and sand burial, while mobile dunes and especially fixed dunes (also named backed dunes or grey dunes in North Atlantic areas) become progressively less exposed to these harsh environmental constraints (Carboni et al., 2009; Fenu et al., 2012; Ciccarelli, 2014; Ruocco et al., 2014). These vegetation zones also represented are typical for three different habitats recognized in the Habitat Directive (92/43/CEE Directive): 2110 Embryonic shifting dunes, 2120 Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes) and 2130* Fixed coastal dunes with herbaceous vegetation (grey dunes). The last one is classified as a Priority Conservation habitat (The European Commission, 2013).

Biodiversity is a multifaceted concept which goes further than simply counting the number of species present in a given place (Villéger et al., 2013). Variation can be assessed at different levels: alpha refers to local diversity, beta to spatial differentiation and gamma to regional diversity (Cardoso et al., 2014). Alpha diversity takes into account how diversified the species are within a site, while beta diversity focuses on how diversified the sites are in species composition within a region (Legendre and De Cáceres, 2013). Patterns and processes determining species diversity change across spatial scales (Turner, 1989; Whitaker, 1998; Ricklefs, 2005). Three magnitudes could be taken into account: global scale, regional scale and local scale (Isserman 2010). In our study we considered local and regional scales.

This study measures taxonomic diversity, functional diversity and phylogenetic diversity at alpha level as phylogenetic and functional components add valuable information to species richness (Ahrendsen et al., 2016). Using taxonomic, functional and phylogenetic diversity together allows us to test predictions about the different effects of competition and environmental filtering on phylogenetic and functional diversity (Arnan et al., 2016). Indeed, phylogenetic diversity and functional diversity are less often quantified, but these forgotten dimensions may be equally or more important (Swenson, 2011). Also, alpha diversity is useful to identify the mechanism underlying local-scale co-occurrence (Swenson et al., 2012). Functional and phylogenetic components of diversity are related to environment and biotic interactions. Environmental filtering which filters species on the basis of their tolerance to abiotic conditions (Weiher and Keddy, 1995). Competitive interactions among species playing a role in their long-term coexistence (Leibold, 1998).

In relation to phylogenetic diversity, phylogenetic clustering takes place when closely related species tend to co-occur as a consequence of environmental filtering. In contrast, under competitive exclusion, closely related species compete leading to phylogenetic overdispersion (Cavender-Bares et al., 2006). Species from the same lineage are more likely to compete, leading to trait differentiation or exclusion in the same lineage. This could result in patterns of high trait dispersion and low phylogenetic dispersion (Prinzing et al., 2008). Finally, neutral processes, which lead to randomly assembled communities, give less importance to the niches assuming that all taxa are demographically and ecologically equivalent and that dispersal limitation plays a role in structuring of communities (Hubbell, 2001).

This study took place along a 750 km coastal stretch in northern Spain and southwestern France. Abundances of vascular plants were recorded. We expected a change in species composition along the ecological gradient from sea-to-inland. Then, we investigated if this change was followed by changes in phylogenetic and functional diversity or if species richness was affected.

3.2. Material and methods

3.2.1. Study area

The present study was conducted along 750 km of the Atlantic coast of north Spain and southwest France (Figure 3.1). From a biogeographic point of view the study area is included in the Atlantic European Province, Cantabrian

Atlantic Subprovince. The French area belongs to the Aquitaine-Landes (AL) biogeographic sector. The Spanish area includes three different biogeographic sectors: Cantabrian and Basque (CB), North Galicia and Asturias (GA) and Galicia and North Portugal (GP) (Rivas-Martínez, 1982, 2007). A detailed bioclimatic characterization of each sector is presented on Table 3 of Torca et al., 2019.

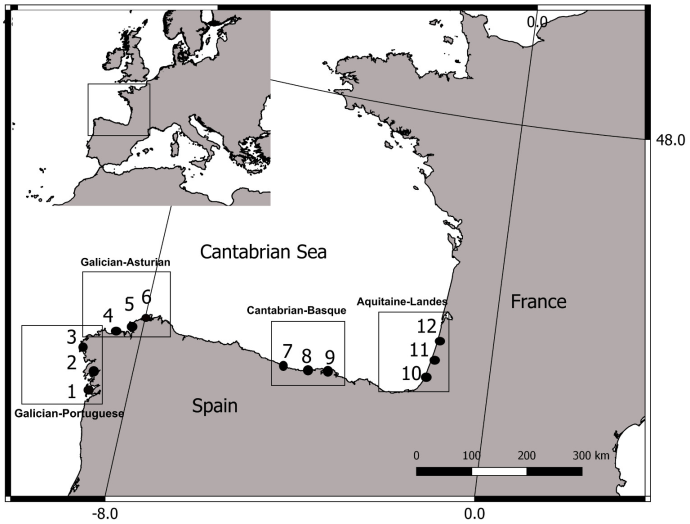

Figure 3.1: Study area. Twelve locations sampled from Galicia (Spain) to France grouped by biogeographic sectors. Galicia and Noth Portugual: 1. La Lanzada 2. As Furnas 3. Carnota North Galicia and Asturias: 4. Barrañán 5. San Xurxo 6. Valdoviño Cantabrian and Basque: 7. Oyambre 8. Liencres 9. Noja Aquitaine-Landes 10. Tarnos 11. Casernes 12. Messanges.

Concerning the main vegetation types, different plant formations were identified along the sea-inland gradient and most of them are changing because different human and environmental pressures. Specifically the following syntaxa are present: on embryo dunes (Habitat Directive code 2110), to date, *Euphorbio paraliae-Agropyretum junceiformis* is the only association present with no important changes along the study area (Rivas-Martínez et al., 2011). Embryo dunes are exposed to wind and waves, which makes it a very stressful system. This dune vegetation is characterized by anual specialized species and some perennial ones creating some grasslands dominated by *Elytrigia juncea* (Gracia et al., 2009). On mobile dunes (Habitat Directive code 2120), the associations *Otantho maritimi-Ammophiletum australis* in Spain and *Sileno thorei-Ammophiletum arenariae* and *Galio arenarii-Hieracietum eriophori* in France have been mentioned (Demartini, 2016). Mobile dunes begin to accumulate sand by wind deposition due to the stoloniferous stems of plant species and because the wind speed is lower than in embryo dunes. The dominant species is *Ammophila arenaria* (Gracia, 2009). On fixed dunes (Habitat Directive code 2130), two different orders are recognized in the study area: *Crucianelletalia maritimae* including the *Helichrysion picardii* alliance and *Artemisio lloydii-Koelerietalia albescentis* order including *Euphorbio portlandicae-Helichrysion stoechadis alliance* (Mucina et al., 2016. Marcenò et al., 2018). On fixed dunes wind intensity decreases and allows soil stability and accumulation of organic matter. This habitat is colonized by herbaceous species and little shrubs (Gracia and Muñoz, 2009).

3.2.2. Sampling

Vegetation sampling was performed on a set of representative tracts of the Atlantic coasts distributed along the four biogeographic sectors and in which the three main dune vegetation types were present (Figure 3.1). Deeply disturbed locations were avoided. Sites ranged from 180 to 7000 m of longitude and from 20 to 500 m of width. In France there was a continuum of beach and dunes along the coast.

In each location, and for each different coastal dune vegetation type, four 100 m^2 (10 x 10 m) plots were sampled. In every plot, two 10 m^2 subplots were set in the corners following Dengler (2009). In each 10 m^2 subplot the total list of the vascular plant species encountered was registered. Mosses and lichens were listed but not taken into account for this study. The extended Braun-Blanquet scale (Westhoff and Van Der Maarel, 1978) was used, in which value r= rare + = sparse, 1 = <4%, 2 is divided in 2m = 5%, 2a = 5-12% and 2b = 12-25%, 3 = 25-49%, 4 = 50-74%, 5 = 75-100%. The index is based on frequency-abundancy and the percentages are vegetation cover. Sampling took place during the months of June and July of 2014 and 2015.

3.2.3. Traits

Ten different traits were taken into account (Table 3.1). Traits were selected under the hypothesis of a change from Atlantic to Mediterranean conditions in both the ecological and biogegraphical gradients. This include the adaptations to more Mediterranean conditions.

For the LHS (leaf-height-seed) framework (Westoby, 1998) specific leaf area (SLA), plant height and seed mass of the most abundant species were measured. Height was directly recorded in the field, while SLA and seed mass were measured *a posteriori* in the laboratory following Pérez-Harguindeguy et al. (2013). For less abundant species and other traits data were collected from online databases (see bibliographic references in Torca et al., 2019) and regional and national floras (Castroviejo, 1986; Aizpuru et al., 2007). Value of the traits measured or gathered from databases are given on Table S1 of Torca et al., 2019.

3.2.4. Diversity indices

Taxonomic, functional and phylogenetic diversity were studied at the alpha level. For taxonomic diversity we calculated species richness (number of species per subplot) and Shannon's Index, which is a common index to measure species diversity in many habitats, included coastal dunes (Carboni et al., 2009; Honrado et al., 2009, Malavasi et al., 2018).

Table 3.1: List of traits analysed with decomposition in categories for discrete ones.

Trait	**Description**	**Data Type**	**Attribute**
Life form	Raunkiaer life form	Nominal	Chamaephyte, Geophyte, Hemicryptophyte, Phanerophyte, Therophyte
Geographical distribution	Geographical range	Nominal	Eurosiberian, Mediterranean, Non-European, Pluriregional
Flowering onset	Beginning of flowering	Quantitative	1-12
Flowering span	Flowering duration	Quantitative	1-12
Pollination	Pollination vector	Nominal	Selfing, Wind, Animals
Fruit type	Fruit type	Nominal	Capsule, Caryopsis, Follicle, Legume, Nut, Schizocarp, Siliqua
Seed dispersal	Seed dispersal vector	Nominal	Anemochorous, Autochorous, Barochorous, Hydrochorous, Without Adaptations, Zoochorous
SLA	Specific Leaf Area (Leaf area / dry weight)	Quantitative	cm^2/g
Plant height	Plant height at maturity	Quantitative	m
Seed mass	Weight of dried dispersules	Quantitative	g

In order to measure phylogenetic diversity two indices were calculated: NRI (Net Relatedness Index) and NTI (Nearest Taxon Index). NRI and NTI values were multiplied by -1 so positive values indicate phylogenetic clustering while negative values overdispersion. To measure NRI and NTI a phylogenetic tree was constructed using the species list and the *Brranching* package of R (R Core Team, 2015). To calculate the random distributions the null model used was taxa.label from the R-package *Picante* (Kembel et al., 2010). In this model names are randomly swapped 999 times across the phylogenetic tree, holding species richness of plots and species turnover among them constant (Brunbjerg et al., 2015). This null model has been frequently used in studies of alpha dispersion (Swenson et al., 2012).

Other studies have measured functional traits in coastal dunes taking into account the relationship between phylogenetic and functional diversity of plant communities (Ricotta et al., 2012; Carboni et al., 2013; Brunbjerg et al., 2014; Marcantonio et al., 2014). In our study two indices were calculated to estimate functional diversity: CWM (Community Weighted Mean) and RaoQ (Garnier et al., 2004; Pavoine and Dolédec, 2005; Leps et al., 2006).

3.2.5. Data analysis

First, in order to explore if species composition changes along the ecological gradient, NMDS was performed using package *Vegan* (Oksanen et al., 2016). Braun-Blanquet cover values were back-transformed to percentages according to van der Maarel (1979) in the following way: r = 0.02, + = 0.1, 1 = 2.5, 2m = 5, 2a = 8.75, 2b = 18.75, 3 = 37.5, 4 = 62.5 and 5 = 87.5. Then, square-root transformation was applied in order to balance the highest and lowest cover values. The dissimilarity matrix was constructed using Bray-Curtis distance.

The differences in floristic composition of biogeographic sectors were tested by nested permutational multivariate analyses of variance (PERMANOVA) (Anderson, 2001) using PERMANOVA+ for Primer software (Clarke and Gorley, 2006). This was also applied to calculated diversity indices: Shannon, species richness, NRI, NTI, RaoQ and CWM. Then, to detect characteristic or indicator species for each coastal dune vegetation type, *IndVal*, Indicator Value (Dufrene and Legendre, 1997), was calculated. The *IndVal* coefficient combines the relative abundance of the species and its relative frequency of occurrence in a group of replicates. For *IndVal* analyses *indicspecies* R package (Cáceres and Legendre, 2009) was used. Species were sorted by *IndVal* value.

For functional diversity a detailed analysis was conducted and every trait was analysed separately for CWM and RaoQ indices. Moreover, for CWM, discrete traits were decomposed in their different categories establishing the percentage of contribution of each category to the CWM. Then, for an overall estimation of the functional diversity an integrated value of RaoQ was calculated using *SYNCSA* R package (Debastiani and Pillar, 2012). Gower distance was used in order to include both continuous and discrete traits. Gower's formula can be applied to a mixture of different measurement scales and it allows the inclusion of ordinal variables (Ricotta and Burrascano, 2008).

In the case of phylogenetic diversity NRI and NTI indices were applied using *Picante* R package (Kembel et al., 2010). NRI and NTI were calculated for each site in order to detect any pattern along the biogeographic gradient. Then, the number of plots with significant patterns of clustering or overdispersion were calculated and compared.

In order to make comparisons for each index, linear mixed effects models were applied as they are useful when taking into account the nested design of plots and locations (Zuur et al., 2009). Coastal dune vegetation type was considered as a fixed factor while 10 m^2 subplots nested in 100 m^2 plots and these nested in locations were set for the random factor. To construct the models, in particular for the categorical decomposition of traits in CWM, analysis was performed only when at least 75% of the plots had a CWM percentage or RaoQ value higher than zero. Also, square root or log transformation were applied to response variables in some cases to meet model assumptions. Models were calculated with *lme4* R package (Bates et al., 2015). Finally, to test differences between coastal dune vegetation types, pairwise comparisons were conducted using R package *lmeans* (Lenth, 2016).

3.3. Results

Overall, 110 vascular plant taxa were identified in this study. The most widely represented family was *Poaceae* with a total of 25 taxa, followed by *Asteraceae* with 13 and *Fabaceae* with 10. Most genera presented one or two taxa with the exception of *Euphorbia* and *Ononis* with 4 taxa and *Cerastium*, *Festuca*, *Linaria*, *Medicago*, *Plantago*, *Silene* and *Vulpia* with 3 taxa each. Herbaceous species dominated with 40 therophytes, 39 hemicryptophytes and 6 geophytes. Woody species had almost no presence in embryo and mobile dune, while they appeared more frequently in fixed dunes. No ferns were found in this study.

3.3.1. Changes in species composition

The ordination analysis (NMDS) (Figure 3.2) showed a clear difference in floristic composition of the three vegetation types of coastal dune zonation (NMDS1), with fixed dunes that also differed according with their biogeographic characteristics (NMDS2). For fixed dunes two groups were differentiated, eastern (AL, CB) and western (GA, GP) biogeographic sectors.

PERMANOVA results (Table 1 of Torca et al., 2019 or Table A1 on Appendix) showed no differences in species composition of the embryo dunes between different biogeographic regions. But differences in species composition in mobile dunes and are most visible in fixed dunes. There was 1 indicator species in embryo dunes, 4 in mobile dunes and 34 in fixed dunes (Table S2 of Torca et al., 2019).

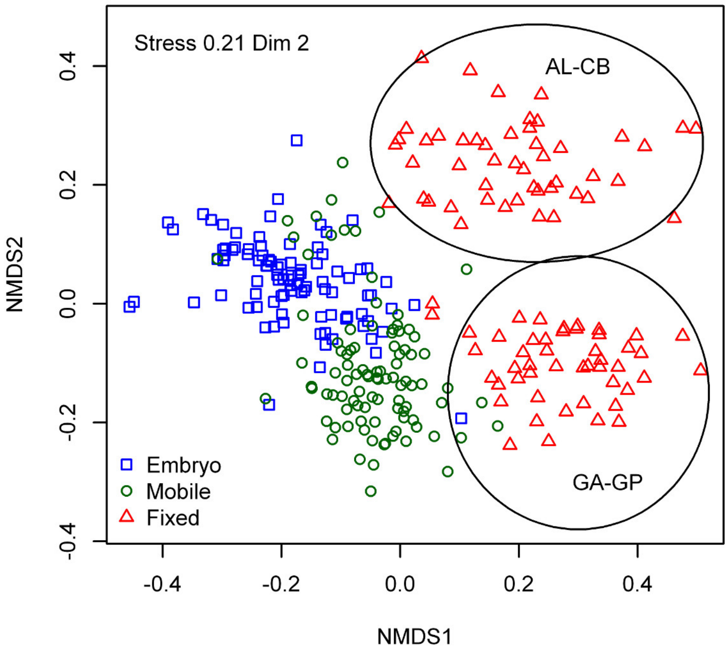

Figure 3.2: NMDS ordination of species composition using square root of abundances and Bray-Curtis distance for embryo, mobile and fixed dunes. Circles show eastern and western biogeographic sector plots grouping in fixed dunes. AL = Aquitaine-Landes, CB = Cantabrian and Basque, GA = North Galicia and Asturias and GP = Galicia and North Portugal.

3.3.2. Overall taxonomic, functional and phylogenetic diversities

The PERMANOVA results showed no differences at biogeographic sector level for any dune habitat in any diversity index (Table 2 of Torca et al., 2019 or Table A2 on Appendix). Data about taxonomic diversity measured by the Shannon index showed higher values on fixed dunes than in mobile and embryo dunes. Overall functional diversity calculated with RaoQ presented the same trend from embryo to fixed dunes. There were differences between fixed dunes and embryo and mobile dunes for the Shannon Index and RaoQ. Relative to phylogenetic diversity calculated with NRI and NTI, there were differences between fixed and embryo dunes and between fixed and mobile dunes (Figure 3.3). In summary, in all cases there were not differences between embryo and mobile dunes, while there were between fixed dunes and the other two vegetation types. From ecological point of view, it means that a higher values on taxonomic diversity for fixed dunes is followed by higher values of trait divergence; so the more diversity in species, the more diverse in traits.

Analysis of the percentage of significant phylogenetic patterns showed higher values of overdispersion in mobile dunes and the lowest values in fixed dunes. NTI differences between embryo and mobile dunes and fixed dunes were

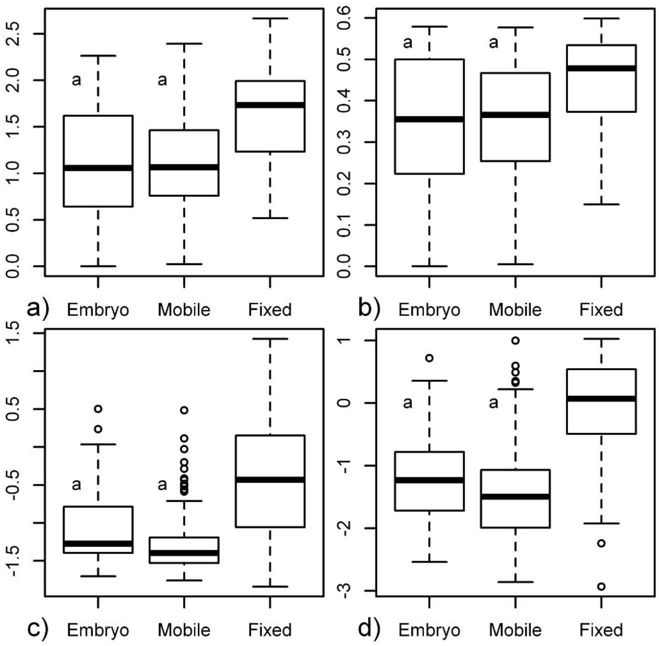

Figure 3.3: Distribution of Shannon index (a), RaoQ (b), NRI (c) and NTI (d) for the three dune vegetation types. Letters indicate no significant differences ($p<0.05$) after pairwise comparison of the factor dune vegetation types in the linear mixed models.

significant (post hoc $p < 0.02$ mobile dune; $p<0.03$ embryo dune). For NRI, there were significant differences between mobile and fixed dunes ($p < 0.018$) (Figure 3.4). This means that species would tend to be more phylogenetically related in fixed dunes than in embryo and mobile dunes.

3.3.3. Functional diversity in detail

CWM of discrete traits were split into their categories. Only trait categories used in the model comparison analysis were reported (Table 3.2 and Table 3.3).

With reference to plant biotype, percentage of contribution of chamaephytes to CWM was higher in fixe dunes, while geophytes decreased along the sea-inland gradient. Therophytes showed higher values in fixed dunes. Looking at the geographical origin, in proportion, the most abundant species in embryo dunes were species of Eurosiberian origin, while in mobile and fixed dunes were Mediterranean species most abundant. Pollination by wind presented lower values from embryo to fixed dunes and in contrast zoophily showed higher values on fixed dunes. Regarding fruit type, the most characteristic types were caryopsis in embryo and mobile dunes and nuts in fixed dunes. Then, dispersion by wind was more frequent in fixed dunes, followed by embryo dunes. Dispersion without adaptations was higher on mobile dunes. Flowering onset was about late April and early May in the three vegetation types, and flower-

Table 3.2: Mean values of functional diversity for CWM for each dune vegetation type. Discrete traits decomposed in categories (sd = standard deviation). Letters indicate no significant differences ($p<0.05$) after pairwise comparison of the factor dune vegetation type in the linear mixed models.

	Embryo		Mobile		Fixed	
	Mean	sd	Mean	sd	Mean	sd
Life form chamephyte	0.14	0.18a	0.14	0.19a	0.58	0.24
Life form geophyte	0.71	0.28	0.21	0.20	0.06	0.08
Life form therophyte	0.04	0.11a	0	0.01	0.15	0.15a
Mediterranean	0.08	0.11	0.69	0.29a	0.65	0.2a
Pluriregional	0.23	0.20a	0.17	0.15a	0.21	0.15a
Eurosiberian	0.54	0.33	0.14	0.23a	0.14	0.18a
Flowering onset	5.01	0.38a	4.97	0.29a	4.93	0.44a
Flowering span	4.17	0.69	3.67	0.66	4.60	0.63
Pollination wind	0.56	0.29a	0.37	0.26a	0.27	0.18
Pollination zoophily	0.44	0.29a	0.63	0.26a	0.72	0.19
Fruit nut	0.04	0.09a	0.07	0.12a	0.46	0.23
Fruit capsule	0.26	0.22	0.19	0.2a	0.18	0.19a
Fruit caryopsis	0.55	0.29a	0.61	0.27a	0.21	0.15
Dispersal anemochorous	0.28	0.23a	0.25	0.20a	0.53	0.22
Dispersal without adaptations	0.08	0.16a	0.6	0.28	0.20	0.2a
Dispersal zoochorous	0.03	0.08a	0.04	0.08a	0.24	0.17
SLA	104.21	16.83a	101.73	32.57a	133.97	38.42
Plant height	0.44	0.1	0.71	0.24	0.31	0.06
Seed mass	0.05	0.06a	0.05	0.09a	0.08	0.09

Table 3.3: Mean values of functional diversity for RaoQ for each dune vegetation type. Discrete traits decomposed in categories (sd = standard deviation). Letters indicate no significant differences ($p<0.05$) after pairwise comparison of the factor dune vegetation type in the linear mixed models.

	Embryo		Mobile		Fixed	
	Mean	sd	Mean	sd	Mean	sd
Life form	0.08	0.06a	0.08	0.04a	0.10	0.03
Geographical range	0.08	0.05a	0.08	0.04a	0.10	0.04
Flowering onset	0.23	0.29a	0.16	0.17a	0.79	1.01
Flowering span	0.25	0.42a	0.28	0.36a	0.51	0.33
Pollination	0.11	0.05a	0.11	0.04a	0.11	0.05a
Fruit type	0.06	0.03a	0.06	0.03a	0.08	0.03
Dispersal	0.08	0.04a	0.08	0.04a	0.08	0.02a
Plant height	1.11	1.12a	3.20	1.73a	0.65	0.73a
Seed mass	0.26	0.51a	0.33	0.68ab	0.43	0.73b
SLA	0.14	0.20a	0.27	0.24a	0.73	0.42

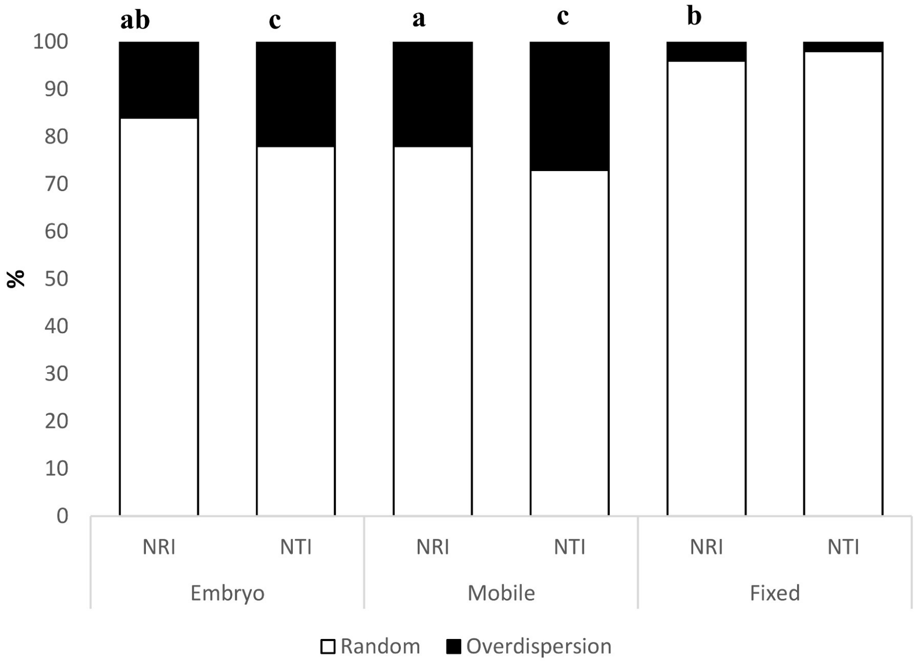

Figure 3.4: Percentages of significantly phylogenetic patterns (overdispersion, random) for NRI and NTI for each dune vegetation type. Letters indicate no significant differences ($p < 0.05$) for overdispersion.

ing span lasted for about four months. Relating LHS scheme, SLA was almost equal in embryo and mobile dune vegetation types and showed a higher value in fixed dunes. The highest growth height was recorded in mobile dunes. Seed mass remained almost the same in embryo and mobile dunes and it increased significant in fixed dunes.

Analysis of traits using RaoQ (taking into account that RaoQ measures the dispersion or divergence of the trait while CWM measures the mean) showed higher values on fixed dunes in life form, geographical range, fruit type, flowering span and onset, seed mass and SLA. The rest of traits presented a mixed pattern with higher values on embryo and mobile dunes or equal values between dune vegetation types.

3.4. Discussion

We expected differences in species composition across dune vegetation types in correspondence with strong environmental gradient from sea-to-inland (Van der Maarel, 2003). Indeed, different phytosociological associations have been traditionally recognised (Feola et al., 2011; Frederiksen et al., 2006). Then we proposed that this change could be followed by a change in functional and phylogenetic diversity (Carboni et al., 2009; Malavasi et al., 2018). In this study we analysed the patterns of taxonomic, functional and phylogenetic diversity and if there were related in some way in the coastal dune ecosystems of northwest Spain and southwest France.

3.4.1. Exploration of changes in species composition

Species composition of dune vegetation types in embryo dunes presented one group, which matches with the unique phytosociological association described for the Cantabrian Atlantic Subprovince: *Euphorbio paraliae-Agropyretum junceiformis.* These communities are dominated by *Elytrigia juncea* subsp. *boreoatlantica*, *Calystegia soldanella* and *Eryngium maritimum*, species of broad coastal distribution in Europe (Kadereit and Westberg, 2007). Also, the habitat is exposed to stress, as it occurs in the case of embryo dunes, the more its vegetation is habitat-related and independent from the biogeographic region in which it is located (Wiedemann and Pickart, 2004; Feola et al., 2011; Mahdavi et al., 2017).

With regard to mobile dunes, our results confirm the differences between biogeographic sectors. This is in accordance with the two different associations accepted in the French sector for mobile dunes: *Sileno thorei-Ammophiletum arenariae* and *Galio arenarii-Hieracietum eriophori* (Demartini, 2016). These associations are characterized by species as *Silene uniflora* subsp. *thorei*, *Galium arenarium*, *Hieracium eriophorum* and *Linaria thymifolia* (Table S2 of Torca et al., 2019), which are not present along the northern Atlantic coast of Spain. Along the other Iberian biogeographic sectors, the communities of mobile dunes were floristically and structurally very similar among them (Figure 2) and were included in the *Otantho maritimi-Ammophiletum australis* association, well characterized by *Ammophila arenaria* subsp. *australis.* This characteristic species agrees with stated in Marceno et al., 2018.

On fixed dune vegetation two main groups were evident corresponding one to Galicia and North Portugal and North Galicia and Asturias and the other to Cantabrian and Basque and Aquitaine-Landes biogeographic sectors (Figure 3.2). This is in accordance with the two phytosociological alliances recognized: the *Helichrysion picardii* in the western areas and *Euphorbio portlandicae-Helichrysion stoechadis* in the eastern ones (Marcenò et al., 2018). Some indicator species, such as *Helichrysum stoechas* subsp. *maritimum*, *Koeleria albescens* or *Phleum arenarium*, were only present in eastern biogeographic sectors; while other species, such as *Andryala integrifolia*, *Helichrysum italicum* subsp. *picardii*, *Iberis procumbens* or *Mibora minima*, were only in western biogeographic sectors (Table S2 of Torca et al., 2019). There were also some western endemic species as *Silene scabriflora* subsp. *gallaecica.*

The presence of a unique association in embryo dunes and the homogeneus composition along the coast in the study could be related to azonality. The vegetation of communities next to sea could be considered azonal; while in inner, more stable dunes species composition would be more related to local climatic conditions (Buffa et al., 2012). Indeed, Jiménez-Alfaro et al., (2015) found climatic variables to be more important in fixed dunes for the Iberian peninsula.

3.4.2. Taxonomic, functional and phylogenetic diversity overall

Coastal dunes show a sea-land gradient where environmental conditions change from more exposed to more sheltered ones (Carboni et al., 2011; Bazzichetto et al., 2016). Some studies have found a change (generally an increase) in species richness along this environmental gradient, with a peak at the intermediate position (Fenu et al., 2012), sometimes depending on the shoreline stability or accretion trend (Prisco et al., 2016). In our study we found that taxonomic diversity increased from embryo to fixed dunes. This agrees with the results found by Isermann (2005) and Acosta et al.,(2009). Moreover, the number of specialist indicator species increased from 1 in embryo dunes to 34 in fixed dunes.

Overall functional diversity showed an increase along the sea-inland gradient through different coastal dune vegetation types as Ricotta et al. (2012) also reported. Embryo dunes present specific plant species well adapted to this extreme environment (Maun, 1994). In our study the most frequent species in embryo dunes were *Calystegia soldanella*, *Elytrigia juncea* subsp. *boreatlantica*, *Eryngium maritimum* and *Euphorbia paralias*. Carboni et al. (2016) found that vegetation types closer to the sea, such as embryo dunes, showed a higher proportion of specialist species and higher average specialization levels. They listed five most specialized species (*Chamaesyce peplis, Cutandia maritima, Eryngium maritimum, Polygonum maritimum* and *Salsola kali*), typical of beaches and dunes. Four of them were also present in our vegetation plots. Nevertheless, in dunes vegetation is formed by a reduced set of specialized species (Angiolini et al., 2017). This specialization is congruent with the lower trait divergence (low value of RaoQ) found in our embryo dunes, and environmental filtering is suggested to increase functional similarity among species site (Kembel and Hubbell, 2006). For fixed dunes, trait divergence was higher than in embryo dunes (Figure 3.3). Competition for resources results in trait divergence and encourages coexistence between organisms in relation to limiting similarity (Pacala and Tilman, 1994). Moreover, trait divergence is assumed to originate from biotic filters and it is expected under low environmental stress (Conti et al., 2017), which would be the case for fixed dunes.

When looking at phylogenetic diversity, there was a general increase of values from embryo to fixed dunes, with fixed dunes being significantly different from the other two coastal dune vegetation types. Phylogenetic diversity presented decreasing overdispersion values from embryo to fixed dunes (Figure 3.4). Embryo dunes showed a mean species/family ratio of close to 1 while in fixed dunes it was 1.64 (Table S2 of Torca et al., 2019). Then, although fixed dunes have more absolute species diversity, this diversity tends to be clustered around main families. There are more species, but also more closely related, which would be in accordance with the lower overdispersed values of phylogenetic diversity, both NRI and NTI, and the lower percentage of significant overdispersed plots (Figure 3.4).

Our results showed trait convergence and phylogenetic overdispersion on embryo dunes. When adaptations are evolutionary convergent environmental filtering could cause phylogenetic overdispersion (Webb, 2000; Webb et al., 2002). Distantly related species may be found in communities with similar environmental conditions due to evolutionary convergence of the traits (Ackerly et al., 2006; Davies, 2006). In our case the similar environmental conditions would be the strong winds and waves that communities next to sea are exposed to. For fixed dunes we found a pattern of trait divergence and phylogenetic less overdispersion. This agrees with Brunbjerg et al., (2012), who found in general a clustered phylogenetic community structure on stable dunes. Phylogenetic clustering and phenotypic overdispersion would take place when co-ocurring close relative species differ in one or more important traits (Kawano, 2002).

Dune ecosystems are harsh environments and the stressful conditions constrain the range of plant physiological responses as result of a process of environmental filtering (Meinzer, 2003). Only species with particular adaptations can survive in these ecosystems (Maun, 2009). This would apply to embryo dunes in particular as the most exposed habitat to wind and waves. Under the environmental filtering paradigm, environmental conditions at a site are assumed to drive the optimal trait values or within limits (Swenson et al., 2012). This species assemblage would lead to high phylogenetic diversity, while trait convergence is related to environmental filtering. Also at a local scale, when disturbance tolerance requires specific traits, the process of environmental filtering leads to convergent trait composition (Weiher and Keddy, 1995).

In fixed dunes we found the opposite pattern: higher trait divergence and more phylogenetic clustering. This could be explained by negative ecological interactions leading to the competitive exclusion of similar species or by past negative interactions responsible for trait divergence (Prinzing et al., 2008). Negative biotic interactions would result in co-occurring species that are dissimilar in traits relating to competition (Swenson et al., 2012). Competitive exclusion could lead to divergence of relevant traits (Bello et al., 2013; Carboni et al., 2013). Therefore, we found different plant communities, which could be the response to different ecological processes. This could be related to a hierarchical model of community assembly where species sequentially pass through historical, abiotic, and biotic filters to result in the local assemblage observed (Webb et al., 2002, 2008).

With reference to the diversity indices and biogeographic sectors, we found no differences at regional scale (Table 2 of Torca et al., 2019 or Table A2 on Appendix), despite the species composition change between mobile and fixed dunes. This agrees with Mahdavi et al. (2017), who found changes in species pools and vegetation types in four different regions and functionally analogous species in coastal ecosystems including dune habitats.

3.4.3. Functional diversity

We found a change from Eurosiberian distribution range in embryo dunes to a Mediterranean in fixed dunes. The Eurosiberian distribution could be related to azonality, as this habitat presented an homogeneus species composition along the study area. Wind strategies (wind pollination) were higher in embryo dunes while animal strategies (animal pollination) characterized fixed dunes (Table 3.2). Mahdavi and Bergmeier (2016) reported entomophilous species to be found more frequently in fixed dunes. We found that the most abundant species in mobile dunes were taller than species in other coastal dune vegetation types. Phenological phases are prone to be related to local climate following mild temperatures and precipitations. In our study the onset of flowering was set about May extending during 3 or 4 months. There were not differences along the sea-inland gradient.

Height is an indirect characteristic of the ability to compete for light (Westoby et al. 2002). It was minimum in fixed dunes and maximum in mobile dunes, maybe due to the height of *Ammophila arenaria* subsp. *australis*, which is the tallest and most dominant species in mobile dunes. Taller plants compete more effectively for light (Cavender-Bares et al., 2004) and this would be the strategy of *Ammophila arenaria* subsp. *australis*. Smaller plants in embryo dunes could be explained since they are more resilient under high disturbance (Westoby, 1998). In embryo dunes taller plants such as *Elytrigia juncea* subsp. *boreoatlantica* coexisted with smaller ones such as *Calystegia soldanella* or *Eryngium maritimum*. This would be another case where smaller and taller species tend to coexist more frequently indicating differences in light acquisition strategies (Bello et al., 2011). Seed mass could be used to represent the trade-off between the number and size of seeds produced (Moles and Westoby, 2006). We found lighter seeds in embryo dunes and heavier on fixed dunes. A reduced seed mass would have a positive effect on competitive ability and a negative effect on colonisation or dispersal ability (Kisdi and Geritz, 2003). Embryo dune species often have a strategy based on high capacity of long distance dispersal. SLA could be used to represent the leaf economics spectrum such as structural investment, long leaf life spans, and low photosynthetic rates (Wright et al., 2004). Also it is a good surrogate for the plant ability to use light efficiently (Westoby et al., 2002). We found the highest values of SLA in fixed dunes and the lowest in mobile dunes.

Conclusions

We found different species composition for each coastal dune vegetation types. In embryo dunes species assemblage was constant along biogeographic sectors, while it changed in mobile and fixed dunes. Taxonomic, functional and phylogenetic diversity indices did not show changes at biogeographic sector level despite the species change in mobile and fixed dunes. We also found an increase in taxonomic diversity from embryo to fixed dunes followed by an increase in functional divergence. In habitats more exposed to sea, wind and waves, such as embryo dunes, few species phylogenetically dispersed were selected by their traits leading to functional convergence. This could be due to environmental filtering. Some traits would be selected regardless of the family so that could explain the more phylogenetic overdispersion found. Fixed dunes, a more sheltered habitat, showed higher taxonomic diversity and trait divergence, which could be related to competitive exclusion of similar functional species. In conclusion, on the one hand coastal dunes showed different biodiversity patterns along a sea-inland gradient at small scale, and on the other hand, despite a change in species, functional and phylogenetic diversity remained without changes at larger scale along a geographical gradient.

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Abbreviations

CWM	community weighted mean
FD	functional diversity
NMDS	non-metric multidimensional scaling
NRI	net relatedness index
NTI	nearest taxon index
PD	phylogenetic diversity
SLA	specific leaf area
TD	taxonomic diversity

References

Ackerly, D.D., Schwilk, D.W., Webb, C.O., 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology 87, S50-61.

Acosta, A., Carranza, M.L., Izzi, C.F., 2009. Are there habitats that contribute best to plant species diversity in coastal dunes? Biodivers. Conserv. 18, 1087-1098. https://doi.org/10.1007/s10531-008-9454-9

Ahrendsen, D.L., Aust, S.K., Roxanne Kellar, P., 2016. Biodiversity assessment using next-generation sequencing: comparison of phylogenetic and functional diversity between Nebraska grasslands. Plant Syst. Evol. 302, 89–108. https://doi.org/10.1007/s00606-015-1246-6

Aizpuru, I., Aseginolaza, C., Uribe-Echebarría, P.M., Urrutia, P. & Zorrakin, I., 2007. Claves ilustradas de la flora del País Vasco. Servicio de publicaciones del Gobierno Vasco, Vitoria-Gasteiz. 831pp.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Angiolini, C., Bonari, G., Landi, M., 2017. Focal plant species and soil factors in Mediterranean coastal dunes: An undisclosed liaison? Estuar.

Coast. Shelf Sci. Available on-line. https://doi.org/10.1016/j.ecss.2017.06.001

Arnan, X., Cerdá, X., Retana, J., 2016. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40, 448–457. https://doi.org/10.1111/ecog.01938

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed Efects Models Using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Bazzichetto, M., Malavasi, M., Acosta, A., Carranza, M., 2016. How does dune morphology shape coastal EC habitats occurrence? A remote sensing approach using airborne LiDAR on the Mediterranean coast. Ecological Indicators 71, 618–626. https://doi.org/10.1016/j.ecolind.2016.07.044

Bello, F. de, Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F., Thuiller, W., 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography 36, 393–402. https://doi.org/10.1111/j.1600-0587.2012.07438.x

Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š., Lepš, J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity: Intraspecific variability in functional diversity. Methods Ecol. Evol. 2, 163–174. https://doi.org/10.1111/j.2041-210X.2010.00071.x

Brown, A.C., McLachlan, A., 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environ. Conserv. 29, 62-77. https://doi.org/10.1017/S037689290200005X

Brunbjerg, A.K., Borchsenius, F., Eiserhardt, W.L., Ejrnaes, R., Svenning, J.-C., 2012. Disturbance drives phylogenetic community structure in coastal dune vegetation. Journal of Vegetation Science 23, 1082–1094. https://doi.org/10.1111/j.1654-1103.2012.01433.x

Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., Ejrnaes, R., Aarssen, L.W., Buckley, H.L., Forey, E., Jansen, F., Kattge, J., Lane, C., Lubke, R.A., Moles, A.T., Monserrat, A.L., Peet, R.K., Roncal, J., Wootton, L., Svenning, J.-C., 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. J. Plant Ecol. 7, 101–114. https://doi.org/10.1093/jpe/rtt069

Brunbjerg, A.K., Jørgensen, G.P., Nielsen, K.M., Pedersen, M.L., Svenning, J.-C., Ejrnæs, R., 2015. Disturbance in dry coastal dunes in Denmark promotes diversity of plants and arthropods. Biol. Conserv. 182, 243–253. https://doi.org/10.1016/j.biocon.2014.12.013

Buffa, G., Fantinato, E., Pizzo, L., 2012. Effects of disturbance on sandy coastal ecosystems of N-Adriatic coasts (Italy), in: Lameed, G.A. (Ed.), Biodiversity Enrichment in a Diverse World. InTech, pp. 338–372. https://doi.org/10.5772/47480

Cáceres, M.D., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1

Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? J. Veg. Sci. 24, 932–941. https://doi.org/10.1111/jvs.12095

Carboni, M., Carranza, M.L., Acosta, A.T.R, 2009. Assessing conservation status on coastal dunes: a multiscale approach. Landsc Urban Plan. 91, 17–25. https://doi.org/10.1016/j.landurbplan.2008.11.004

Carboni, M., Santoro, R., Acosta, A.T.R., 2011. Dealing with scarce data to understand how environmental gradients and propagule pressure shape fine-scale alien distribution patterns on coastal dunes: Drivers of alien patterns on coastal dunes. J. Veg. Sci. 22, 751–765. https://doi.org/10.1111/j.1654-1103.2011.01303.x

Carboni, M., Zelený, D., Acosta, A.T.R., 2016. Measuring ecological specialization along a natural stress gradient using a set of complementary niche breadth indices. J. Veg. Sci. 27, 892–903. https://doi.org/10.1111/jvs.12413

Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius, M., Borges, P.A.V., Podani, J., Schmera, D., 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. J. Biogeogr. 41, 749–761. https://doi.org/10.1111/jbi.12239

Castroviejo, S. (coord. gen.). 1986-2012. Flora iberica 1-8, 10-15, 17-18, 21. Real Jardín Botánico, CSIC, Madrid.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A., Bazzaz, F.A., 2004. Phylogenetic overdispersion in Floridian oak communities. Am. Nat. 163, 823–843. https://doi.org/10.1086/386375

Cavender-Bares, J., Keen, A., Miles, B., 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87, S109–S122. https://doi.org/10.1890/0012-9658(2006)87[109:PSOFPC]2.0.CO;2

Ciccarelli, D., 2014. Mediterranean coastal sand dune vegetation: influence of natural and anthropogenic factors. Environ. Manage. 54, 194–204. https://doi.org/10.1007/s00267-014-0290-2

Clarke, K., Gorley, R., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E. Plymouth 192.

Conti, L., de Bello, F., Lepš, J., Acosta, A.T.R., Carboni, M., 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. J Veg Sci 28, 762–773. https://doi.org/10.1111/jvs.12533

Davies, T.J., 2006. Evolutionary ecology: when relatives cannot live together. Curr. Biol. 16, 645–647.

Debastiani, V.J., Pillar, V.D., 2012. SYNCSA—R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28, 2067–2068. https://doi.org/10.1093/bioinformatics/bts325

Del Vecchio, S., Jucker, T., Carboni, M., Acosta, A.T.R., 2017. Linking plant communities on land and at sea: The effects of Posidonia oceanica wrack on the structure of dune vegetation. Estuar. Coast. Shelf Sci. 184, 30–36. https://doi.org/10.1016/j.ecss.2016.10.041

Demartini, C., 2016. Les végétations des côtes Manche-Atlantique françaises: essai de typologie et de cartographie dynamic-caténales. Université de Bretagne Occidentale. 675pp.

Dengler, J., 2009. A flexible multi-scale approach for standardised recording of plant species richness patterns. Ecol. Indic. 9, 1169–1178. https://doi.org/10.1016/j.ecolind.2009.02.002

Drius, M., Malavasi, M., Acosta, A.T.R., Ricotta, C., Carranza, M.L., 2013. Boundary-based analysis for the assessment of coastal dune landscape integrity over time. Appl. Geogr. 45, 41–48. https://doi.org/10.1016/j.apgeog.2013.08.003

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.2307/2963459

EEA, 2015. State of nature in the EU Results from reporting under the nature directives 2007–2012. Publications Office of the European Union, Luxembourg. 173 pp. https://doi.org/10.2800/603862

Fenu, G., Cogoni, D., Ferrara, C., Pinna, M.S., Bacchetta, G., 2012. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 146, 586-602. https://doi.org/10.1080/11263504.2012.656727

Feola, S., Carranza, M.L., Schaminée, J.H.J., Janssen, J. a. M., Acosta, A.T.R., 2011. EU habitats of interest: an insight into Atlantic and Mediterranean beach and foredunes. Biodivers Conserv 20, 1457–1468. https://doi.org/10.1007/s10531-011-0037-9

Frederiksen, L., Kollmann, J., Vestergaard, P., Bruun, H.H., 2006. A multivariate approach to plant community distribution in the coastal dune zonation of NW Denmark. Phytocoenologia 36, 321–342. https://doi.org/10.1127/0340-269X/2006/0036-0321

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., others, 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637. https://doi.org/10.1890/03-0799

Gómez-Pina, G., Muñoz-Pérez, J.J., Ramírez, J.L., Ley, C., 2002. Sand dune management problems and techniques, Spain. J. Coast. Res. 36, 325–332. https://doi.org/10.2112/1551-5036-36.sp1.325

Gracia, F., 2009. 2120 Dunas móviles de litoral con Ammophila arenaria (dunas blancas)., in: VVAA., Bases Ecológicas Preliminares Para La Conservación de Los Tipos de Hábitat de Interés Comunitario En España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, p. 48.

Gracia, F., Hernández, L., Hernández, A.I., San Jaume, E., Flor, G., 2009. 2110 Dunas móviles embrionarias, in: VVAA., Bases Ecológicas Preliminares Para La Conservación de Los Tipos de Hábitat de Interés Comunitario En España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, p. 54.

Gracia, F., Muñoz, J.C., 2009. 2130 Dunas costeras fijas con vegetación herbácea (dunas grises)., in: VVAA., Bases Ecológicas Preliminares Para La Conservación de Los Tipos de Hábitat de Interés Comunitario En España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, p. 40.

Honrado, J., Vicente, J., Lomba, A., Alves, P., Macedo, J.A., Henriques, R., Granja, H., Caldas, F.B., 2009. Fine-scale patterns of vegetation assembly in the monitoring of changes in coastal sand-dune landscapes. Web Ecol. 10, 1–14. https://doi.org/10.5194/we-10-1-2010

Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press. 392 pp.

Isermann, M., 2005. Soil pH and species diversity in coastal dunes. Plant Ecol. 178, 111–120. https://doi.org/10.1007/s11258-004-2558-8

Isermann, M., 2010. Phytodiversity in relation to scale. Habilitation-Manuscript to gain the Venia Legendi in the field of ecology. Bremen. 140 pp. http://elib.suub.uni-bremen.de/edocs/00101844-1.pdf

Jiménez-Alfaro, B., Marcenò, C., Guarino, R., Chytrý, M., 2015. Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages. J. Biogeogr. 42, 452–462. https://doi.org/10.1111/jbi.12437

Kawano, K., 2002. Character displacement in giant rhinoceros beetles. Am. Nat. 159, 255–271. https://doi.org/10.1086/338512

Kadereit, J.W., Westberg, E., 2007. Determinants of phylogeographic structure: a comparative study of seven coastal flowering plant species across their European range. Watsonia 26, 229–238.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kembel, S.W., Hubbell, S.P., 2006. The phylogenetic structure of a neotropical forest tree community. Ecology 87, S86–S99. https://doi.org/10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2

Kisdi, E., Geritz, S.A.H., 2003. On the coexistence of perennial plants by the competition-colonization trade-off. Am. Nat. 161, 350–354. https://doi.org/10.1086/345855

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. https://doi.org/10.1111/ele.12141

Leibold, M.A., 1998. Similarity and local co-existence of species in regional biotas. Evol. Ecol. 12, 95–110. https://doi.org/10.1023/A:1006511124428

Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. 69, 1–33. https://doi.org/10.18637/jss.v069.i01

Leps, J., De Bello, F., Lavorel, S., Berman, S., 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. Preslia 78, 481–501.

Mahdavi, P., Bergmeier, E., 2016. Plant functional traits and diversity in sand dune ecosystems across different biogeographic regions. Acta Oecol. 74, 37–45. https://doi.org/10.1016/j.actao.2016.06.003

Mahdavi, P., Isermann, M., Bergmeier, E., 2017. Sand habitats across biogeographical regions at species, community and functional level. Phytocoenologia 139–165. https://doi.org/10.1127/phyto/2017/0127

Malavasi, M., Bartak, V., Carranza, M.L., Simova, P., Acosta, A.T.R., 2018. Landscape pattern and plant biodiversity in Mediterranean coastal dune ecosystems: Do habitat loss and fragmentation really matter? J. Biogeogr. 45, 1367–1377. https://doi.org/10.1111/jbi.13215

Marcantonio, M., Rocchini, D., Ottaviani, G., 2014. Impact of alien species on dune systems: a multifaceted approach. Biodivers. Conserv. 23, 2645–2668. https://doi.org/10.1007/s10531-014-0742-2

Marcenò, C., Guarino, R., Loidi, J., Herrera, M., Isermann, M., Knollová, I., Tichý, L., Tzonev, R., Acosta, A.T.R., FitzPatrick, Ú., Iakushenko, D., Janssen, J., Jiménez-Alfaro, B., Kacki, Z., Keizer-Sedláková, I., Kolomiychuk, V., Rodwell, J., Schaminée, J., Šilc, U., Chytry, M., 2018. Classification of the European and Mediterranean coastal dune vegetation. Appl. Veg. Sci. 21, 533–559. https://doi.org/10.1111/avsc.12379

Martínez, M.L., Silva, R., Lithgow, D., Mendoza, E., Flores, P., Martínez, R., Cruz, C., 2017. Human impact on coastal resilience along the coast of Veracruz, Mexico. J. Coast. Res. 77, 143–153. https://doi.org/10.2112/SI77-015.1

Maun, M.A., 2009. The Biology of Coastal Sand Dunes. Oxford University Press, New York. 280pp.

Maun, M.A., 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio 111, 59–70. https://doi.org/10.1007/BF00045577

McLachlan, A., Brown, A., 2006. The Ecology of Sandy Shores, 2nd Edition. Academic Press, Burlington. 396pp. Meinzer, F., 2003. Functional convergence in plant responses to the environment. Oecologia 134, 1–11. https://doi.org/10.1007/s00442-002-1088-0

Moles, A.T., Westoby, M., 2006. Seed size and plant strategy across the whole life cycle. Oikos 113, 91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., García, R.G., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., Tichý, L., 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl. Veg. Sci. 19, 3–264. https://doi.org/10.1111/avsc.12257

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2.3-5.

Pacala, S.W., Tilman, D., 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. Am. Nat. 143, 222–257.

Pavoine, S., Dolédec, S., 2005. The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. Environ. Ecol. Stat. 12, 125–138. https://doi.org/10.1007/s10651-005-1037-2

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167-234. https://doi.org/10.1071/BT12225

Prinzing, A., Reiffers, R., Braakhekke, W.G., Hennekens, S.M., Tackenberg, O., Ozinga, W.A., Schamine, J.H.J., van Groenendael, J.M., 2008. Less lineages more trait variation: phylogenetically clustered plant communities are functionally more diverse. Ecol. Lett. 11, 809–819. https://doi.org/10.1111/j.1461-0248.2008.01189.x

Prisco, I., Stanisci, A., Acosta, A.T.R., 2016. Mediterranean dunes on the go: evidence from a short term study on coastal herbaceous vegetation. Estuar. Coast. Shelf Sci. 182, 40–46. https://doi.org/10.1016/j.ecss.2016.09.012

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/, Vienna, Austria. Ricotta, C., Burrascano, S., 2008. Beta diversity for functional ecology. Preslia 80, 61–71.

Ricotta, C., Pavoine, S., Bacaro, G., Acosta, A.T.R., 2012. Functional rarefaction for species abundance data: On functional rarefaction functions. Methods Ecol. Evol. 3, 519–525. https://doi.org/10.1111/j.2041-210X.2011.00178.x

Ricklefs, R.E., 2005. Historical and ecological dimensions of global patterns in plant diversity. Biol. Skr. 55, 583–603. Rivas-Martínez, S., 1982.

Series de vegetación de la región Eurosiberiana de la Península Ibérica. Lazaroa 4, 155–166.

Rivas-Martínez, S., Díaz, T.E., Penas, A., Fernández (Eds.), 2011. Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. Itinera Geobot. 18 (1), 5-424.

Rivas-Martínez, S., 2007. Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. Itinera Geobot. 17, 5-436. Ruocco, M., Bertoni, D., Sarti, G., Ciccarelli, D., 2014.

Mediterranean coastal dune systems: Which abiotic factors have the most influence on plant communities? Estuar. Coast. Shelf Sci. 149, 213–222. `https://doi.org/10.1016/j.ecss.2014.08.019`

Swenson, N.G., 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. Am. J. Bot. 98, 472–480. `https://doi.org/10.3732/ajb.1000289`

Swenson, N.G., Erickson, D.L., Mi, X., Bourg, N.A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J.K., Liu, X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S.J., Ye, W., Zhang, J., Zimmerman, J.K., Kress, W.J., 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. Ecology 93, S112–S125. `https://doi.org/10.1890/11-0402.1`

The European Comission, 2015. The State of Nature in the European Union. Report on the status of and trends for habitat types and species covered by the Birds and Habitats Directives for the 2007-2012 period as required under Article 17 of the Habitats Directive and Article 12 of the Birds Directive. Brussels, `http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:52015DC0219&from=EN.`

The European Commission, 2013. Interpretation manual of European Union habitats. Eur 28. `http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf.`

Torca, M., Campos, J.A., Herrera, M., 2019. Species composition and plant traits of south Atlantic European coastal dunes and other comparative data. Data in Brief 22, 207–213. `https://doi.org/10.1016/j.dib.2018.12.005`

Turner, M.G., 1989. Landscape Ecology: The Effect of Pattern on Process. Annual Review of Ecology and Systematics 20, 171–197. `https://doi.org/10.1146/annurev.es.20.110189.001131`

Van Der Maarel, E., 2003. Some remarks on the functions of European coastal ecosystems. Phytocoenologia 33, 187–202. `https://doi.org/10.1127/0340-269X/2003/0033-0187`

Van Der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114.

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional beta-diversity reveals that low functional beta-diversity is driven by low functional turnover in European fish assemblages: Decomposing functional beta-diversity. Glob. Ecol. Biogeogr. 22, 671–681. https://doi.org/10.1111/geb.12021

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Amer. Naturalist 156, 145–155.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and Community Ecology. Annu. Rev. Ecol. Syst. 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Webb, C.O., Cannon, C.H., Davies, S.J., 2008. Ecological organization, biogeography, and the phylogenetic structure of tropical forest tree communities, in: P. Carson, W., A. Schnitzer, S. (Eds.), Tropical Forest Community Ecology. Wiley-Blackwell, pp. 79–97.

Weiher, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. Oikos. 73, 323–335.

Westhoff, V., Van der Maarel, E., 1978. The Braun-Blanquet approach, in: Whittaker, R.H. (Ed.), Classification of Plant Communities. Dr. W. Junk Publishers, The Hague, pp. 287–399.

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729

Westoby, M., S. Falster, D., Moles, A., Vesk, P., J. Wright, I., 2002. Plant ecological strategies: some leading dimensions of variation between species. Annu. Rev. Ecol. Evol. Syst. 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Wiedemann, A.M., Pickart, A., 2004. Temperate zone coastal dunes, in: Martínez, M.L., Psuty, N.P. (Eds.), Coastal Dunes, Ecological Studies. Springer Berlin Heidelberg, pp. 53–65. https://doi.org/10.1007/978-3-540-74002-5_2

Whittaker, R.J., 1998. Island Biogeography: Ecology, evolution and Conservation. Oxford University Press, Oxford. 416 pp.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, Statistics for Biology and Health. Springer New York. 574pp.

Chapter 4

Ecological gradient have a greater effect than biogeographical gradient on taxonomic, functional and phylogenetic beta diversity

4.1. Introduction

Ecologists have long been interested in the mechanisms that influence the assembly of species into biological communities (Diamond, 1975; Keddy, 1992; Götzenberger et al., 2012; Gerhold et al., 2015). These mechanisms fall into two broad groups: environmental filtering, in which species functional traits determine which species are sufficiently adapted to abiotic environmental factors, and competitive interactions, by which species vie with other species for limited resources (Cornwell and Ackerly, 2009; Spasojevic and Suding, 2012). In competitive interactions, which often occur on a local scale of centimeters to meters, plant size and abundance can be the main arbitrators of interspecific effects (Goldberg, 1987). In addition, competitive effects that are associated with standing crop may themselves be contingent on environmental factors, such as amount of soil organic matter (Wilson and Keddy, 1986). In environmental filtering, in contrast, landscape and plot-specific physical, chemical and climatic factors act to influence species composition in plant communities (Lebrija-Trejos et al., 2010; Boukili and Chazdon, 2017). Bazzaz (1991) compares environmental filtering to habitat selection in the sense that both involve responses that result from the differential adaptation of species to environmental conditions. As dispersing propagules, species in the regional pool enter these processes, which influence patterns of composition and diversity in local communities (Fukami, 2004). Dispersing individuals from the regional species pool are first subject to environmental variation. Those that pass these filters establish successfully, and are subsequently subject to biotic interactions that influence both local composition and relative abundance (Ricklefs, 1987). While the biotic interactions–environmental filters dichotomy provides a framework for understanding the importance of local mechanisms for community structure, we lack sufficient understanding of how regional differences influence these processes to structure biotic community (Gonçalves-Souza et al., 2014; Heino et al., 2017).

Variation among communities in terms of taxonomic, functional and phylogenetic diversity can help us understand the structure, composition and dynamics of community assembly (Maherali and Klironomos, 2007). Phylogenetic methods capture a significant portion of the variability in plant functional traits, which is important because it is often difficult to know exactly which traits confer the ability to establish and persist in communities (Kraft and Ackerly, 2010). Both phylogenetic and functional community trait variation change as communities undergo succession (Kunstler et al., 2012). Further, studies of relationship between phylogenetic diversity and environmental variation have usually focused on local variation (alpha diversity; Meynard et al., 2011), while among-site (beta) diversity in phylogenetic, taxonomic and functional community structure has received less attention (Cardoso et al., 2014; Pool et al., 2014). Examination of beta diversity in these components of community structure can help develop understanding of how the evolutionary history of traits and local ecological factors interact to influence diversity across broad spatial scales (Siefert et al., 2013). For example, Graham and Fine (2008) report beta diversity in phylogenetic structure to provide insight into environmental and historical factors that influence species richness. Understanding how community assembly changes across larger spatial scales will entail consideration of both alpha and beta diversity in community structure.

Coastal dune systems provide an excellent opportunity for the study of geographical variation in community assembly. Coastal dunes generally present an ecological gradient from more-exposed communities next to sea to increasingly more sheltered communities as one moves inland (Barbour et al., 1985; Brown and McLachlan, 1990). Along this gradient biotic conditions, including rates of sand movement and burial, moisture availability, salt exposure and nutrient levels, change systematically (Forey et al., 2008; Fenu et al., 2012). As a result, portions of the gradient are characterized by consistent differences in vegetation. Embryo dunes, those closest to water and waves, present low vegetation coverage and biomass, and are characterized by pioneer species, such as the grass *Elytrigia juncea* and additional plants highly tolerant to seawater inundation (Gracia et al., 2009; Montreuil et al., 2013). Mobile dunes are further inland and have greater sand accumulation but little organic matter. In Europe, the dominant species in these dunes is often the grass *Ammophila arenaria* (Nicolson, 1960; Gracia, 2009). Even further inland, fixed dunes experience less exposure to wind than dunes closer to open water, and have more organic matter and greater soil depth than other dune habitats. Fixed dunes also are less dominated by single species and present substantial species and community diversity (Lemauviel et al., 2003; Gracia and Muñoz, 2009). These three habitats correspond to different vegetation types or plant communities, according to phytosociological classification (Rivas-Martínez et al., 2011). In our study area embryo dunes have been included in the association *Euphorbio paraliae-Agropyretum junceiformis.* On mobile dunes there are three associations, one in Spain, *Otantho maritimi-Ammophiletum australis*, and two in France, *Sileno thorei-Ammophiletum arenariae* and *Galio arenarii-Hieracietum eriophori* (Demartini, 2016). On fixed dunes we have two orders with their alliances. One is the *Crucianelletalia maritimae* including the *Helichrysion picardii* alliance and the other is *Artemisio lloydii-Koelerietalia albescentis* order including *Euphorbio portlandicae-Helichrysion stoechadis alliance* (Mucina et al., 2016; Marcenò et al., 2018).

The obvious heterogeneity in dune systems along this complex gradient suggest variation in both functional and phylogenetic diversity within and among local communities. In fact, a close relationship between functional and phylogenetic diversity can exist in coastal dunes (Carboni et al., 2013), while processes that promote phylogenetic clustering and regional diversification can also influence assembly in dune communities (Brunbjerg et al., 2014). Additional evidence suggests that environmental filtering mechanisms dominate in dune communities in the absence of invasive species (Marcantonio et al., 2014). Consequently, we anticipate that the greater taxonomic and phylogenetic diversity of fixed dunes provides opportunity for species turnover and changes in phylogenetic and functional diversity (Losos, 2008). These changes should be lower in embryo dune communities that are exposed to harsh conditions than more-sheltered fixed dune communities, because exposure to demanding conditions promotes the functionally similarity of species (Chesson and

Huntly, 1997; Machac et al., 2011). Over substantial (sub continental) geographic distances, species in embryo dunes, which are nearer to sea, should be functionally more similar than those in fixed dunes because of predominating physical disturbance, exposure to wind and salt, and poorly developed soil.

We study coastal dunes across four biogeographical sectors, spanning about 750 km along the coasts of north Spain and southwest France (Rivas-Martínez, 1982; Rivas-Martínez et al., 2017b). We analyze beta diversity of taxonomic, functional and phylogenetic community components in two gradients, one ecological along the sea-inland and another along the coast and four biogeographical regions. We wonder which of these two gradients played the main role. We decompose plant beta diversity into richness and replacement components in order to assess whether or not the number of species or species identity play important roles in assembly. Finally we calculated Local Beta Diversity Contributors in order to asses if any site showed a particular species composition.

4.2. Materials and methods

4.2.1. Study area

The study area was located in the Atlantic coast of southern Europe (Figure 4.1), extending from southern French coast to northwest corner of Spain and it was included in the Cantabroatlantic subprovince. It included four biogeographical sectors: Galicia and North Portugal (GP), North Galicia and Asturias (GA), Cantabrian and Basque (CB) and Aquitaine-Landes (AL) (Rivas-Martínez, 1982; Rivas-Martínez et al., 2017b). In the western sectors, temperate hyperoceanic submediterranean conditions predominate, while in the eastern sectors a temperate oceanic bioclimate is dominant (Rivas-Martínez et al., 2017a). A detailed bioclimatic description of each sector can be found in Torca et al., (2019a).

4.2.2. Sampling and data collection

We selected three study locations in each of the four biogeographical sectors. Locations were selected due to their natural status avoiding very disturbed places and with enough area in order to set the plots. Three different dune vegetation types were considered in each location: embryo, mobile and fixed dunes. For each vegetation type in each location four 100 m^2 (10 x 10 m) plots were set randomly. In each 100 m^2 we included two 10 m^2 subplots in opposite corners following Dengler (2009). In each 10 m^2 subplot the vascular flora was identified and the cover was visually estimated following the Braun-Blanquet scale (See chapter 3). First we gave a cover estimate for the most abundant species and finally for the less frequent. Those species not identified in the field were brought to the lab for further identification.

For functional diversity analysis 10 traits were recorded: life form, geographical distribution, flowering onset and span, pollination, fruit type,

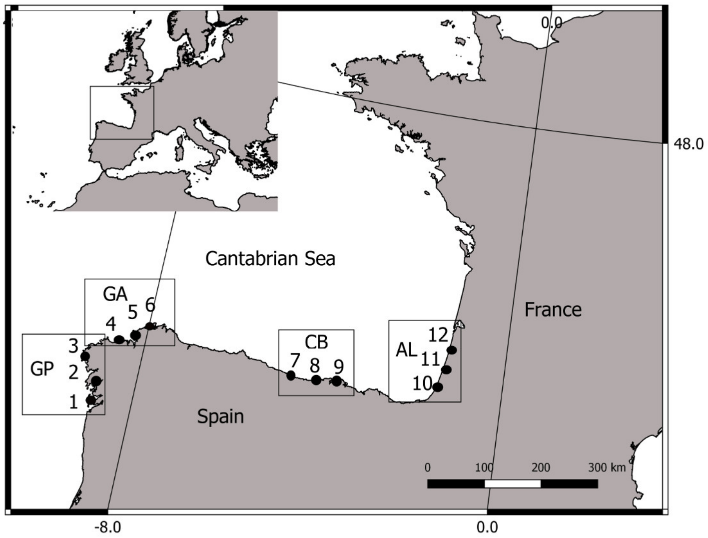

Figure 4.1: Study area. Twelve locations sampled from Galicia (Spain) to France grouped by biogeographic sectors. Galicia and North Portugal: 1. La Lanzada 2. As Furnas 3. Carnota North Galicia and Asturias: 4. Barrañán 5. San Xurxo 6. Valdoviño Cantabrian and Basque: 7. Oyambre 8. Liencres 9. Noja. Aquitaine-Landes: 10. Tarnos 11. Casernes 12. Messanges.

seed dispersal, specific leaf area (SLA), plant height and seed mass. For the LHS (leaf-height-seed) framework (Westoby, 1998) the traits of most abundant species were measured both in the field directly (plant height) or later in the laboratory (SLA and seed mass). For other traits and less abundant species data were collected from regional and national floras and from online database. More detailed information can be found in Torca et al., (2019a) See chapter 3.

For phylogenetic diversity a phylogenetic tree was constructed with the *brranching* R package (Chamberlain, 2015). We used the reference tree R20120829 (Bermer et al., 2009) because it was the tree that most of our species included. Then, polytomies were removed randomly and one species not included in the tree was manually added.

4.2.3. Diversity indices

Ecological studies often rely on similarity coefficients between pairs of species assemblages (or communities, plots, sites, quadrats, etc.) to explore the mechanisms driving community assembly (Ricotta et al., 2015). In this work taxonomic, functional and phylogenetic diversity were studied.

Taxonomic diversity

For beta taxonomic diversity Bray-Curtis index of dissimilarity (Bray and Curtis, 1957) was calculated. The index is based on both species occurrence and abundances at each site. The dissimilarity matrix was constructed using squared-rooted values of cover to equalize the relative importance of common and rare species.

Phylogenetic diversity

Beta phylogenetic diversity was measured with NRI (Net Relatedness Index) and NTI (Nearest Taxon Index) beta equivalents, which are D_{pw} and D_{nn} (Gonzalez-Caro et al., 2014). NRI is a standardized effect size (SES) of the observed mean pairwise phylogenetic distance (MPD) of all individuals or species in an assemblage. D_{pw} is based pairwise phylogenetic measure and is highly correlated with the more broadly known metric Rao's D (Rao, 1982) (Swenson et al., 2012). Also, D_{pw} has a long history of usage in community ecology (Gonzalez-Caro et al., 2014). D_{pw} is likely better at detecting major compositional turnover from community to community (Swenson et al., 2012).

D_{nn} calculates the mean nearest phylogenetic or functional neighbour between two communities (Ricotta and Burrascano, 2008) and it is an extension to beta diversity of Mean Nearest Taxon Distance (MNTD) (Swenson, 2014). The nearest-neighbour metric is ideal for detecting subtle turnover in composition from subplot-to-subplot that may not be detected with pairwise metrics (Swenson et al., 2012). Moreover this metric is similar to traditional metrics of species turnover such as the Bray-Curtis index (Swenson, 2011).

Functional diversity

Gower distance was used to get a functional dissimilarity matrix for functional beta diversity. Gower distance allows inclusion of both continuous and discrete traits (Ricotta and Burrascano, 2008). Then, the resulting matrix was used with D_{pw} index in order to obtain a beta diversity measure. The NRI and NTI are measures of phylogenetic diversity, but similar measures of functional diversity were calculated using trait dendrograms or trait distance matrices allowing for direct comparisons between trait and phylogenetic results (Swenson et al., 2012). In this case, for functional D_{pw} we used trait matrix based on Gower distance.

4.2.4. Beta diversity partitioning and local contributors

We expect a change of beta diversity along the study area, but this index does not specify if it is due to species replacement or richness. So we will try beta diversity decomposition. Decomposition of beta diversity provides a suitable tool to elucidate the mechanisms of assembly of plant sand dune communities along the sea-inland gradient (Tordoni et al., 2018). In order to decompose beta diversity in richness and replacement Ružička index, Jaccard equivalent for abundance data was calculated. Furthermore, in order to see how each site contributed to beta diversity LCBD (Local Contribution to Beta Diversity) was used. LCBD is a comparative indicator of site singularity and are useful to detect unusual species combinations. These combinations could be the result of the presence of high conservation value species or maybe due to the effect of invasive species in plant communities (Legendre and De Cáceres, 2013).

4.2.5. Data analysis

To assess possible spatial patterns in the plots multivariate ordination was applied. Then, a constrained variable was used. This variable was the distance along the coast in order to express the biogeographical gradient along the four sectors. The variable was measured starting in the furthest beach in the west, La Lanzada. Distance-based Redundance Data Analysis (db-RDA; Legendre and Anderson, 1999) was performed to conduct the constrained ordination. Distance-based Redundance Data Analysis is a multivariate multiple regression (Geffen et al., 2004) and is a suitable tool for distance measures that are not Euclidean, such as the Bray-Curtis and Gower measures (Legendre and Anderson, 1999; McHardle and Anderson, 2001). It is also an invaluable tool for modelling communities through environmental predictors (Peres-Neto et al., 2006).

We used the *capscale* function of *Vegan* R package (Oksanen et al., 2016; R Core Team, 2015) to conduct db-RDA ordination on taxonomic, functional and phylogenetic diversity. Ordinations were performed for each dune type separately. We did later an ANOVA analysis to see if the constraining variable, distance along the coast, explained the ordination. Then to disentangle variation partitioning *varpart* function in the *Vegan* package was applied. It automatically conducts variation partitioning of a response table using RDA-adjusted r^2 values (Peres-Neto et al., 2006). For the species composition matrix total beta diversity and replacement and richness components were calculated with *adespatial* R package (Legendre, 2014; Dray et al., 2016).

4.3. Results

In embryo dunes there were 49 species, 76 in mobile dunes and 94 in fixed dunes (Table 4.1). In western sectors (GA, GP) there were 20 species in embryo dunes, 24 in mobile dunes and 28 in fixed dunes. In eastern sectors (AL, CB) there were 12 species, 31 in mobile dunes and 19 in fixed dunes. There were 4 species common to the four sectors in embryo dunes, 8 in mobile dunes and 13 in fixed dunes.

4.3.1. Taxonomic, functional and phylogenetic diversity

First, we analysed taxonomic diversity. In embryo dune, the distribution of plots in the db-RDA was explained significantly by the variable biogeographical gradient, as well as in mobile and fixed dune habitats (Table 4.2). In mobile dunes there was a gradient from east to west in which French sites (AL) were separated. In fixed dune east and west localities were grouped. Western sites (GP, GA) presented a more mixed pattern than eastern ones CB, AL (Figure 4.2 a-c). The ecological gradient contributed 29% of variation while the biogeographical gradient only 7% (Figure 4.3a).

Table 4.1: Total number of species and divided by presence in the easter sectors (AL-CB), western sectors (GA, GP) and common to the four sectors.

Sector	Embryo	Mobile	Fixed
Total	49	76	94
AL-CB	12	31	19
GA-GP	20	24	28
Common to 4 sectors	7	8	13

Table 4.2: ANOVA for db-RDA variables for beta TD, PD (D_{pw} and D_{nn}) and FD in embryo, mobile and fixed dune habitats. df = degrees of freedom

Beta Index	Habitat	Variable	df	F	p
Taxonomic	Embryo	biogeographic	1	3.35	0.006
	Mobile	biogeographic	1	9.72	0.001
	Fixed	biogeographic	1	39.38	0.001
Functional	Embryo	biogeographic	1	1.39	0.141
	Mobile	biogeographic	1	3.54	0.004
	Fixed	biogeographic	1	4.77	0.001
D_{pw}	Embryo	biogeographic	1	0.74	0.549
	Mobile	biogeographic	1	1.01	0.39
	Fixed	biogeographic	1	2.99	0.001
D_{nn}	Embryo	biogeographic	1	4.05	0.07
	Mobile	biogeographic	1	8.02	0.015
	Fixed	biogeographic	1	32.97	0.001

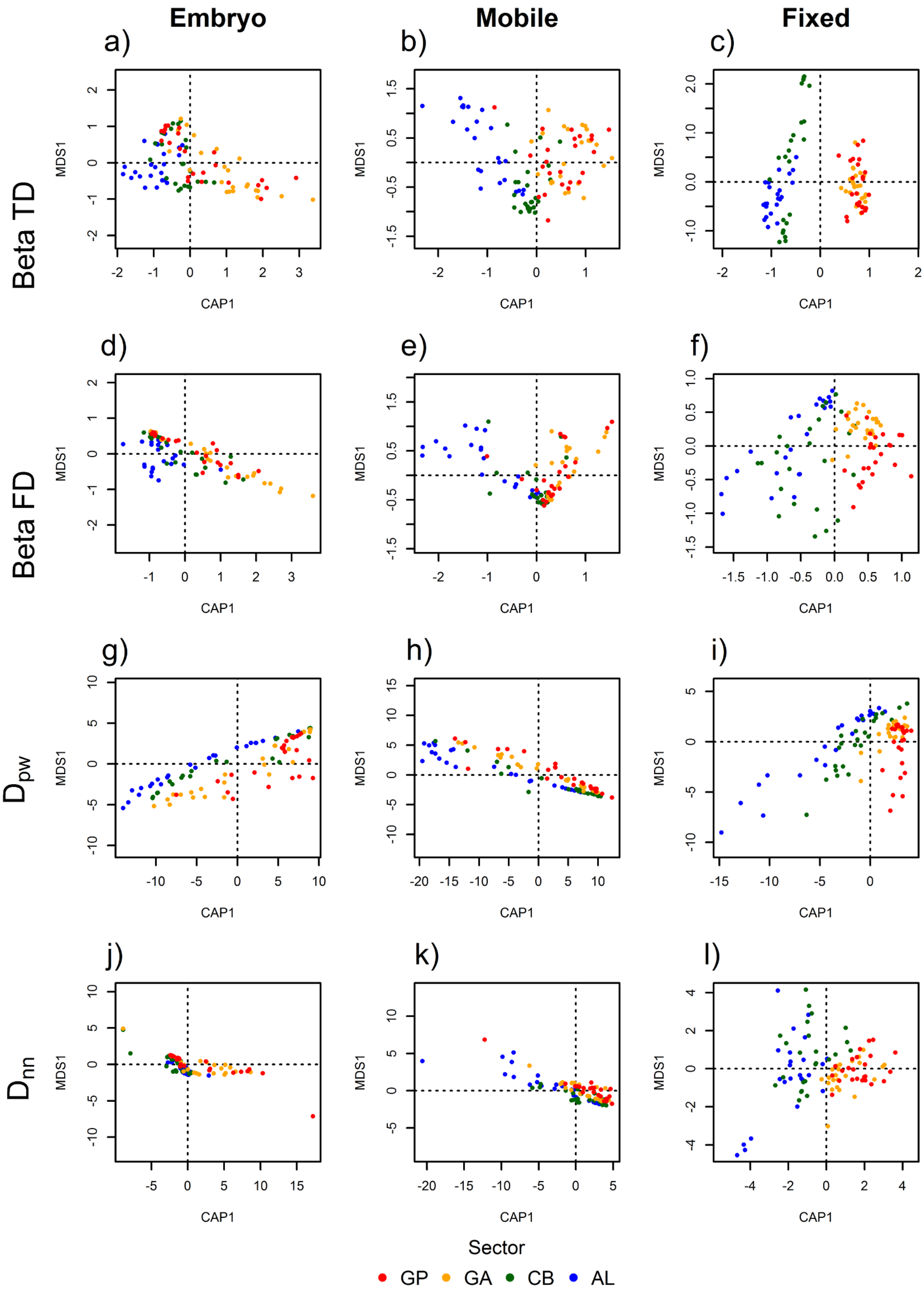

Figure 4.2: Spatial ordinations for taxonomic (TD), functional (FD) and phylogenetic (D_{nn} and D_{pw}) beta diversity on each dune habitat. Embryo dunes (a, d, g, j) showed pattern, where plots were mixed. In fixed dunes (c, f, i, l) plots split in western and eastern sectors.

Functional diversity showed a similar pattern as taxonomic diversity. For embryo dunes no clear differences in functional diversity were present. In mobile and fixed dune biogeographical gradient explained the distribution of the plots in the db-RDA (Table 4.2). In mobile dune French plots ordered apart. For fixed dune regional separation was shown in the ordination (Figure 4.2 d-f). When three dune habitats were taken together both variables, distance and habitat, showed significant differences (Table 4.3). About variation partitioning 26% was due to dune habitat and just 1% to the biogeographical gradient (Figure 4.3b). No variation was shared between variables.

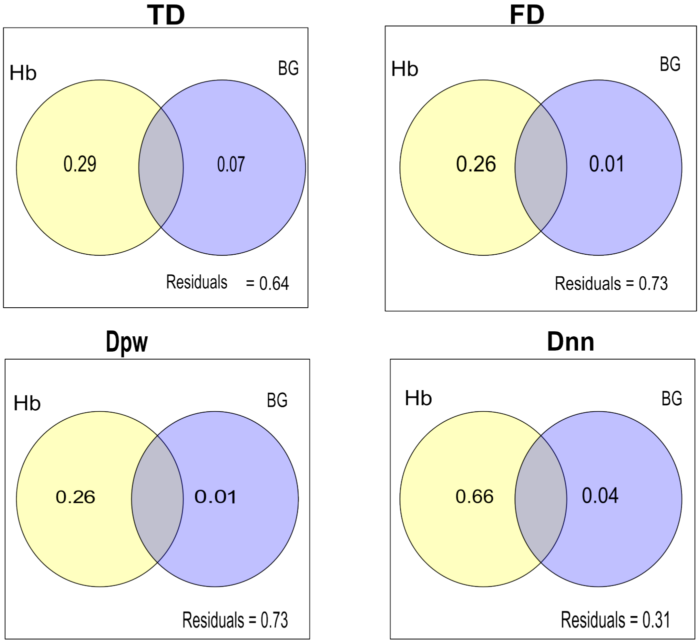

Figure 4.3: Variation partitioning for biogeographical gradient (BG) and dune habitat (Hb) for each diversity index. Values <0 not shown.

For phylogenetic diversity and for embryo and mobile dunes, Dpw index and biogeographical gradient did not explain significantly the ordination (Table 4.2). However, fixed dune habitats presented a pattern with biogeographical gradient (Figure 4.2g-i). When the three dune habitats were taken into account just biogeographical gradient explained the distribution of plots in the db-RDA (Table 4.3). 19% of variation was due to habitat type (Figure 4.3c). For Dnn index and for mobile and fixed dune habitats biogeographical gradient explained significantly the ordination, (Table 4.2). In ordination plots fixed dunes showed a clear difference between east and west zones, while in mobile and embryo dune habitats this pattern was not so evident (Figure 4.2j-l). Taking into account all the habitats both dune habitat and biogeographical gradient explained the distribution of plots in the ordination (Table 4.3). Dune habitat explained 66% of the variation while 4% was due to biogeographical gradient. No variation was shared between these two variables (Figure 4.3d).

In general, we found an increasing clear pattern in the ordinations from embryo to fixed dunes. In embryo dunes plots appeared more mixed and in fixed dunes two groups, eastern (AL, CB) and western (GA, GP) sectors,

Table 4.3: ANOVA for db-RDA variables for TD, PD (Dpw and Dnn) and FD for biogeographical gradient (distance along the coast) and dune habitats gathered (ecological gradient) at local scale. df = degrees of freedom

Index	Habitat	Variable	df	F	p
Taxonomic	Global	biogegraphic	1	32.41	0.001
		dune habitat	2	65.69	0.001
Functional	Global	biogeographic	1	6.6	0.001
		dune habitat	2	51	0.001
D_{pw}	Global	biogeographic	1	1.58	0.131
		dune habitat	2	52.8	0.001
D_{nn}	Global	biogeographic	1	37.84	0.001
		dune habitat	2	307.76	0.001

were differentiated. This trend is present regardless of the diversity index considered.

4.3.2. Beta diversity partitioning and local contributors

Decomposition of beta diversity in richness and replacement showed the highest value in fixed dune and the lowest in mobile dune (Table 4.4). The proportion of richness and replacement in embryo dune was higher for richness beta diversity component, which accounted for the 53% of total beta diversity while species replacement accounted for the 47%. In mobile dune proportion was 55% replacement and 45% species richness. Fixed dune communities were dominated by replacement with 64% of total beta diversity while species richness accounts for the 36%. Species richness increased from sea to inland in most of the sites (Figure 4.4).

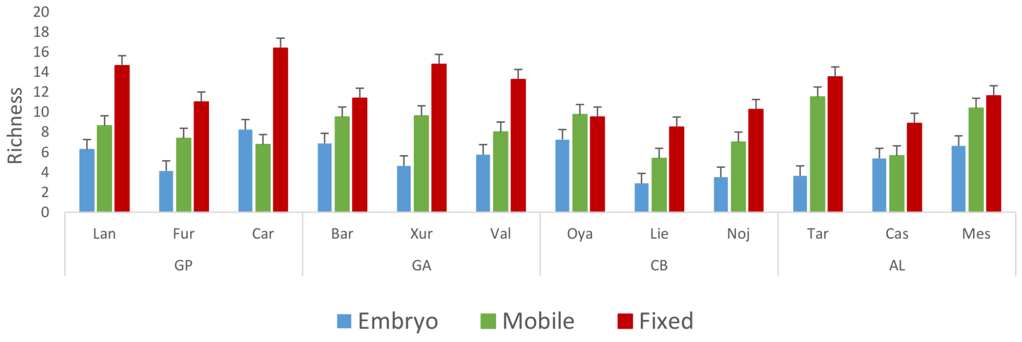

Figure 4.4: Mean of species richness for embryo, mobile and fixed dunes along the geographical gradient. Bars = standard error. Lan = La Lanzada, Fur = As Furnas, Car = Carnota, Bar = Barrañán, Xur = San Xurxo, Val = Valdoviño, Oya = Oyambre, Lie = Liencres, Noj = Noja, Tar = Tarnos, Cas = Casernes, Mes = Messanges.

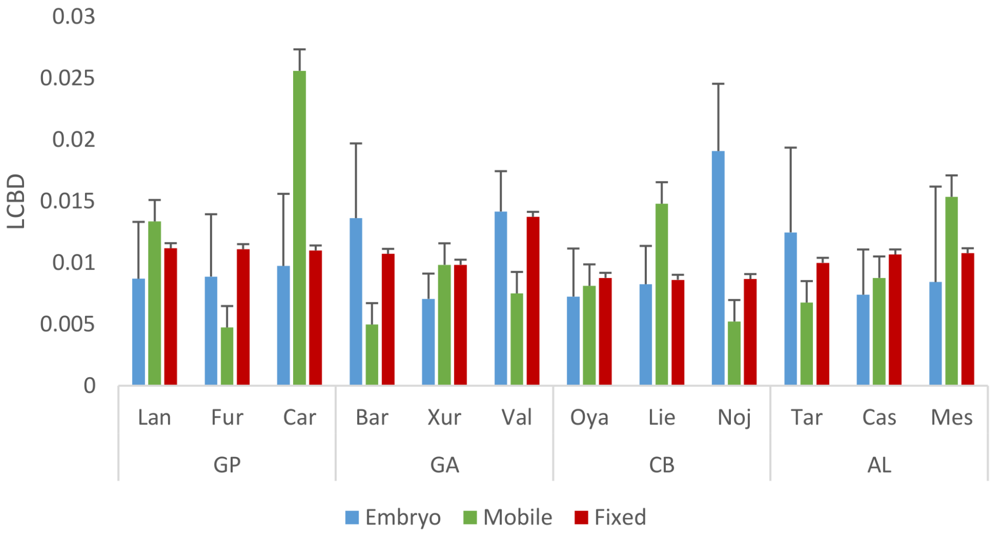

Figure 4.5: Means of Local Contributors to Beta Diversity (LCBD) for embryo, mobile and fixed dunes. Bars = standard error. For abbreviation of sites see Figure 4.4.

Table 4.4: Total beta diversity (BD), replacement (repl) and richness (richness) for embryo, mobile and fixed dune habitats.

Dune habitat	BD Total	Total repl	Total rich	Total repl /Total BD	Total rich / Total BD
Embryo	0.375	0.178	0.197	47%	53%
Mobile	0.37	0.202	0.168	55%	45%
Fixed	0.443	0.283	0.16	64%	36%

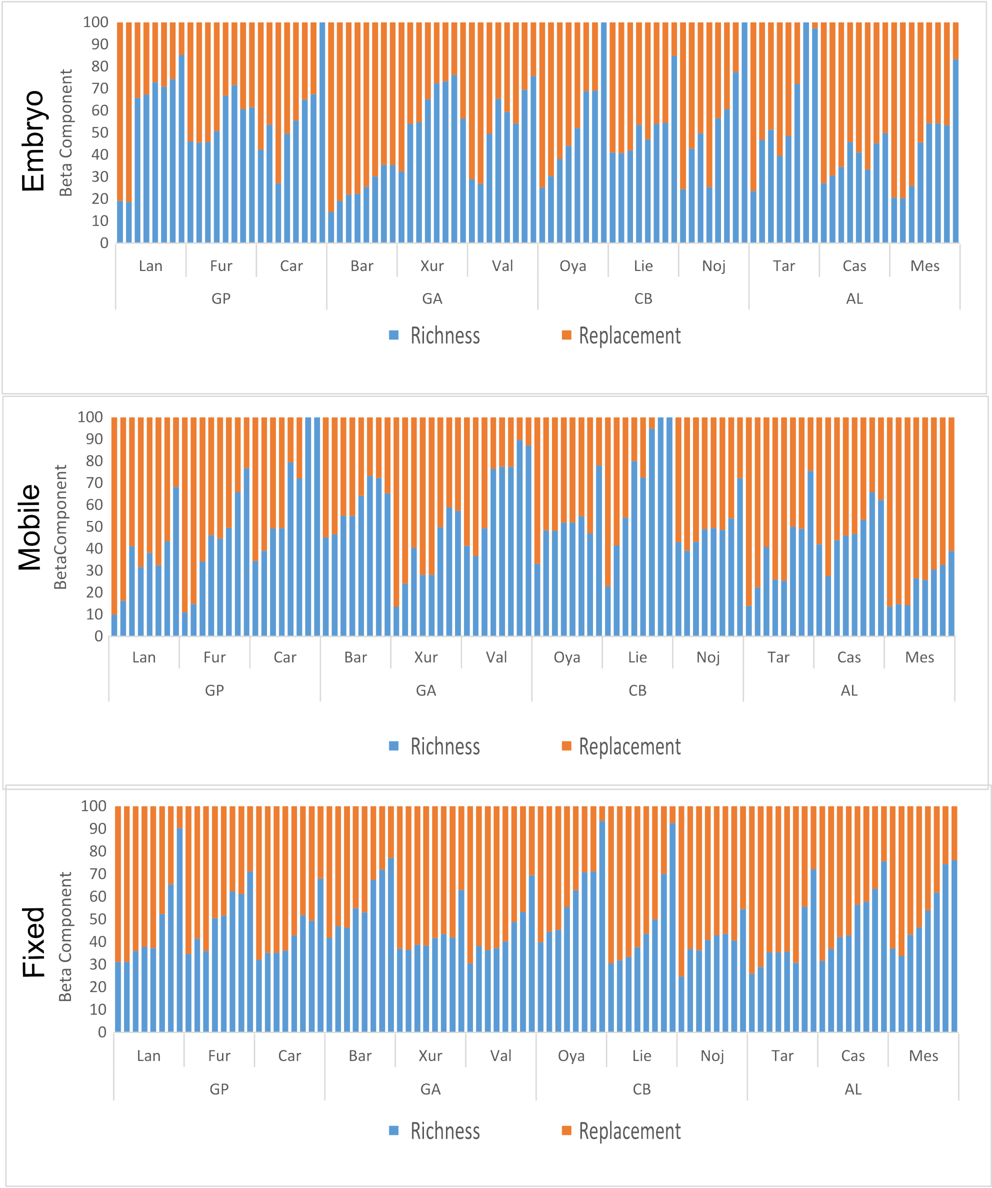

Figure 4.6: Values of beta diversity components of richness and replacement on each dune habitat: embryo (a), mobile (b) and fixed (c). For abbreviation of sites see Figure 4.4.

LCBD values were not higher in one dune habitat type or in other. Embryo and mobile dunes presented more variable values from higher to lower, whereas fixed dune tended to be more stable (Figure 4.5). Embryo dunes presented 6 significant values and fixed dunes again 6 significant values. Decomposition of beta diversity in its two components, richness and replacement (Figure 4.6), showed no clear pattern of which component dominates. In some locations was replacement and in others richness. Indeed, within the plots of the same site again no clear pattern appeared excepting Casernes (France) and Barrañán (W Spain) for embryo dunes and Messanges (France) and La Lanzada (W Spain) for mobile dunes, where replacement dominated.

4.4. Discussion

4.4.1. Taxonomic, functional and phylogenetic beta diversity

We proposed coastal dunes as a suitable ecosystem to study geographical variation as they have a unique and particular ecological gradient. We expected greater changes in community assembly in fixed dunes due to the lower effect of environmental filtering (Torca et al., 2019b). In general, we found that biogeographical gradient partially explained beta diversity patterns for taxonomic, functional and phylogenetic diversity.

For embryo dune, taxonomic beta diversity was mainly explained by the biogeographical gradient. Most common and abundant species such as *Elytrigia juncea* subsp. *boreoatlantica*, *Calystegia soldanella*, *Eryngium maritimum* or *Euphorbia paralias* were recorded in the four biogeographical sectors; however, there were some species only present in one sector. For example, considering the Galicia and North Portugal (GP) sector we found *Artemisia campestris*, *Crithmum maritimum* or *Cuscuta campestris*. In the sector Aquitaine-Landes (AL) we found species such as *Galium arenarium* or *Silene uniflora* subsp. *thorei*. Indeed, there were species only present in the border of the study area. *Astragalus baionensis*, *Linaria thymifolia* or *Silene portensis* were only recorded for embryo dune in Messanges, which is the site most in the east. In the western side, in La Lanzada, for embryo dune we recorded *Cyperus capitatus*, *Matthiola sinuata* and *Scolymus hispanicus*, which were not found in other embryo dune sites. This situation could explain why taking into account biogeographical sectors as groups only embryo dune it is not significant (Torca et al., 2019b). In this study distance between sites was assessed, so local differences were able to arise. Phylogenetic beta diversity for embryo dune showed no significant differences for any index. Despite the species change families remain without differences. Furthermore, species present in the four biogeographical sectors were mainly from the *Poaceae* and *Asteraceae* families: *Ammophila arenaria* subsp. *australis*, *Elytrigia juncea* subsp. *boreoatlantica*, *Leontodon saxatilis* or *Hypochaeris radicata*. In embryo dune no differences were found in functional diversity. This agrees with the low functional alpha diversity (Torca et al., 2019b). Highly stressful habitats act as an environmental filter, that selects the few tolerant species with morphological and physiological traits that are suitable (Gallego-Fernández and Martínez, 2011; Bermúdez and Retuerto, 2013).

Distribution of plots of the ordination in mobile dunes was explained by biogeographical gradient for taxonomic and functional diversity (Table 4.2). This agrees with Rivas-Martínez et al. (2011) and Demartini (2016), who recognized three different associations for mobile dunes, one in north of Spain and two in France. For phylogenetic diversity biogeographical gradient partially explained the ordination only for the D_{nn} index. Dnn is a nearest-neighbour metric ideal for detecting subtle turnover composition that may be not detected by pairwise metrics (Swenson et al., 2012). Changes of species for the French sector are not at the family level, with the exception of *Thesium humifusum*, which is included in *Santalaceae*, as this family was absent from north Spain sites. Most of changes were at level of genus or even species such as *Linaria supina* subsp. *maritima* in the Cantabrian and Basque sector and *Linaria thymifolia* in the AL sector. About functional diversity, the lower abundances or even the absence in some plots in France of *Ammophila arenaria* subsp. *australis* would make a difference, as it is the tallest species and most abundant species in most of mobile dunes.

Distribution of plots in fixed dunes was explained by biogeographical gradient for taxonomic, functional and phylogenetic diversity regardless of what phylogenetic index used. The clear grouping between sectors for taxonomic diversity that we have found would support the phytosociological classification. From a total of 94 species 19 belonged to eastern sectors, 28 to the western sectors and just 13 were common to the four sectors (Table 4.1). In this context there was a replacement of species at family level. For example, for the *Asteraceae* family in France we found *Hieracium eriophorum* and in western sectors *Andryala integrifolia* and *Scolymus hispanicus*. In North Galicia and Asturias and Galicia and North Portugal sectors there are species from *Caprifoliaceae*, *Gentianaceae* and *Brassicaceae* families. These families were not recorded in fixed dunes in Aquitaine-Landes and Cantabrian and Basque sectors. In a subtler differentiation we found a replacement at species level for some genera such as *Linaria*, *Helichrysum* or *Jasione*.

The variation partitioning showed higher values for habitat factor than biogeographical gradient for the four diversity indices measured. For functional diversity we found a greater influence of dune habitat. This agrees with Mahdavi and Bergmeier (2016), who found higher functional affiliation of sand dune species shaped by habitat rather than by climatic region. This relation of species and habitat is in accordance with Mahdavi et al. (2017), whose results showed functional diversity between different four regions of sand dunes studied related to the change in species composition. However, for species composition results of Mahdavi and Bergmeier (2016) showed a higher influence of climate and phytogeography than our results, which for taxonomic diversity showed a greater variation of dune habitat. Mahdavi and Bergmeier (2016) sampled three different biogeographic regions, which one included inland dunes. While spatial processes overall affect turnover across plant communities, the influence of the space is much weaker than changes in the abiotic environment (Fig. 4.4a).

4.4.2. Beta diversity partitioning and local contributors

Our results showed an increasing beta diversity from embryo to fixed dunes (Table 4.4). This increase could be related to the increasing richness in the sea-inland gradient (Tordoni et al., 2018). Embryo and mobile dunes have fewer species than fixed dunes and are dominated by some such as *Elytrigia juncea* subsp. *boreatlantica* and *Ammophila arenaria* subsp. *australis*. In the samples of embryo dune there was great heterogeneity with plots plenty of *Elytrigia* and others almost without species. For mobile dunes something similar happened with plots with high abundances of *Ammophila* and other sites such as Tarnos (France, AL) or La Lanzada (Galicia, GP) with almost no presence of this characteristic species of mobile dunes.

Then, changes in species richness and abundances could lead to the mixed patterns presented on Figure 4.5 for LCBD. For example, in embryo dune Barrañán (Galicia, GA), had higher values of *Crucianella maritima*, a species mainly present in western sectors, than *Elytrigia juncea* subsp. *boreatlantica*. This could make this site suitable for high values of LCBD. In the case of mobile dunes, those places with low values of *Ammophila* (La Lanzada, Carnota, Messanges) showed higher values of LCBD. Fixed dunes showed a smaller range of variation for LCBD (Table 4.4). As there are more species without a highly dominant one, turnover of species would not lead to such drastic changes as in embryo and mobile dunes. Oyambre (Spain, CB) presented higher values of LCBD in most of the plots (Figure 4.6). This location was next to a parking and was one of the ways to access the beach, then trampling could act as an eroding factor. Extensive human activity in littoral areas and the presence of coastal roads favour the entry of alien species (Campos et al., 2004, 2010) ruderal and wide distribution species (*Plantago coronopus* and *P. lanceolata*) into dune plant communities (Acosta et al., 2006). Also human activities, including trampling, threaten the natural biodiversity of sandy shore ecosystems (Andersen, 1995), reducing richness and relative abundance of typical species (Campos et al., 2004; Mahdavi and Bergmeier, 2016).

About decomposition of beta diversity in richness and replacement no clear pattern appeared as in Tordoni et al., (2018), where there was richness over replacement for coastal dune communities. So changes were due to gain or loss of species. This would be an expectable result as they only sampled in two sites separated by less than twenty kilometres. In our case there could be a balance between richness and species turnover, where in some plots would dominate one or the other, even within the same site. However, in some places such as Barrañán (Galicia, GA) and Casernes (France, AL) for embryo dune, and Messanges (France, AL) and La Lanzada (Galicia, GP) for mobile dune replacement component dominated. Indeed, for embryo dune five of six significant values were in Casernes. This trend of replacement dominance could be based on the larger adaptations of the species to the harsh conditions of the habitats (Tordoni et al., 2018). In our case in particular it could be also due to the larger distance studied, 750 km along the coast, including a whole biogeographical Subprovince.

Conclusions

We found a relation with the biogeographical gradient for all biodiversity components in fixed dunes, while it was only for taxonomic diversity in embryo dunes. A stressful environment would select similar species in embryo dunes, while at the same time there could be some specific species from some sites. In fixed dunes softer conditions would allow the differentiation of species between sectors, which would be followed by a change in functional and phylogenetic diversity. Comparing variation percentages due to biogeographical or ecological gradients, the ecological one dominated. Therefore, the ecological gradient was stronger than the biogeographical one. This would reinforce the biogeographical classification of the study area in the same subprovince. Decomposition of beta diversity in richness and replacement showed higher values of richness in embryo dune and replacement for fixed dunes. In embryo dunes main species remained constant along the biogeographical gradient and only some less abundant species changed, which would give more importance to richness component. In fixed dunes species change would be greater because environmental filtering would be lower. Then, environmental would select some main species in embryo dunes, while in fixed dunes the milder conditions would promote species replacement.

References

Acosta, A., Ercole, S., Stanisci, A., Blasi, C., 2006. Sandy coastal ecosystems and effects of disturbance in Central Italy. J. Coast. Res. 39, 985–989.

Andersen, U.V., 1995. Resistance of Danish coastal vegetation types to human trampling. Biol. Conserv. 71, 223–230. https://doi.org/10.1016/0006-3207(94)00031-K

Barbour, M.G., De Jong, T.M., Pavlik, B.M., 1985. Marine beach and dune plant communities, in: Chabot, B.F., Mooney, H.A. (Eds.), Physiological Ecology of North American Plant Communities. Springer Netherlands, Dordrecht, pp. 296–322. https://doi.org/10.1007/978-94-009-4830-3_14

Bazzaz, F.A., 1991. Habitat Selection in Plants. Am. Nat. 137, S116–S130.

Bermer, B., Bremer, K., Chase, M.W., Fay, M.M., Reveal, J.L., Soltis, D.E., Soltis, P.S., Stevens, P.F., Anderberg, A.A., Moore, M.J., Olmstead, R.G., Rudall, P.J., Sytsma, K.J., Tank, D.C., Wurdack, K., Xiang, J.Q., Zmarzty, S., 2009. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161, 105–121. https://doi.org/10.1111/j.1095-8339.2009.00996.x

Bermúdez, R., Retuerto, R., 2013. Living the difference: alternative functional designs in five perennial herbs coexisting in a coastal dune environment. Funct. Plant Biol. 40, 1187–1198. https://doi.org/10.1071/FP12392

Boukili, V.K., Chazdon, R.L., 2017. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. Perspect. Plant Ecol. Evol. Syst. 24, 37–47. https://doi.org/10.1016/j.ppees.2016.11.003

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349. https://doi.org/10.2307/1942268

Brown, A.C., McLachlan, A., 1990. Ecology of sandy shores, 2nd ed. Elsevier, Amsterdam.

Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., Ejrnaes, R., Aarssen, L.W., Buckley, H.L., Forey, E., Jansen, F., Kattge, J., Lane, C., Lubke, R.A., Moles, A.T., Montserrat, A.L., Peet, R.K., Roncal, J., Wootton, L., Svenning, J.-C., 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. J. Plant Ecol. 7, 101–114. https://doi.org/10.1093/jpe/rtt069

Campos, J.A., García-Mijangos, I., Loo, J., Herrera, M., 2010. Datos sobre la vegetación psamófila ruderal de la costa cantábrica. Braun-Blanquetia 46, 146–155.

Campos, J.A., Herrera, M., Biurrun, I., Loidi, J., 2004. The role of alien plants in the natural coastal vegetation in central-northern Spain. Biodivers. Conserv. 13, 2275–2293. https://doi.org/10.1023/B:BIOC.0000047902.27442.92

Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? J. Veg. Sci. 24, 932–941. https://doi.org/10.1111/jvs.12095

Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius, M., Borges, P.A.V., Podani, J., Schmera, D., 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. J. Biogeogr. 41, 749–761. https://doi.org/10.1111/jbi.12239

Chamberlain S., 2018. brranching: Fetch 'Phylogenies' from Many Sources. R package version 0.3.0. https://CRAN.R-project.org/package=brranching

Chesson, P., Huntly, N., 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am. Nat. 150, 519–553. https://doi.org/10.1086/286080

Cornwell, W.K., Ackerly, D.D., 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecol. Monogr. 79, 109–126. https://doi.org/10.1890/07-1134.1

Demartini, C., 2016. Les végétations des côtes Manche-Atlantique françaises: essai de typologie et de cartographie dynamic-caténales. Université de Bretagne Occidentale.

Dengler, J., 2009. A flexible multi-scale approach for standardised recording of plant species richness patterns. Ecol. Indic. 9, 1169–1178. https://doi.org/10.1016/j.ecolind.2009.02.002

Diamond, J.M., 1975. Assembly of species communities., in: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge, MA, USA.

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Legendre, P., Wagner, H., 2016. adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.0-3. `http://CRAN.R-project.org/package=adespatial`.

Fenu, G., Cogoni, D., Ferrara, C., Pinna, M.S., Bacchetta, G., 2012. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). Plant Biosyst. 146, 586–602. `https://doi.org/10.1080/11263504.2012.656727`

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. J. Veg. Sci. 19, 493–502. `https://doi.org/10.3170/2008-8-18392`

Fukami, T., 2004. Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. Popul. Ecol. 46. `https://doi.org/10.1007/s10144-004-0182-z`

Gallego-Fernández, J.B., Martínez, M.L., 2011. Environmental filtering and plant functional types on Mexican foredunes along the Gulf of Mexico. Écoscience 18, 52–62. `https://doi.org/10.2980/18-1-3376`

Geffen, E., Anderson, M.J., Wayne, R.K., 2004. Climate and habitat barriers to dispersal in the highly mobile grey wolf. Mol. Ecol. 13, 2481–2490. `https://doi.org/10.1111/j.1365-294X.2004.02244.x`

Gerhold, P., Cahill, J.F., Winter, M., Bartish, I.V., Prinzing, A., 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). Funct. Ecol. 29, 600–614. `https://doi.org/10.1111/1365-2435.12425`

Goldberg, D.E., 1987. Neighborhood Competition in an Old-Field Plant Community. Ecology 68, 1211–1223. `https://doi.org/10.2307/1939205`

Gonçalves-Souza, T., Romero, G.Q., Cottenie, K., 2014. Metacommunity versus biogeography: a case study of two groups of Neotropical vegetation-Dwelling Arthropods. PLOS ONE 9, e115137. `https://doi.org/10.1371/journal.pone.0115137`

Gonzalez-Caro, S., Umana, M.N., Alvarez, E., Stevenson, P.R., Swenson, N.G., 2014. Phylogenetic alpha and beta diversity in tropical tree assemblages along regional-scale environmental gradients in northwest South America. J. Plant Ecol. 7, 145–153. `https://doi.org/10.1093/jpe/rtt076`

Götzenberger, L., Bello, F. de, Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., Zobel, M., 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. Biol. Rev. 87, 111–127. `https://doi.org/10.1111/j.1469-185X.2011.00187.x`

Gracia, F.J., 2009. Dunas móviles de litoral con Ammophila arenaria (dunas blancas), in: VV.AA (Ed.), Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Ministerio de Medio Ambiente, y Medio Rural y Marino., Madrid, p. 48.

Gracia, F.J., Hernández, L., Hernández, A.I., SanJaume, E., Flor, G., 2009. Dunas móviles embrionarias, in: VV.AA (Ed.), Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Ministerio de Medio Ambiente, y Medio Rural y Marino, Madrid, p. 54.

Gracia, F.J., Muñoz, J.C., 2009. Dunas costeras fijas con vegetación herbácea (dunas grises), in: VV.AA (Ed.), Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Ministerio de Medio Ambiente, y Medio Rural y Marino, Madrid, p. 40.

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., Virtanen, R., 2017. Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. Oecologia 183, 121–137. `https://doi.org/10.1007/s00442-016-3750-y`

Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164. `https://doi.org/10.2307/3235676`

Kraft, N.J.B., Ackerly, D.D., 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecol. Monogr. 80, 401–422. `https://doi.org/10.1890/09-1672.1`

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Kattge, J., Coomes, D.A., 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. Ecol. Lett. 15, 831–840. `https://doi.org/10.1111/j.1461-0248.2012.01803.x`

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., Poorter, L., 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91, 386–398. `https://doi.org/10.1890/08-1449.1`

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity: Replacement and richness difference components. Glob. Ecol. Biogeogr. 23, 1324–1334. `https://doi.org/10.1111/geb.12207`

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1. `https://doi.org/10.2307/2657192`

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. `https://doi.org/10.1111/ele.12141`

Lemauviel, S., Gallet, S., Rozé, F., 2003. Sustainable management of fixed dunes: example of a pilot site in Brittany (France). C. R. Biol. 326, 183–191. https://doi.org/10.1016/S1631-0691(03)00056-8

Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecol. Lett. 11, 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Machac, A., Janda, M., Dunn, R.R., Sanders, N.J., 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography 34, 364–371. https://doi.org/10.1111/j.1600-0587.2010.06629.x

Mahdavi, P., Bergmeier, E., 2016. Plant functional traits and diversity in sand dune ecosystems across different biogeographic regions. Acta Oecologica 74, 37–45. https://doi.org/10.1016/j.actao.2016.06.003

Mahdavi, P., Isermann, M., Bergmeier, E., 2017. Sand habitats across biogeographical regions at species, community and functional level. Phytocoenologia 139–165. https://doi.org/10.1127/phyto/2017/0127

Maherali, H., Klironomos, J.N., 2007. Influence of Phylogeny on Fungal Community Assembly and Ecosystem Functioning. Science 316, 1746–1748. https://doi.org/10.1126/science.1143082

Marcantonio, M., Rocchini, D., Ottaviani, G., 2014. Impact of alien species on dune systems: a multifaceted approach. Biodivers. Conserv. 23, 2645–2668. https://doi.org/10.1007/s10531-014-0742-2

Marcenò, C., Guarino, R., Loidi, J., Herrera, M., Isermann, M., Knollová, I., Tichý, L., Tzonev, R.T., Acosta, A.T.R., FitzPatrick, Ú., Iakushenko, D., Janssen, J.A.M., Jiménez-Alfaro, B., Kącki, Z., Keizer-Sedláková, I., Kolomiychuk, V., Rodwell, J.S., Schaminée, J.H.J., Šilc, U., Chytrý, M., 2018. Classification of European and Mediterranean coastal dune vegetation. Appl. Veg. Sci. https://doi.org/10.1111/avsc.12379

McHardle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., Mouquet, N., 2011. Beyond taxonomic diversity patterns: how do alpha, beta and gamma components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob. Ecol. Biogeogr. 20, 893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x

Montreuil, A.-L., Bullard, J.E., Chandler, J.H., Millett, J., 2013. Decadal and seasonal development of embryo dunes on an accreting macrotidal beach: North Lincolnshire, UK. Earth Surf. Process. Landf. 38, 1851–1868. https://doi.org/10.1002/esp.3432

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., García, R.G., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., Tichý, L., 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl. Veg. Sci. 19, 3–264. https://doi.org/10.1111/avsc.12257

Nicolson, T.H., 1960. Mycorrhiza in the Gramineae: II. Development in different habitats, particularly sand dunes. Trans. Br. Mycol. Soc. 43, 132-IN10. https://doi.org/10.1016/S0007-1536(60)80017-4

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2.3-5.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614–2625.

Pool, T.K., Grenouillet, G., Villéger, S., 2014. Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. Divers. Distrib. 20, 1235–1244. https://doi.org/10.1111/ddi.12231

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/, Vienna, Austria.

Rao, C.R., 1982. Diversity and dissimilarity coefficients: A unified approach. Theor. Popul. Biol. 21, 24–43. https://doi.org/10.1016/0040-5809(82)90004-1

Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science 235, 167–171.

Ricotta, C., Bacaro, G., Caccianiga, M., Cerabolini, B.E.L., Moretti, M., 2015. A classical measure of phylogenetic dissimilarity and its relationship with beta diversity. Basic Appl. Ecol. 16, 10–18. https://doi.org/10.1016/j.baae.2014.10.003

Ricotta, C., Burrascano, S., 2008. Beta diversity for functional ecology. Preslia 80, 61–71.

Rivas-Martínez, S., 1982. Series de vegetación de la región Eurosiberiana de la Península Ibérica. Lazaroa 4, 155–166.

Rivas-Martínez, S., Díaz, T.E., Penas, A., Fernández (Eds.), 2011. Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. Itinera Geobotanica 18, 5–424.

Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T.E., Rivas-Sáenz, S., 2017a. Bioclimatology of the Iberian Peninsula and the Balearic Islands, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 29–80. https://doi.org/10.1007/978-3-319-54784-8_2

Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Cantó, P., del Río, S., Costa, J.C., Herrero, L., Molero, J., 2017b. Biogeographic Units of the Iberian Peninsula and Balearic Islands to District Level. A Concise Synopsis, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 131–188. https://doi.org/10.1007/978-3-319-54784-8_5

Siefert, A., Ravenscroft, C., Weiser, M.D., Swenson, N.G., 2013. Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. Glob. Ecol. Biogeogr. 22, 682–691. https://doi.org/10.1111/geb.12030

Spasojevic, M.J., Suding, K.N., 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. J. Ecol. 100, 652–661. https://doi.org/10.1111/j.1365-2745.2011.01945.x

Swenson, N.G., 2014. Functional and phylogenetic ecology in R, Use R! Springer New York, New York, NY.

Swenson, N.G., 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. Am. J. Bot. 98, 472–480. https://doi.org/10.3732/ajb.1000289

Swenson, N.G., Erickson, D.L., Mi, X., Bourg, N.A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J.K., Liu, X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S.J., Ye, W., Zhang, J., Zimmerman, J.K., Kress, W.J., 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. Ecology 93, S112–S125. https://doi.org/10.1890/11-0402.1

Torca, M., Campos, J.A., Herrera, M., 2019a. Species composition and plant traits of south Atlantic European coastal dunes and other comparative data. Data Brief 22, 207–213. https://doi.org/10.1016/j.dib.2018.12.005

Torca, M., Campos, J.A., Herrera, M., 2019b. Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. Estuar. Coast. Shelf Sci. 218, 39–47. https://doi.org/10.1016/j.ecss.2018.11.016

Tordoni, E., Napolitano, R., Maccherini, S., Re, D.D., Bacaro, G., 2018. Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline. Ecol. Res. 1–12. https://doi.org/10.1007/s11284-018-1629-6

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729

Wilson, S.D., Keddy, P.A., 1986. Measuring Diffuse Competition Along an Environmental Gradient: Results from a Shoreline Plant Community. Am. Nat. 127, 862–869. https://doi.org/10.1086/284530

Chapter 5

Habitat specialist species drive diversity area relationships (DARs) in southern European Atlantic coastal dunes

5.1. Introduction

Spatial scale is important when considering community assembly and different components of biodiversity. Biodiversity has a hierarchical nature, including a wide spectrum of diversity components at different scales. This spectrum goes from species to ecosystem and landscape level, taking into account their processes and interactions (Whittaker, 1972; UNEP, 1992; Primack, 2004). Increasing species richness (S) with increasing area of investigation (A) is one of the most fundamental «laws» in ecology (Lomolino, 2001; Helmus and Ives, 2012). This is call the Species-Area Relationship (SAR). The SAR is one of the most important patterns in biodiversity research and the increase in species richness with area is often considered one of the few «rules» in ecology (He and Legendre, 2002).

SARs have been recognized since the 19th century and is important for many issues in ecology, biogeography, evolution, and conservation (Rosenzweig, 1995; Lomolino, 2000; Tjørve, 2003; Scheiner et al., 2011). SAR appears to be ubiquitous having been observed in a wide array of taxa from diatoms to vertebrates and including vascular plants (Connor and McCoy, 2001). H.G. Watson was the first describing the SAR in 1835; in the 1960s and 1970 the interest in explaining the mechanisms underlying SAR arises, while since 1980 the discussion involves the use of SARs and its application to conservation biology (Connor and McCoy, 2001). Scheiner, 2003 described four main types of SARs: nested plots in continuous systems (Type I), non-nested plots in continuous systems (Type II) and non-contiguous systems (Type III) and those base on isolated units as islands (Type IV). Type II and III had two variants depending on the analysis method. For a review on this classification see Dengler et al., 2009a. In this study we used nested plots. Maybe it is not the most used system, because it implies a specific sampling design and data cannot usually be retrieved from databases of relevés. However, nested plots represent the «purest» form of SAR, as data points represent the same environmental conditions and the only variable changing is plot size (Dengler, 2008; Dengler and Boch, 2008).

SARs have focused on species richness, but other diversity components can be measured at different spatial scales. Helmus and Ives, (2012) and Morlon et al., (2011) studied Phylogenetic Diversity-Area Relationships (PDAR) to indicate and describe the relationship between phylogenetic diversity and area. Phylogenetic diversity is connected to SARs as information on the phylogenetic relationships of species may help to determine the ecological processes that underlie SARs (Helmus and Ives, 2012). We should see the scaling area approach as a standard methodology for gaining deeper insight from community phylogenetic analyses (Swenson et al., 2006). Wang et al., (2013) and Mazel et al., (2014) explored Functional Diversity-Area Relationships (FDAR), which are similar to species-area relationship, but plots are a measure of phenotypic trait diversity as a function of spatial scale (Smith et al., 2013). Other studies have measured functional diversity at different scales, although not following an area-relationship scheme (Swenson et al., 2012; Hu et al., 2014).

On coastal dunes we found no study about area-relationship for taxonomic, functional or phylogenetic diversity, just spatial patterns. Spatial patterns addressed species association or how site and regional scales changed relating disturbance and environmental stress (Forey et al., 2008, 2009). Acosta et al., (2000, 2003) analysed the spatial pattern of dune communities linked to quality and disturbance. Carranza et al., (2010) and Carboni et al., (2011) studied the spatial distribution of alien species in coastal dunes. Furthermore, in coastal dunes live highly specialist species restricted to this environment (Acosta et al., 2009; Biondi et al., 2009) with other of broader requirements called generalists. Generalists often include nitrophilous and ruderal species. Ruderals are those plants, which live in anthropic sites, need high amount of nutrients and which are poor tolerant to the competition with other species (Matesanz et al., 2005). Specialists are constrained to particular habitats for which they are well adapted, while generalists have higher environmental tolerances so they appear in more diverse habitats (Büchi and Vuilleumier, 2014). Specialists would have a better performance than generalists in their optimal habitats (Futuyma and Moreno, 1988; Wilson and Yoshimura, 1994; Jasmin and Kassen, 2007). Specialists depend more on specific resources than generalists, so specialists could be more likely affected by disturbance. Indeed, disturbances like habitat destruction and degradation may increase the competition with generalists and the extinction of specialists (Clavel et al., 2011). This leads to the «specialization-disturbance hypothesis», in which generalists perform better than specialists under disturbance conditions (Vázquez and Simberloff, 2002). Just one study in the Mediterranean area has addressed the differences between specialists and generalists linked to increasing area in coastal dunes (Carboni et al., 2016). They found a higher degree of specialization, higher specialized species, in embryo and mobile dunes, while inland habitats were dominated by generalists.

Towards land we usually find human infrastructures, such as holiday resorts. In the surrounding of these resorts species composition changes to more common ruderal generalists (Grunewald, 2006). In Italy, as in other parts of the world, sometimes dunes are planted with a variety of different species, which is a source of invasive alien species (Carboni et al., 2010). In general, inland presents greater habitat heterogeneity and it provides more opportunities for alien species as well as natives (Deutschewitz et al., 2003; Kumar et al., 2006). In contrast, extreme environmental conditions in communities next to sea, e.g. low soil fertility, sand burial, salt spray; (Packham and Willis, 1997), could be a filtering mechanism too strong for incoming alien species. Then, we would expect to find more species in the communities inland, such as fixed dunes, with an increasing number of generalists.

In this paper we analyse diversity area relationships in coastal dunes for total species and specialists and generalists. As coastal dunes present an environmental gradient (Frederiksen et al., 2006) we studied the communities in that gradient from sea to inland. Those communities are embryo (habitat 2110 of 92/43/EEC directive), mobile (2120) and fixed (2130) dunes. We used data of 12 sites along 750 kilometres in the coast of north Spain and southwest France including 4 biogeographical sectors. We calculated the SAR, FDAR and PDAR for embryo, mobile and fixed dunes, both for total species and generalist and specialists. As species richness increases from sea to land (Fenu et al., 2012) we expect a stepper slope of SAR in fixed dunes (H1). We found an increase on functional diversity (Torca et al., 2019a) along the environmental gradient on coastal dunes, so we expect an increasing slope in FDAR (H2). We also found lower values of PD in fixed dunes, then we could expect a decreasing value in the slope of PDAR in fixed dunes when compared with the other two vegetation types (H3). Regarding to biodiversity patterns shown by dune specialist species and generalist species, we could expect different diversity area relationships, in particular in functional diversity as specialist are constrained to a narrow range of environmental tolerance so they would be less functionally diverse than generalists (H4). We test the hypothesis of a connection between the slope of diversity-area relationships and the position of the vegetation along an environmental gradient in coastal dunes, both for total species and specialists and generalists (H5). Also that this connection depends on the vegetation type analysed.

5.2. Material and methods

5.2.1. Study area and sampling method

This work is located in the coasts of north Spain and southwest France. We sampled 12 sites (Fig. 5.1). The sites were included in four biogeographical sectors: Galicia and North Portugal, North Galicia and Asturias, Cantabrian and Basque and Aquitaine-Landes (Rivas-Martínez, 1982; Rivas-Martínez et al., 2017), three sites per biogeographical sector. In each site we sampled three vegetation types: embryo, mobile and fixed dunes. For each vegetation type we set four 100 m^2 (10 x 10 m) plots. In each 100 m^2 plot we arranged two 10 m^2 (3.16 x 3.16 m) subplots and for each 10 m^2 subplot two 1 m^2 squares (Fig. 5.2). Then, for each 1 m^2 sample we set a unique series from 0.1 m^2 to 1 cm^2. For the arrangement of the plots we followed Dengler (2009).

For 1 m^2 samples we estimated vegetation cover visually in percentage. For 10 m^2 subplots we applied the extended Braun-Blanquet scale (Westhoff and Van der Maarel, 1978). In remaining sampled areas we recorded species by presence/absence. As we had to use the recordings of all areas we used for this study presence/absence data for species composition matrices.

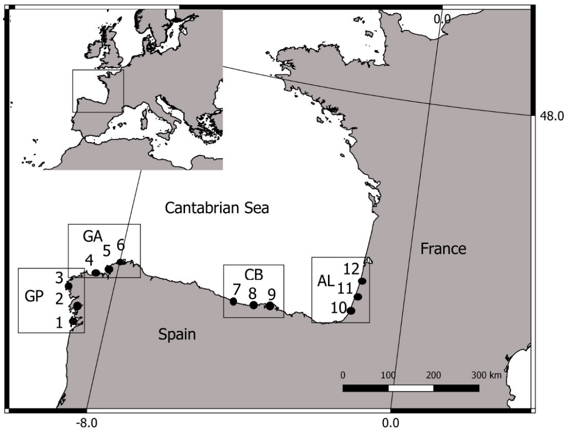

Figure 5.1: Study area. Twelve locations sampled from Galicia (Spain) to France grouped by biogeographic sectors. Galicia and North Portugal 1. La Lanzada 2. As Furnas 3. Carnota North Galicia and Asturias: 4. Barrañán 5. San Xurxo 6. Valdoviño Cantabrian and Basque: 7. Oyambre 8. Liencres 9. Noja. Aquitaine-Landes: 10. Tarnos 11. Casernes 12. Messanges.

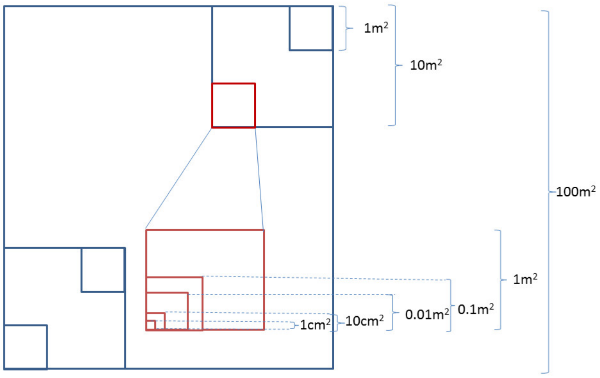

Figure 5.2: Sampling scheme of nested plots of subplots from 100 m^2 to 1 cm^2.

5.2.2. Functional and phylogenetic data

Species composition lists were used to calculate three different types of diversity area relationship. First, classical SAR curves based on species richness. Second, functional diversity index, FD, (Petchey and Gaston, 2006) was calculated using a trait dendrogram. Finally, phylogenetic diversity Faith's Index (PD) was calculated. Faith's Index (Faith, 1992) is described as the sum of the branch lengths connecting all species in an assemblage, where there are n branches with each having a length of l in a phylogeny containing only the species in the assemblage (Swenson, 2014).

$$Faith = \sum_{i}^{n} l_i$$

PD (Faith, 1992) and FD (Petchey and Gaston, 2006) metrics are identical to one another, except that PD utilizes a phylogeny and FD a dendrogram derived from trait data (Wang et al., 2013).

We used PD to calculate PDAR (Wang et al., 2013; Mazel et al., 2014). PD is proportional to species richness for a star phylogeny (i.e. a phylogeny where species share no branch-length), rendering comparisons with the traditional species–area relationship possible. PD has the added advantage of being the phylodiversity metric of choice in conservation research (Faith, 1992; Forest et al., 2007; Nee and May, 1997; Purvis et al., 2005; Rodrigues and Gaston, 2002; Winter et al., 2009). Using FD for FDAR makes results comparable with PD (Mazel et al., 2014). We chose FD and PD metrics because alternative metrics that utilize pairwise distances (Chave et al., 2007; Hardy and Senterre, 2007; Cadotte et al., 2010) are not monotonic with species richness making inferences from these curves less tractable (Wang et al., 2013).

In order to calculate functional and phylogenetic diversity we constructed a trait dendrogram and a phylogenetic tree. To create the phylogenetic tree we used the *Brranching* package (Chamberlain, 2015) of R (R Core Team, 2015) with the *Phylomatic* tree; the reference tree selected was *Phylomatic* tree R20120829 for plants (Bermer et al., 2009). We randomly resolved polytomies with the *multi2di* function of the *APE* package (Paradis et al., 2004) and branch length using BLADJ (Branch Length Adjustment) and an age file according to Wikström et al., (2001) in *Phylocom* (Webb et al., 2008). About trait we requested data from floras and online data bases listed in Torca et al., (2019b). The selected traits were life form, geographical distribution, flowering span and onset, pollination, fruit type, seed dispersal, specific leaf area (SLA), plant height and seed mass. We think they are a good combination to explain species ecology and local adaptation. They have been used in studies for coastal dunes such as Acosta et al., (2006) and Carboni et al., (2013) to test differences in traits for native and alien species or to make comparisons between plant communities.

We calculated species richness, FD and PD for both total of species and for specialist and generalist species. The classification of specialists or generalist was made according to plant habitat distribution, following data from floras and guides such as Castroviejo, (1986) and Aizpuru et al., (2007). Those living exclusively in coastal dunes were considered specialists, while those living in a greater range of habitats were classified as generalists.

5.2.3. Data analysis

The statistical analysis were performed with the R software environment (R Core Team, 2015). PD and FD were calculated using *fd()* function of the *Picante* package (Kembel et al., 2010). In order to perform area relationships regressions power-law functions were applied. The power (log-log) model is one of the most frequently applied and it presents the advantage of producing straight lines in log-log space for intermediate and larger sampling areas (Tjørve, 2009). Power law is advised to be used in comparisons and descriptions of any type of SAR (Dengler, 2009) and is a suitable model for

SARs when the areas are contiguous (Dengler et al., 2019). Then we applied the log-log transformation to both species richness (Baumann et al., 2016) and PD (Morlon et al., 2011). The log-log transformation was also applied to FD to follow the same process after observing the fit of the model to the data. Power law function was applied to calculate FDAR in Karadimou et al., (2016).

For SAR power-law functions takes the form of $S = c\ A^z$, where S is the number of species, A the plot area and c and z the two fitted parameters (Baumann et al., 2016). The parameter z can be interpreted as a scaling factor describing how fast the response of species richness to area changes along the SAR curve (Lomolino, 2001) and the parameter c represents the expected mean number of species per unit area (Fattorini et al., 2017).

In order to get a unique series from 1 cm^2 to 100 m^2 for each 100 m^2 plot, arithmetic mean values of diversity measures from each corner were taken for each area. Models in which smallest plots were not replicated and averaged have a worse performance (Dengler et al., 2019). In the case where the smaller subplots in both corners had 0 values we considered the value of 0.1 as a constant to deal with the cases of $\log_{10}$ of 0. In addition scale dependence of z-values was assessed by calculating within each 100 m^2 plot for each transition between two subsequent plot sizes the local slope (Baumann et al., 2016). A Tukey post-hoc test was applied to test significant differences. Then ANOVA was performed to test whether the local z-values change across these grain-size transitions. ANOVA was used to search for differences between habitats in the z-values for each diversity component. In the case of specialist and generalist the ANOVA analysis included the grouping between specialists and generalist. In each case the nested design of sectors and sites was taken into account. Finally, we calculated the correlation between the number of specialist and generalist and set a correlation. We looked if the correlation was significant and in that case if it was positive or negative.

5.3. Results

5.3.1. Descriptive data

The mean of overall z-values for species richness, functional diversity and phylogenetic diversity for total species increased from embryo to fixed dunes (Table 5.1). Species richness in embryo dunes mean ranged from 0.54 on 1 cm^2 to 7.19 on 100 m^2, in mobile dunes from 0.73 to 13.38 and in fixed dunes from 0.66 to 17.48 (Table 5.2). For functional diversity in embryo dunes mean ranged from 0.14 to 1.41, in mobile dunes from 0.19 to 2.37 and in fixed dunes from 0.17 to 2.89. For phylogenetic diversity in embryo dunes mean ranged from 53.28 to 335.74, in mobile dune from 72.54 to 466.90 and in fixed dunes from 62.71 to 581.

Then, data were analysed by generalists and specialists. About the percentages, we found little changes between biogeographical sectors (Table 5.3). In embryo and mobile dunes specialists present higher values, while in fixed dunes specialists and generalists are more balanced. In the case of

Table 5.1: Descriptive data of z values for total, generalist and specialist species in each vegetation type. SD = Standard Deviation.

		Embryo				Mobile				Fixed			
		Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
Total species	TD	0.1	0.33	0.2	0.06	0.13	0.43	0.23	0.06	0.16	0.39	0.25	0.05
	FD	0.08	0.32	0.18	0.05	0.09	0.46	0.2	0.06	0.13	0.32	0.22	0.04
	PD	0.07	0.62	0.16	0.1	0.07	0.7	0.17	0.12	0.09	0.51	0.19	0.09
Generalists	TD	0	0.34	0.11	0.12	0	0.35	0.23	0.1	0.15	0.42	0.28	0.06
	FD	0	0.2	0.05	0.07	0	0.25	0.13	0.07	0.13	0.31	0.21	0.04
	PD	0	0.7	0.27	0.3	0	0.74	0.32	0.2	0.08	0.74	0.39	0.23
Specialists	TD	0.1	0.29	0.18	0.05	0.12	0.41	0.21	0.06	0.15	0.38	0.24	0.05
	FD	0.08	0.27	0.17	0.05	0.08	0.32	0.18	0.05	0.12	0.3	0.21	0.04
	PD	0.07	0.62	0.16	0.1	0.06	0.78	0.17	0.13	0.08	0.65	0.2	0.12

Table 5.2: Descriptive data of richness, PD and FD for each dune habitat for total species. SD = Standard Deviation

		Embryo				Mobile				Fixed			
	m^2	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
Richness	0.0001	0	3	0.54	0.57	0	3	0.73	0.59	0	4	0.66	0.67
	0.001	0	4	0.77	0.73	0	3	1.02	0.75	0	4	1.12	0.92
	0.01	0	5	1.3	0.91	0	5	1.51	1.02	0	8	2.14	1.38
	0.1	0	6	2.24	1.16	0	7	2.83	1.47	0	12	4.21	1.86
	1	1	9	3.69	1.75	0	11	5.29	2.33	0	15	7.96	2.58
	10	1	17	5.43	2.65	3	15	8.3	2.92	6	21	12.03	3.5
	100	3	19	7.19	3.56	5	23	13.38	4.35	11	30	17.48	4.52
FD	0.0001	0	0.73	0.14	0.15	0	0.73	0.19	0.15	0	0.89	0.17	0.17
	0.001	0	0.93	0.19	0.18	0	0.73	0.26	0.18	0	0.89	0.27	0.21
	0.01	0	1.14	0.32	0.21	0	1.21	0.37	0.23	0	1.71	0.49	0.29
	0.1	0	1.39	0.53	0.25	0	1.54	0.65	0.3	0	2.3	0.9	0.34
	1	0.26	1.79	0.81	0.34	0	2.21	1.09	0.43	0	2.62	1.53	0.42
	10	0.26	3.13	1.12	0.48	0.61	2.76	1.58	0.49	1.15	3.26	2.15	0.51
	100	0.61	3.31	1.41	0.61	1	4.07	2.37	0.68	1.91	4.48	2.89	0.57
PD	0.0001	0	230	53.28	55.48	0	290	72.54	57.93	0	260	62.71	58.53
	0.001	0	238.33	73.28	64.54	0	290	98.25	68.22	0	270	95.51	69.35
	0.01	0	308.33	118.11	71.43	0	315	132.47	74.47	0	408.33	158.93	80.68
	0.1	0	367.5	181.03	70.61	0	425.83	206.27	76.26	0	512.08	247.11	80.36
	1	100	450.83	243.43	74.45	0	492.5	286.56	80.96	0	588.7	356.77	90.19
	10	100	511.62	291.68	82.02	207.5	551.04	362.12	85.82	252.78	747.04	459.95	108.23
	100	208.33	575.09	335.74	87.44	251.67	712.5	466.9	103.08	340.37	840.07	581	115.09

Table 5.3: Percentages of generalist and specialist species in the three dune vegetation types by biogeographical sector. GP = Galicia and North Portugal, GA = North Galicia and Asturias, CB = Cantabrian and Basque, AL = Aquitaine-Landes.

	Embryo		Mobile		Fixed	
	Generalist	Specialist	Generalist	Specialist	Generalist	Specialist
GP	26%	74%	26%	74%	43%	57%
GA	21%	79%	41%	59%	34%	66%
CB	22%	78%	37%	63%	41%	59%
AL	14%	86%	33%	67%	38%	62%

generalist species richness embryo dunes mean ranged from 0.01 on 1 cm^2 to 1.13 on 100 m^2, in mobile dunes from 0.01 to 3.71 and in fixed dunes from 0.18 to 6.92 (Table 5.4). For functional diversity embryo dunes mean had a minimum of 0.003 and a maximum of 0.26, in mobile dunes 0.003 and 0.79 and in fixed dunes 0.05 and 1.33. For phylogenetic diversity in embryo dunes mean ranged from 1.04 to 64.06, in mobile dunes from 1.04 to 175.03 and fixed dunes from 17.50 to 319.62. Mean overall z-values for species richness, functional and phylogenetic diversity increased from embryo to fixed dunes (Table 5.1).

About specialist species richness we found a ranging mean value in embryo dunes from 0.53 on 1 cm^2 to 6.06 on 100 m^2, in mobile dunes from 0.72 to 9.67 and in fixe dunes from 0.48 to 10.56 (Table 5.5). For functional diversity in embryo dunes mean ranged from 0.14 to 1.18, in mobile dunes from 0.18 to 1.74 and in fixed dunes from 0.12 to 1.92. For phylogenetic diversity in embryo dunes mean ranged from 52.24 to 321.61, in mobile dune from 71.55 to 407.37 and in fixed dunes from 46.93 to 421.36. Mean overall mean z-values showed increasing values from embryo to fixed dunes for species richness, functional and phylogenetic diversity (Table 5.1).

5.3.2. Scale dependence

For total of species, in all cases there was scale dependence and the effect of the scale relating grain-size was significant, excepting for mobile dunes in phylogenetic diversity. The local z-values insignificantly peaked at the transition from 0.01 to 0.1 m^2 (Fig. 5.3). For generalist species there was no a clear peak in the area transitions (Fig. 5.4). Again there was scale dependence for all cases, excepting mobile dunes in phylogenetic diversity. For specialist species the pattern was similar to the total species one. A small peak at the transition from 0.01 to 0.1 m^2 (Fig. 5.5). There was no scale dependence for mobile and fixed dunes in phylogenetic diversity.

Table 5.4: Descriptive data of richness, PD and FD for each dune habitat for generalist species. SD = Standard Deviation

		Embryo				Mobile				Fixed			
	m^2	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
Richness	0.0001	0	1	0.01	0.1	0	1	0.01	0.1	0	2	0.18	0.43
	0.001	0	1	0.02	0.12	0	1	0.05	0.21	0	3	0.4	0.65
	0.01	0	1	0.03	0.16	0	2	0.13	0.38	0	5	0.83	1.02
	0.1	0	1	0.03	0.16	0	4	0.37	0.67	0	8	1.41	1.39
	1	0	3	0.26	0.54	0	5	0.91	1.17	0	9	3.18	1.84
	10	0	5	0.65	1.09	0	7	1.76	1.64	1	10	4.6	2.1
	100	0	5	1.13	1.52	0	11	3.71	2.61	2	13	6.92	2.6
FD	0.0001	0	0.27	0.003	0.03	0	0.27	0.003	0.03	0	0.52	0.05	0.11
	0.001	0	0.27	0.004	0.03	0	0.27	0.01	0.06	0	0.74	0.1	0.16
	0.01	0	0.27	0.01	0.04	0	0.52	0.03	0.1	0	1.16	0.2	0.23
	0.1	0	0.27	0.01	0.04	0	0.84	0.09	0.16	0	1.38	0.34	0.3
	1	0	0.74	0.07	0.14	0	1.08	0.22	0.27	0	1.63	0.69	0.34
	10	0	1.01	0.16	0.25	0	1.48	0.4	0.34	0.27	1.82	0.94	0.35
	100	0	1.16	0.26	0.33	0	1.98	0.79	0.49	0.49	2.38	1.33	0.4
PD	0.0001	0	100	1.04	10.18	0	100	1.04	10.18	0	200	17.5	39.96
	0.001	0	100	1.56	12.43	0	100	4.69	21.19	0	230	36.34	57.46
	0.01	0	100	2.6	15.97	0	200	11.52	33.7	0	325	71.7	78.76
	0.1	0	100	2.6	15.97	0	278.33	31.94	53.57	0	489.58	109.46	91.44
	1	0	208.33	23.25	47.54	0	336.67	69.73	81.61	0	497.92	207.99	90.44
	10	0	212.5	42.93	64.22	0	361.3	110.8	86.5	100	482.08	257.16	87.85
	100	0	242.5	64.06	74.98	0	393.06	175.03	100.26	130	602.08	319.62	108.77

Table 5.5: Descriptive data of richness, PD and FD for each dune habitat for specialist species. SD = Standard Deviation

		Embryo				Mobile				Fixed			
	m^2	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
Richness	0.0001	0	3	0.53	0.57	0	2	0.72	0.57	0	3	0.48	0.61
	0.001	0	4	0.76	0.72	0	3	0.97	0.74	0	3	0.72	0.75
	0.01	0	4	1.27	0.87	0	5	1.38	0.94	0	4	1.31	0.92
	0.1	0	6	2.16	1.12	0	7	2.46	1.21	0	5	2.61	1.1
	1	1	8	3.44	1.55	0	9	4.38	1.82	0	10	4.78	1.66
	10	1	12	4.78	2	2	14	6.54	2.25	2	13	7.43	2.33
	100	3	14	6.06	2.44	4	18	9.67	3.25	4	18	10.56	2.7
FD	0.0001	0	0.74	0.14	0.15	0	0.52	0.18	0.15	0	0.68	0.12	0.15
	0.001	0	0.93	0.19	0.18	0	0.74	0.25	0.18	0	0.68	0.18	0.18
	0.01	0	0.93	0.32	0.2	0	1.09	0.34	0.22	0	0.89	0.32	0.21
	0.1	0	1.12	0.52	0.23	0	1.58	0.57	0.26	0	1.18	0.6	0.23
	1	0.26	1.63	0.75	0.28	0	1.75	0.91	0.34	0	1.88	1.01	0.32
	10	0.26	2.25	0.98	0.35	1	2.4	1.26	0.38	0.52	2.29	1.45	0.4
	100	0.6	2.5	1.18	0.41	1	3.08	1.74	0.52	0.75	2.72	1.92	0.43
PD	0.0001	0	230	52.24	55.53	0	200	71.55	56.71	0	260	46.93	58.1
	0.001	0	238.33	72.2	64.08	0	290	93.83	67.21	0	260	66.35	65.5
	0.01	0	298.33	116.52	70.64	0	315	125.36	73.97	0	360	109.12	71.36
	0.1	0	367.5	177.78	69.55	0	368.33	193.93	71.76	0	360	178.76	69.54
	1	100	443.33	238.23	72.18	0	438.33	265.07	72.79	0	438.33	251.74	78.68
	10	100	467.31	283.65	75.48	200	517.04	330.52	74.65	138.15	553.15	334.35	88.19
	100	208	517.31	321.61	77.65	246	674.68	407.37	86.4	233.47	666.76	421.36	93.06

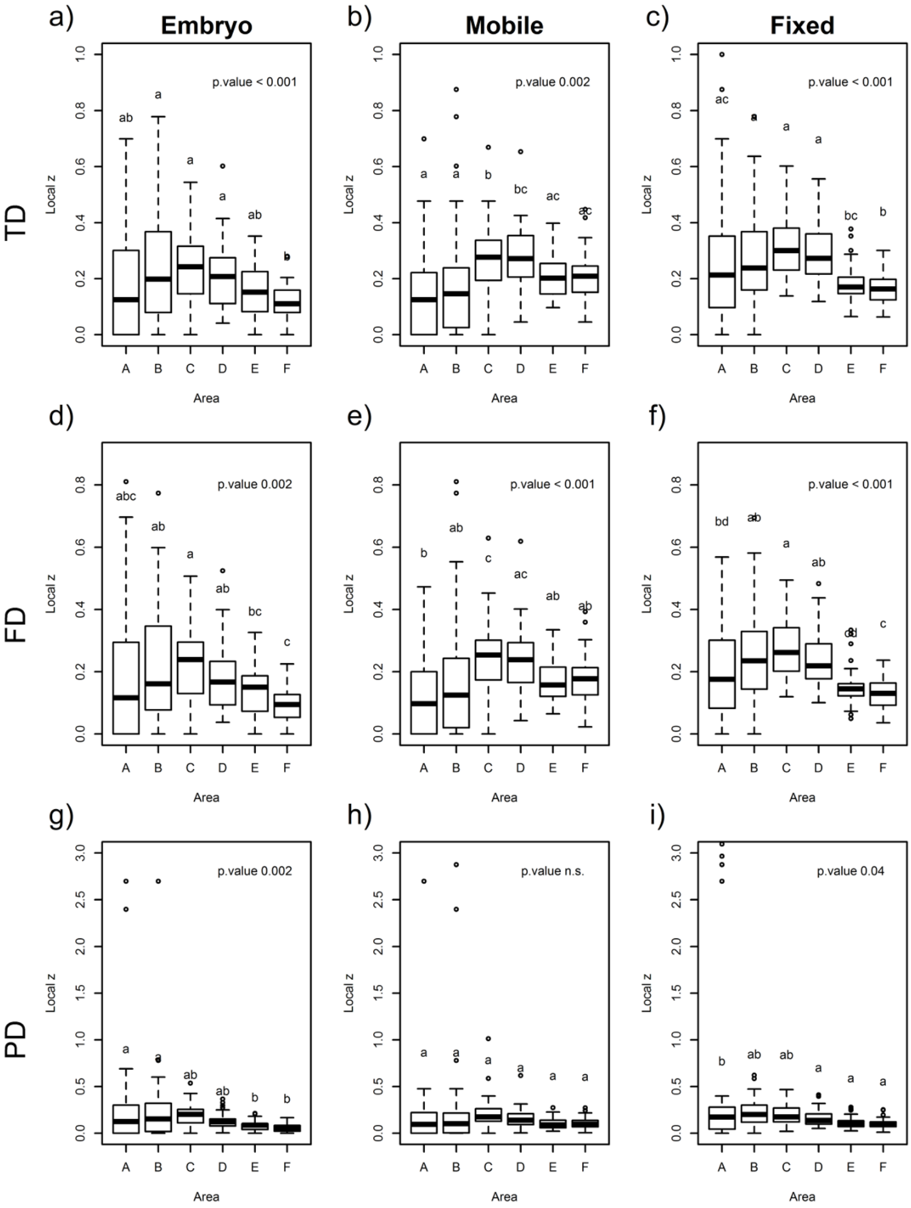

Figure 5.3: Box–whisker plots of the scale-dependence of the power-law z-values of TD (a-c), FD (d-f) and PD (g-i) of total species. Local z-values refer to the transition from one plot size to the next larger plot size (A = 0.0001-0.001 m^2, B = 0.001-0.01 m^2, C = 0.01-0.1 m^2, D=0.1-1 m^2, E=1-10 m^2, F=10-100 m^2).

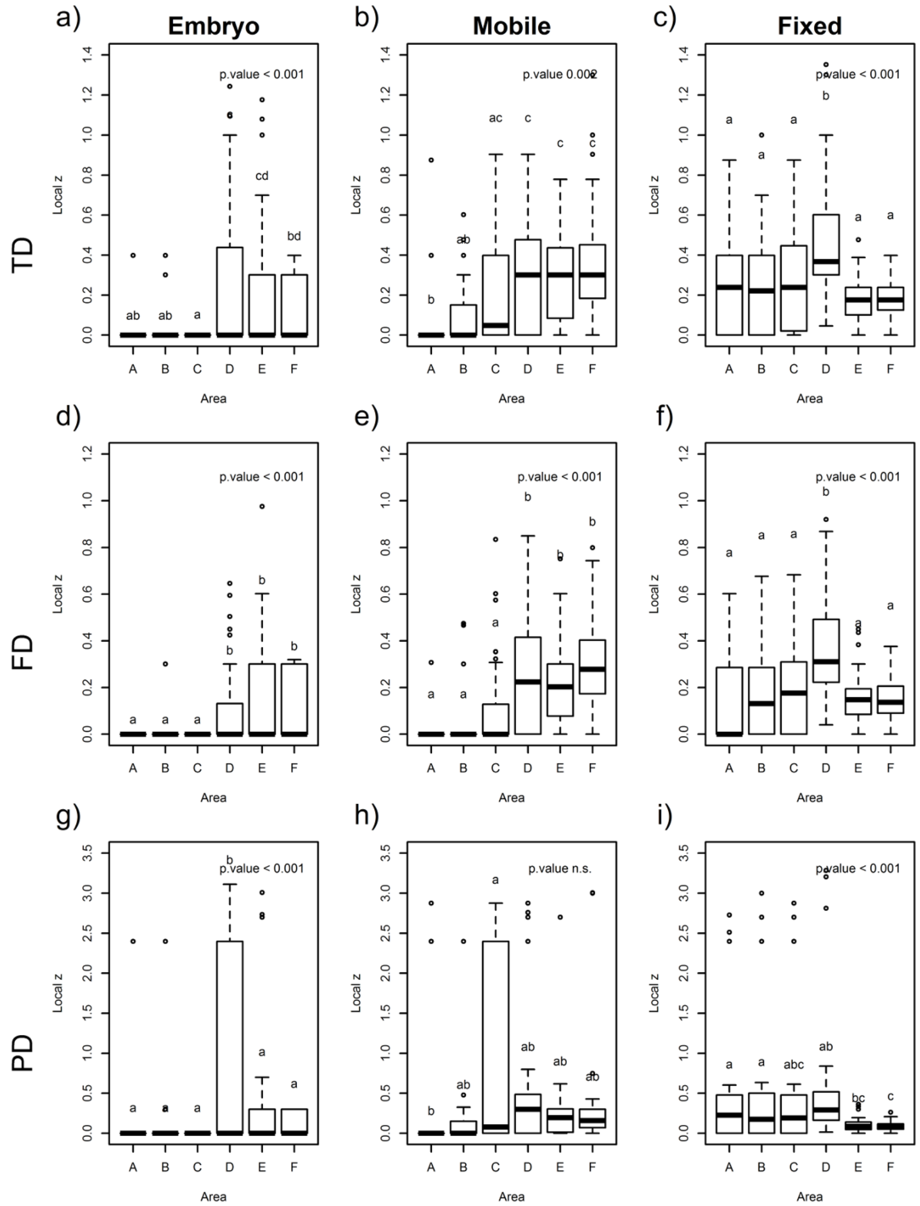

Figure 5.4: Box–whisker plots of the scale-dependence of the power-law z-values of TD (a-c), FD (d-f) and PD (g-i) of generalist species. Local z-values refer to the transition from one plot size to the next larger plot size (A = 0.0001-0.001 m^2, B = 0.001-0.01 m^2, C = 0.01-0.1 m^2, D=0.1-1 m^2, E=1-10 m^2, F=10-100 m^2).

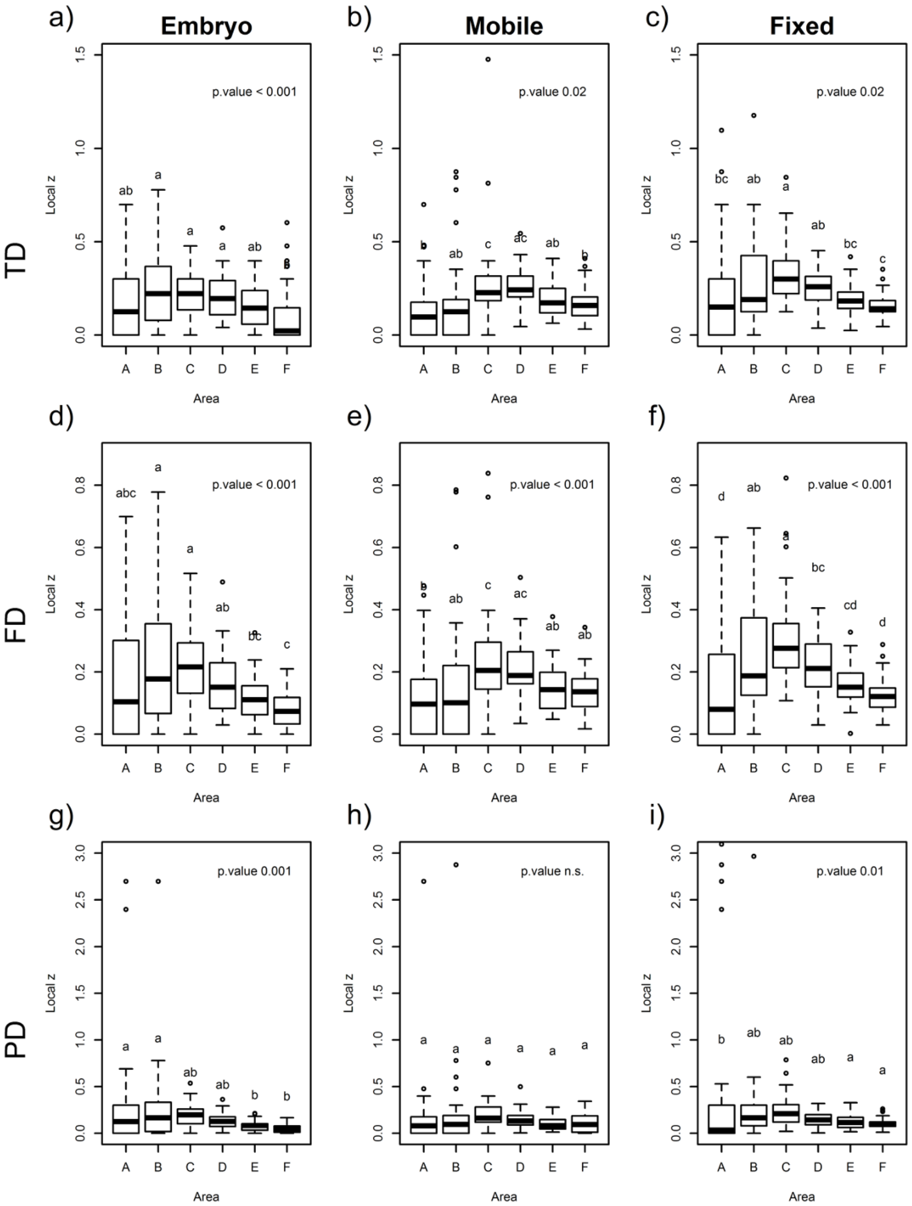

Figure 5.5: Box–whisker plots of the scale-dependence of the power-law z-values of TD (a-c), FD (d-f) and PD (g-i) of specialist species. Local z-values refer to the transition from one plot size to the next larger plot size (A = 0.0001-0.001 m^2, B = 0.001-0.01 m^2, C = 0.01-0.1 m^2, D=0.1-1 m^2, E=1-10 m^2, F=10-100 m^2).

5.3.3. Correlation between specialist and generalist species

In embryo dune small areas were no significant, while areas over 0.1 m^2 showed a positive correlation (Table 5.6). R^2 values increased up to 0.35 for 100 m^2. In mobile dunes smallest and biggest areas presented no significant correlation, only medium areas with a very low r^2 value (0.03). Fixed dunes showed the opposite pattern compared with embryo dunes, where medium

Table 5.6: Relationship between number of generalists and specialists. +/- positive or negative correlation, r^2 of the correlation and stars show the significance. n.s no significant. $p < 0.001^{***}$, $0.001 < p < 0.01^{**}$, $0.01 < p < 0.05^{*}$

Area (m^2)	Embryo	Mobile	Fixed
0.0001 (n = 192)	n.s.	n.s.	- 0.04**
0.001 (n = 192)	n.s.	n.s.	- 0.02*
0.01 (n = 192)	n.s.	n.s.	n.s.
0.1 (n = 192)	+ 0.02*	+ 0.03*	n.s.
1 (n = 192)	+ 0.05**	+ 0.03*	n.s.
10 (n = 96)	+ 0.18***	n.s.	+ 0.06*
100 (n = 48)	+ 0.35***	n.s.	+ 0.21**

Table 5.7: Difference in z-values between habitats and sector for species richness, FD and PD of total species. (Df = degrees of freedom). $p < 0.001^{***}$, $0.001 < p < 0.01^{**}$, $0.01 < p < 0.05^{*}$

		TD		FD		PD	
	Df	F	P-value	F	P-value	F	P-value
VegType	2	14.478	0.001***	44.863	0.001***	0.793	0.455
VegType:Sector	9	1.167	0.324	1.689	0.101	0.726	0.684
VegType:Sector:Site	27	1.963	0.008**	2.179	0.003**	1.494	0.078
Residuals	105						

areas showed no significant correlation and smallest and biggest areas were significant. In this case the correlation of smallest areas was negative, while the biggest ones were positive.

5.3.4. Overall z-values comparison

For total species z-values were compared between vegetation types, sectors and sites for each diversity measure. For species richness vegetation type differences were significant ($F = 14.48$ $p = <0.001$) and also for functional diversity ($F = 44.86$, $p = <0.001$). For PD it was not significant ($F = 0.793$, $p = 0.46$). There were no differences for the sector factor and for site just in species richness and functional diversity (Table 5.7). About the comparison between specialists and generalists we found vegetation type for species richness ($F = 26.20$, $p = <0.001$), functional diversity ($F = 146.05$, $p = <0.001$) and phylogenetic diversity ($F = 10.12$, $p = <0.001$) (Table 5.8). Plant group was only significantly different for functional and phylogenetic diversity, while site was for species richness and functional diversity.

Table 5.8: Difference in z-values between, vegetation type (VegType), plant group, sector and site for species TD (species richness), FD and PD of specialists and generalists (PlantGroup). (Df = degrees of freedom). $p < 0.001^{***}$, $0.001 < p < 0.01^{**}$, $0.01 < p < 0.05^{*}$

		TD		FD		PD	
	Df	F	P-value	F	P-value	F	P-value
PlantGroup	1	0.405	0.525	30.182	0.001^{***}	85.058	0.001^{***}
VegType	2	26.204	0.001^{***}	146.047	0.001^{***}	10.118	0.001^{***}
VegType:Sector	9	0.815	0.603	0.709	0.7	1.023	0.422
VegType:Sector:Site	27	1.638	0.028^{*}	1.882	0.007^{**}	1.081	0.363
Residuals	248						

5.4. Discussion

5.4.1. Descriptive data

Taxonomic diversity increased from embryo to fixed dune with a mean range for 0.0001 m^2 to 100 m^2 of 0.55-7.10 and 2.25-24 respectively. This found values are lower than in other studies for temperate grasslands in Europe (Turtureanu et al., 2014; Baumann et al., 2016; Kuzemko et al., 2016; Polyakova et al., 2016). In these studies the lowest value is around 2 species in 0.0001 m^2 and up to 127 100 m^2. Temperate grasslands present a high small scale diversity of vascular plants (Wilson et al., 2012; Chytrý et al., 2015). Coastal dunes are known by highly specialized and often rare on endemic plant species (Del Vecchio et al., 2017).

As area increases functional diversity should also increase, especially in the case of nested plots, where species accumulate (Karadimou et al., 2016). For the three studied habitats we found an increase of functional diversity with area as in (Mazel et al., 2014; Smith et al., 2013; Wang et al., 2013). Small areas are likely to contain just one type of vegetation, and therefore less variation in trait values, whereas large areas may contain more vegetation types and therefore greater variation in trait values (Smith et al., 2013). For the three habitats we found an increase on phylogenetic diversity as in Morlon et al., (2011); Wang et al., (2013) and Mazel et al., (2015). There were 17 species in embryo dunes, 25 in mobile dunes and 27 in fixed dunes. The most common family was *Poaceae*. This increase of PD along the environmental gradient contrasts with the results in Torca et al., (2019a), where we found a decrease and it was what we expected. This could have a relation with the different index applied to calculate phylogenetic diversity. PD in this study could be more affected by species richness due to a high correlation (Rodrigues et al., 2005, 2011). Therefore, our hypothesis H1 and H2 are confirmed, while H3 of a decreasing PD not.

Carboni et al., (2016) found higher number of specialists in embryo and mobile dunes, while in communities more sheltered the generalists outnumbered specialist species. In their study in the Mediterranean area they hypothesized that very specialize fore-dune species were able to tolerate a high amount of perturbation, related to high environmental stress, due to the lack of competition from generalist species. Most of the generalist species were ruderals such as *Plantago lanceolata* and *Crepis capillaris* or typical of dry grasslands such as *Lotus corniculatus* and *Lolium perenne.* Our results showed higher z-values of specialists for the three dune vegetation types for the three diversity components. Then, our expectation of lower functional diversity of specialists (H4) is not supported.

For fixed dune we could apply the «specialist-disturbance» hypothesis, which states that generalist species are favored by disturbance, while specialists are negatively affected (Futuyma and Moreno, 1988; Vázquez and Simberloff, 2002). In our study area behind fixed dunes there were pine plantations, roads, parkings or walking zones. Then it could lead the increase of generalist arrival and maintenance, in addition to the lower exposition to wind, waves and sand burial, which provides higher opportunities to grow. Our results agree with Devictor et al., (2008), who showed that specialist species tended to be located in less fragmented and less disturbed landscapes than generalists. In our case the less human disturbed habitats would be embryo and mobile dunes, which present a higher proportion of specialist species (Table 5.3).

5.4.2. Scale dependence

Biodiversity is scale-dependent as all measures of diversity necessarily increase nonlinearly with increasing sampling effort and spatial scale (Chase et al., 2018). For taxonomic measures in all species we found scale dependence of z-values of SARs as in Russian steppes or dry grasslands of Transylvania (Turtureanu et al., 2014; Polyakova et al., 2016). In contrast, in the steppe grasslands of Ukraine and alpine grasslands of Italy scale dependence was not found (Baumann et al., 2016; Kuzemko et al., 2016). In the aforementioned studies they used a similar nested plot design as in our study. Our results presented a steepest difference in the 0.01-0.01 range as in Turtureanu et al., 2014; Baumann et al., 2016; Polyakova et al., 2016. Specialists presented similar results as all species data, in particular in embryo and mobile dunes, as they were the more represented species. Generalists were almost no present in smallest areas, so specialists would play an important role in presenting scale dependence.

Functional and phylogenetic diversity followed species richness patterns. As there are more species there are more chances of finding different functional traits or species from different genera. About functional diversity embryo dunes vegetation is characterized by highly specialized plant species with similar functional traits that are well adapted to this extreme environment, while the vegetation of the mobile dunes and the fixed dunes is less affected by physical limiting factors, thus showing an increasingly higher functional dissimilarity (Ricotta et al., 2012).

5.4.3. Interaction between specialist and generalist species

We only found significant increase of generalists with the number of specialists at the bigger scale, 100 m^2, for embryo and fixed dunes. In larger areas there are more microhabitats, which could allow the inclusion of plant species linked to those microhabitats (Polyakova et al., 2016), both generalists and specialists. At small scales biotic interactions, such as facilitation or competition, are likely to affect species composition in the dunes (Forey et al., 2009; Maltez-Mouro et al., 2010). Competition is the mutually adverse effect of organisms on one another, because they are striving for a common resource (Martínez and García-Franco, 2004). At lower scales (1 cm^2-0.01 m^2) in our ecosystem just one or two species can grow, so the correlation between generalists and specialists is almost a matter of chance. Although competitive exclusion is more apparent at small spatial scales (Swenson et al., 2007), our results do not show a negative correlation between generalists and specialists, excepting fixed dunes but with a very low r^2. At medium scales (0.1-1 m^2) again we find a mixture of non-significant values and low r^2. Then we have different trends in the relationship between the number of generalists and specialists depending on the vegetation type (H5), which could be linked to the more sheltered conditions in fixed dunes, while embryo dunes are more exposed. Also we have a change of no pattern in small scales and a significant one in the biggest size area.

5.4.4. Overall z-values comparison

Total species z-values comparison showed significant differences for vegetation type in species richness and functional diversity. We had an increasing species richness as in Acosta et al., (2009) and Peyrat and Fichtner, (2011), who found an increase of species richness across the environmental gradient in coastal dunes. If there are more species in the same area size, it follows that the increasing rate also changes from embryo to fixed dunes. In functional diversity we found an increase from embryo to fixed dunes (Torca et al., 2019a). Again, if there are higher values of functional diversity as the area remains equal, that means a different increasing rate. As an example, if we look at the trait «height», embryo dunes are dominated by a 40cm tall grass *Elytrigia juncea* subsp. *boreatlantica* and in mobile dunes by *Ammophila arenaria* subsp. *australis*, which is about 1m tall. However, in fixed dunes we find a mixture of sizes from few centimeters as *Phleum arenarium* or *Catapodium rigidum* to 20 cm as *Lagurus ovatus.*

The comparison of z-values between generalists and specialists showed only differences in functional and phylogenetic diversity. Baiser and Li, (2018) found differences in z-values between exotic and native plants. This means that specialists-generalists or native-exotic increase their richness by area at the same rate or at least not at significantly different rate.

About functional diversity at smallest areas we should expect to find the most abundant species, which should be those well adapted to the system and those that present the suitable traits to survive. As coastal dunes are a highly stressful habitat (Hesp, 1991), in particular those sites more exposed to wind and waves, specialist species should show an exclusive combination of traits, which allow them to grow successfully (Bermúdez and Retuerto, 2013). Raw data did not show any particular trait value in specialists, but this would arise in a further analysis or taking into account traits more related to habitat adaptations such as succulence or leaf water economy.

Phylogenetic diversity showed significant differences in z-value comparison. Although the number of species between generalists (65) and specialists (55) is more balanced, there is a remarkable difference in the number of families: generalists (29) and specialists (16). Then, despite having the same number of species generalists would be more diverse in lineages, which would lead a higher z-values in phylogenetic diversity than specialists.

Conclusions

In this study we analyzed the changes in species richness, functional diversity and phylogenetic diversity with increasing scale for total, generalist and specialist species. We found an increasing z-value in embryo, mobile and fixed dunes in both for total and split species groups. As there is a bigger area, more species can grow. With more species the chances are that more traits and families could be present. Our result also showed scale dependence with scale in most of the cases. This means that scale plays an important role defining the value of the biodiversity indices. Besides specialists pattern reflected all species pattern in the distribution of values in each step of the scale. Then, specialists drive the biodiversity structure in the coastal dunes studied. In our results arise a correlation between generalists and specialists at the bigger scale (100 m^2) for embryo and fixed dunes. It seems than only when there is enough area the correlation takes place and at smaller scale it is a matter on chance which species grows. The comparison of z-values between vegetation types showed significant differences for species richness and phylogenetic diversity. Functional diversity showed no differences maybe because traits related to survival in the ecosystem were not analyzed individually.

References

Acosta, A., Blasi, C., Carranza, M.L., Ricotta, C., Stanisci, A., 2003. Quantifying ecological mosaic connectivity and hemeroby with a new topoecological index. Phytocoenologia 623–631. https://doi.org/10.1127/0340-269X/2003/0033-0623

Acosta, A., Carranza, M.L., Izzi, C.F., 2009. Are there habitats that contribute best to plant species diversity in coastal dunes? Biodivers. Conserv. 18, 1087. https://doi.org/10.1007/s10531-008-9454-9

Acosta, A., Izzi, C.F., Stanisci, A., 2006. Comparison of native and alien plant traits in Mediterranean coastal dunes. Community Ecol. 7, 35–41. https://doi.org/10.1556/ComEc.7.2006.1.4

Acosta, A.T.R., Blasi, C., Stanisci, A., 2000. Spatial connectivity and boundary patterns in coastal dune vegetation in the Circeo National Park, Central Italy. J. Veg. Sci. 11, 149–154. https://doi.org/10.2307/3236787

Aizpuru, I., Aseginolaza, C., Uribe-Echebarría, P.M., Urrutia, P., Zorrakin, I., Garín, P., Hermosilla, C.E., Lizaur, X., Patino, S., Pérez Dacosta, J.M., Renobales, G., Valencia, J., 2007. Claves ilustradas de la flora del País Vasco y territorios limítrofes. Publication Service of The Basque Country Government, Vitoria-Gasteiz.

Baiser, B., Li, D., 2018. Comparing species–area relationships of native and exotic species. Biol. Invasions 20, 3647–3658. https://doi.org/10.1007/s10530-018-1802-4

Baumann, E., Weiser, F., Chiarucci, A., Jentsch, A., Dengler, J., 2016. Diversity and functional composition of alpine grasslands along an elevational transect in the Gran Paradiso National Park (NW Italy). Tuexenia 337–358.

Bermer, B., Bremer, K., Chase, M.W., Fay, M.M., Reveal, J.L., Soltis, D.E., Soltis, P.S., Stevens, P.F., Anderberg, A.A., Moore, M.J., Olmstead, R.G., Rudall, P.J., Sytsma, K.J., Tank, D.C., Wurdack, K., Xiang, J.Q., Zmarzty, S., 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161, 105–121. https://doi.org/10.1111/j.1095-8339.2009.00996.x

Bermúdez, R., Retuerto, R., 2013. Living the difference: alternative functional designs in five perennial herbs coexisting in a coastal dune environment. Funct. Plant Biol. 40, 1187. https://doi.org/10.1071/FP12392

Biondi, E., Blasi, C., Burrascano, S., Casavecchia, S., Copiz, R., Del Vico, E., 2009. Italian interpretation manual of the 92/43/EEC directive habitats. MATTM.

Büchi, L., Vuilleumier, S., 2014. Coexistence of Specialist and Generalist Species Is Shaped by Dispersal and Environmental Factors. Am. Nat. 183, 612–624. https://doi.org/10.1086/675756

Cadotte, M.W., Davies, T.J., Regetz, J., Kembel, S.W., Cleland, E., Oakley, T.H., 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecol. Lett. 13, 96–105. https://doi.org/10.1111/j.1461-0248.2009.01405.x

Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? J. Veg. Sci. 24, 932–941. https://doi.org/10.1111/jvs.12095

Carboni, M., Santoro, R., Acosta, A., 2010. Are some communities of the coastal dune zonation more susceptible to alien plant invasion? J. Plant Ecol. 3, 139–147. https://doi.org/10.1093/jpe/rtp037

Carboni, M., Santoro, R., Acosta, A.T.R., 2011. Dealing with scarce data to understand how environmental gradients and propagule pressure shape fine-scale alien distribution patterns on coastal dunes: Drivers of alien patterns on coastal dunes. J. Veg. Sci. 22, 751–765. https://doi.org/10.1111/j.1654-1103.2011.01303.x

Carboni, M., Zelený, D., Acosta, A.T.R., 2016. Measuring ecological specialization along a natural stress gradient using a set of complementary niche breadth indices. J. Veg. Sci. 27, 892–903. https://doi.org/10.1111/jvs.12413

Carranza, M.L., Carboni, M., Feola, S., Acosta, A.T.R., 2010. Landscape-scale patterns of alien plant species on coastal dunes: the case of iceplant in central Italy. Appl. Veg. Sci. 13, 135–145. https://doi.org/10.1111/j.1654-109X.2009.01065.x

Castroviejo, S. (coord. gen.). 1986-2012. Flora iberica 1-8, 10-15, 17-18, 21. Real Jardín Botánico, CSIC, Madrid.

Chamberlain, S., 2015. brranching: Fetch “Phylogenies” from Many Sources. HttpsCRANR-Proj. R package version 0.1.0. Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., Knight, T.M., Purschke, O., Gotelli, N.J., 2018. Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecol. Lett. 21, 1737–1751. https://doi.org/10.1111/ele.13151

Chave, J., Chust, G., Thébaud, C., 2007. The importance of phylogenetic structure in biodiversity studies, in: Storch, D., Marquet, P., Brown, J. (Eds.), Scaling Biodiversity. Cambridge University Press, Cambridge, pp. 150–167. https://doi.org/10.1017/CBO9780511814938.010

Chytrý, M., Dražil, T., Hájek, M., Kalníková, V., Preislerová, Z., Šibík, J., Ujházy, K., Axmanová, I., Bernátová, D., Blanár, D., Dančák, M., Dřevojan, P., Fajmon, K., Galvánek, D., Hájková, P., Herben, T., Hrivnák, R., Janeček, Š., Janišová, M., Jiráská, Š., Kliment, J., Kochjarová, J., Lepš, J., Leskovjanská, A., Merunková, K., Mládek, J., Slezák, M., Šeffer, J., Šefferová, V., Škodová, I., Uhlířová, J., Ujházyová, M., Vymazalová, M., 2015. The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). Preslia 87, 217–278.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228. https://doi.org/10.1890/080216

Connor, E.F., McCoy, E.D., 2001. Species area relationship. Encicl. Biodivers. Acad. Press 5, 397–411.

Del Vecchio, S., Jucker, T., Carboni, M., Acosta, A.T.R., 2017. Linking plant communities on land and at sea: The effects of Posidonia oceanica wrack on the structure of dune vegetation. Estuar. Coast. Shelf Sci. 184, 30–36. https://doi.org/10.1016/j.ecss.2016.10.041

Dengler, J., 2009a. A flexible multi-scale approach for standardised recording of plant species richness patterns. Ecol. Indic. 9, 1169–1178. https://doi.org/10.1016/j.ecolind.2009.02.002

Dengler, J., 2009b. Which function describes the species-area relationship best? A review and empirical evaluation. J. Biogeogr. 36, 728–744. https://doi.org/10.1111/j.1365-2699.2008.02038.x

Dengler, J., 2008. Pitfalls in Small-Scale Species-Area Sampling and Analysis. Folia Geobot. 43, 269–287. https://doi.org/10.1007/s12224-008-9014-9

Dengler, J., Boch, S., 2008. Sampling-Design Effects on Properties of Species-Area Relationships – A Case Study from Estonian Dry Grassland Communities. Folia Geobot. 43, 289–304. https://doi.org/10.1007/s12224-008-9018-5

Dengler, J., Matthews, T.J., Steinbauer, M.J., Wolfrum, S., Boch, S., Chiarucci, A., Conradi, T., Dembicz, I., Marcenò, C., García-Mijangos, I., Nowak, A., Storch, D., Ulrich, W., Campos, J.A., Cancellieri, L., Carboni, M., Ciaschetti, G., Frenne, P.D., Dolezal, J., Dolnik, C., Essl, F., Fantinato, E., Filibeck, G., Grytnes, J.-A., Guarino, R., Güler, B., Janišová, M., Klichowska, E., Kozub, Ł., Kuzemko, A., Manthey, M., Mimet, A., Naqinezhad, A., Pedersen, C., Peet, R.K., Pellissier, V., Pielech, R., Potenza, G., Rosati, L., Terzi, M., Valkó, O., Vynokurov, D., White, H., Winkler, M., Biurrun, I., 2019. Species–area relationships in continuous vegetation: Evidence from Palaearctic grasslands. J. Biogeogr. 0, 1–15. https://doi.org/10.1111/jbi.13697

Deutschewitz, K., Lausch, A., Kühn, I., Klotz, S., 2003. Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Glob. Ecol. Biogeogr. 12, 299–311. https://doi.org/10.1046/j.1466-822X.2003.00025.x

Devictor, V., Julliard, R., Jiguet, F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117, 507–514. https://doi.org/10.1111/j.0030-1299.2008.16215.x

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Fattorini, S., Borges, P.A.V., Dapporto, L., Strona, G., 2017. What can the parameters of the species–area relationship (SAR) tell us? Insights from Mediterranean islands. J. Biogeogr. 44, 1018–1028. https://doi.org/10.1111/jbi.12874

Fenu, G., Cogoni, D., Ferrara, C., Pinna, M.S., Bacchetta, G., 2012. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 146, 586–602. https://doi.org/10.1080/11263504.2012.656727

Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Procheş, Ş., Bank, M. van der, Reeves, G., Hedderson, T.A.J., Savolainen, V., 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445, 757–760. https://doi.org/10.1038/nature05587

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. J. Veg. Sci. 19, 493–502. https://doi.org/10.3170/2008-8-18392

Forey, E., Lortie, C.J., Michalet, R., 2009. Spatial patterns of association at local and regional scales in coastal sand dune communities. J. Veg. Sci. 20, 916–925.

Frederiksen, L., Kollmann, J., Vestergaard, P., Bruun, H.H., 2006. A multivariate approach to plant community distribution in the coastal dune zonation of NW Denmark. Phytocoenologia 36, 321–342. https://doi.org/10.1127/0340-269X/2006/0036-0321

Futuyma, D.J., Moreno, G., 1988. The Evolution of Ecological Specialization. Annu. Rev. Ecol. Syst. 19, 207–233. https://doi.org/10.1146/annurev.es.19.110188.001231

Grunewald, R., 2006. Assessment of Damages from Recreational Activities on Coastal Dunes of the Southern Baltic Sea. J. Coast. Res. 1145–1157. https://doi.org/10.2112/05-0464.1

Hardy, O.J., Senterre, B., 2007. Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. J. Ecol. 95, 493–506. https://doi.org/10.1111/j.1365-2745.2007.01222.x

He, F., Legendre, P., 2002. Species Diversity Patterns Derived from Species-Area Models. Ecology 83, 1185–1198. https://doi.org/10.2307/3071933

Helmus, M.R., Ives, A.R., 2012. Phylogenetic diversity–area curves. Ecology 93.

Hesp, P.A., 1991. Ecological processes and plant adaptations on coastal dunes. J. Arid Environ.

Hu, G., Jin, Y., Liu, J., Yu, M., 2014. Functional diversity versus species diversity: relationships with habitat heterogeneity at multiple scales in a subtropical evergreen broad-leaved forest. Ecol. Res. 29, 897–903. https://doi.org/10.1007/s11284-014-1178-6

Jasmin, J.-N., Kassen, R., 2007. Evolution of a single niche specialist in variable environments. Proc. Biol. Sci. 274, 2761–7. https://doi.org/10.1098/rspb.2007.0936

Karadimou, E.K., Kallimanis, A.S., Tsiripidis, I., Dimopoulos, P., 2016. Functional diversity exhibits a diverse relationship with area, even a decreasing one. Sci. Rep. 6, 35420. https://doi.org/10.1038/srep35420

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial Heterogeneity Influences Native and Nonnative Plant Species Richness. Ecology 87, 3186–3199.

Kuzemko, A.A., Steinbauer, M.J., Becker, T., Didukh, Y.P., Dolnik, C., Jeschke, M., Naqinezhad, A., Uğurlu, E., Vassilev, K., Dengler, J., 2016. Patterns and drivers of phytodiversity in steppe grasslands of Central Podolia (Ukraine). Biodivers. Conserv. 25, 2233–2250. https://doi.org/10.1007/s10531-016-1060-7

Lomolino, M.V., 2001. The species-area relationship: new challenges for an old pattern. Prog. Phys. Geogr. Earth Environ. 25, 1–21. https://doi.org/10.1177/030913330102500101

Lomolino, M.V., 2000. Ecology's most general, yet protean pattern: The species-area relationship. J. Biogeogr. 27, 17–26.

Maltez-Mouro, S., Maestre, F.T., 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, 80–84. https://doi.org/10.1016/j.actao.2009.10.003

Martínez, M.L., García-Franco, J.G., 2004. Plant-plant interactions in coastal dunes, in: Martínez, M.L., Psuty, N.P. (Eds.), Coastal Dunes. Ecology and Conservation. Springer Berlin Heidelberg, pp. 205–220.

Matesanz, S., Ros, F.V., Tena, D., Tenorio, M.C., 2005. Rasgos biogeográficos, florísticos y ecológicos de comunidades herbáceas en taludes de carretera en el sur de España. Ecología 97–112.

Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M.V., Loyola, R., Diniz-Filho, J.A.F., Mouillot, D., Thuiller, W., 2014. Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity. Glob. Ecol. Biogeogr. 23, 836–847. https://doi.org/10.1111/geb.12158

Mazel, F., Renaud, J., Guilhaumon, F., Mouillot, D., Gravel, D., Thuiller, W., 2015. Mammalian phylogenetic diversity-area relationships at a continental scale. Ecology 96, 2814–2822.

Morlon, H., Schwilk, D.W., Bryant, J.A., Marquet, P.A., Rebelo, A.G., Tauss, C., Bohannan, B.J.M., Green, J.L., 2011. Spatial patterns of phylogenetic diversity: Spatial patterns of phylogenetic diversity. Ecol. Lett. 14, 141–149. https://doi.org/10.1111/j.1461-0248.2010.01563.x

Nee, S., May, R.M., 1997. Extinction and the loss of evolutionary history. Science 278, 692–694. Packham, J.R., Willis, A.J., 1997. Ecology of Dunes, Salt Marsh and Shingle. Springer US.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics 20, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Peyrat, S., Fichtner, A., 2011. Plant species diversity in dry coastal dunes of the southern Baltic coast. Community Ecol. 12, 220–226. https://doi.org/10.1556/ComEc.12.2011.2.10

Polyakova, M.A., Dembicz, I., Becker, T., Becker, U., Demina, O.N., Ermakov, N., Filibeck, G., Guarino, R., Janišová, M., Jaunatre, R., Kozub, Ł., Steinbauer, M.J., Suzuki, K., Dengler, J., 2016. Scale- and taxon-dependent patterns of plant diversity in steppes of Khakassia, South Siberia (Russia). Biodivers. Conserv. 25, 2251–2273. https://doi.org/10.1007/s10531-016-1093-y

Primack, R.B., 2004. A Primer of Conservation BiologyPaperback, 3rd edition. ed. Sinauer Associates, Inc.

Purvis, A., Gittleman, J.L., Brooks, T. (Eds.), 2005. Phylogeny and Conservation, 1 edition. ed. Cambridge University Press, New York.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/, Vienna, Austria.

Ricotta, C., Pavoine, S., Bacaro, G., Acosta, A.T.R., 2012. Functional rarefaction for species abundance data: On functional rarefaction functions. Methods Ecol. Evol. 3, 519–525. https://doi.org/10.1111/j.2041-210X.2011.00178.x

Rivas-Martínez, S., 1982. Series de vegetación de la región Eurosiberiana de la Península Ibérica. Lazaroa 4, 155–166.

Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Cantó, P., del Río, S., Costa, J.C., Herrero, L., Molero, J., 2017. Biogeographic Units of the Iberian Peninsula and Baelaric Islands to District Level. A Concise Synopsis, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 131–188. https://doi.org/10.1007/978-3-319-54784-8_5

Rodrigues, A.S.L., Brooks, T.M., Gaston, K.J., 2005. Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference? Cambridge University Press, UK.

Rodrigues, A.S.L., Gaston, K.J., 2002. Maximising phylogenetic diversity in the selection of networks of conservation areas. Biol. Conserv. 105, 103–111. https://doi.org/10.1016/S0006-3207(01)00208-7

Rodrigues, A.S.L., Grenyer, R., Baillie, J.E.M., Bininda-Emonds, O.R.P., Gittlemann, J.L., Hoffmann, M., Safi, K., Schipper, J., Stuart, S.N., Brooks, T., 2011. Complete, accurate, mammalian phylogenies aid conservation planning, but not much. Philos. Trans. R. Soc. B Biol. Sci. 366, 2652–2660. https://doi.org/10.1098/rstb.2011.0104

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press.

Scheiner, S.M., 2003. Six types of species-area curves. Glob. Ecol. Biogeogr. 12, 441–447.

Scheiner, S.M., Chiarucci Alessandro, Fox Gordon A., Helmus Matthew R., McGlinn Daniel J., Willig Michael R., 2011. The underpinnings of the relationship of species richness with space and time. Ecol. Monogr. 81, 195–213. https://doi.org/10.1890/10-1426.1

Smith, A.B., Sandel, B., Kraft, N.J., Carey, S., 2013. Characterizing scale-dependent community assembly using the functional-diversity–area relationship. Ecology 94, 2392–2402. Swenson, N.G., 2014. Functional and phylogenetic ecology in R, Use R! Springer New York, New York, NY.

Swenson, N.G., Enquist, B.J., Pither, J., Thompson, J., Zimmerman, J.K., 2006. The Problem and Promise of Scale Dependency in Community

Phylogenetics. Ecology 87, 2418–2424. https://doi.org/10.1890/0012-9658(2006)87[2418:TPAPOS]2.0.CO;2

Swenson, N.G., Enquist, B.J., Thompson, J., Zimmerman, J.K., 2007. The Influence of Spatial and Size Scale on Phylogenetic Relatedness in Tropical Forest Communities. Ecology 88, 1770–1780. https://doi.org/10.1890/06-1499.1

Swenson, N.G., Erickson, D.L., Mi, X., Bourg, N.A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J.K., Liu, X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S.J., Ye, W., Zhang, J., Zimmerman, J.K., Kress, W.J., 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. Ecology 93, S112–S125. https://doi.org/10.1890/11-0402.1

Tjørve, E., 2009. Shapes and functions of species-area curves (II): a review of new models and parameterizations. J. Biogeogr. 36, 1435–1445. https://doi.org/10.1111/j.1365-2699.2009.02101.x

Tjørve, E., 2003. Shapes and functions of species–area curves: a review of possible models. J. Biogeogr. 30, 827–835.

Torca, M., Campos, J.A., Herrera, M., 2019a. Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. Estuar. Coast. Shelf Sci. 218, 39–47. https://doi.org/10.1016/j.ecss.2018.11.016

Torca, M., Campos, J.A., Herrera, M., 2019b. Species composition and plant traits of south Atlantic European coastal dunes and other comparative data. Data Brief 22, 207–213. https://doi.org/10.1016/j.dib.2018.12.005

Turtureanu, P.D., Palpurina, S., Becker, T., Dolnik, C., Ruprecht, E., Sutcliffe, L.M.E., Szabó, A., Dengler, J., 2014. Scale- and taxon-dependent biodiversity patterns of dry grassland vegetation in Transylvania. Agric. Ecosyst. Environ. 182, 15–24. https://doi.org/10.1016/j.agee.2013.10.028

UNEP, 1992. Convention on Biological Diversity. U. N. Environ. Programme Nairobi. Kenya.

Vázquez, D.P., Simberloff, D., 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. Am. Nat. 159, 606–623. https://doi.org/10.1086/339991

Wang, X., Swenson, N.G., Wiegand, T., Wolf, A., Howe, R., Lin, F., Ye, J., Yuan, Z., Shi, S., Bai, X., Xing, D., Hao, Z., 2013. Phylogenetic and functional diversity area relationships in two temperate forests. Ecography 36, 883–893. https://doi.org/10.1111/j.1600-0587.2012.00011.x

Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24, 2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Westhoff, V., Van der Maarel, E., 1978. The Braun-Blanquet approach, in: Whittaker, R.H. (Ed.), Classification of Plant Communities. Dr. W. Junk Publishers, The Hague, pp. 287–399.

Whittaker, R.H., 1972. Evolution and Measurement of Species Diversity. Taxon 21, 213–251. https://doi.org/10.2307/1218190

Wikström, N., Savolainen, V., Chase, M.W., 2001. Evolution of the angiosperms: calibrating the family tree. Proc. R. Soc. B Biol. Sci. 268, 2211–2220. https://doi.org/10.1098/rspb.2001.1782

Wilson, D.S., Yoshimura, J., 1994. On the Coexistence of Specialists and Generalists. Am. Nat. 144, 692–707.

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. J. Veg. Sci. 23, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didžiulis, V., Hejda, M., Hulme, P.E., Lambdon, P.W., Pergl, J., Pyšek, P., Roy, D.B., Kühn, I., 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proc. Natl. Acad. Sci. 106, 21721–21725. https://doi.org/10.1073/pnas.0907088106

Chapter 6

Climate and soil characteristics drive changes in coastal dune plant diversity patterns

6.1. Introduction

Understanding changes in vegetation patterns along environmental gradients is a long standing issue in ecology (Schimper, 1903; Whittaker, 1956). Gradients have been successfully used to understand many aspects of plant ecology, as they provide an ideal opportunity to study natural variation in abiotic factors that may drive community change (Grime, 1977, 1979; Tilman, 1988; Goldberg, 1990; Bertness and Callaway, 1994; Callaway, 1995, 1997). Understanding that the abiotic environment shapes the distribution of species across the landscape was set before much of the modern study of ecology (Humboldt and Bonpland, 1805; Schimper, 1898). Among the most important factors governing diversity gradients are contemporary factors such as water availability and productivity, area, biotic interactions and environmental heterogeneity, and factors related to historical processes such as phylogenetic niche conservatism and geological or climatic history (Currie, 1991; Hawkins et al., 2003; Kreft and Jetz, 2007; Field et al., 2009).

Coastal dune ecosystems are complex, vulnerable and characterized by a close interaction between abiotic and biotic components (Kim and Yu, 2009; Fenu et al., 2012; Ruocco et al., 2014). Dunes soil characteristics vary along the dune profile in relation to micro-environmental factors such as relative humidity, temperature, light, grain size, organic matter content, pH and conductivity (Maun, 2009). Therefore, there is a marked disparity in soil characteristics along a sea-inland gradient (Fenu et al., 2013). Soil and wind related factors are two major drivers controlling environmental variation along coastal dunes (Maun, 2008, 2009; Frederiksen et al., 2006; Forey et al., 2008), as well as soil chemical variables (Costa et al., 1996; Kim and Ihm, 1988).

Coastal dunes have long been useful model systems for analyzing natural variation in abiotic factors that drive community change (Oosting and Billings, 1942; Barbour and DeJong, 1977). Coastal dune ecosystems consist of highly permeable and generally xeric substrates, soils that are pedogenetically uninvolved, and specialized psammophilous vegetation (Fenu et al., 2012). This psammophilous vegetation is mainly made up of the specialist species, which are well adapted and can only live there (Hesp, 1991). In contrast, those species that can grow in many different habitats apart from coastal dunes are named generalists (Castillo and Moreno-Casasola, 1996).

Belt-like patches of plant communities are determined by sequence of plant species showing fairly distinct range of tolerance (Daubenmire, 1968). Then, we can distinguish between embryo, mobile and fixed dunes in relation to the vegetation of coastal dunes following the aforementioned gradient. Furthermore, these communities are recognized in the Habitats Directive (92/43/EEC) with the codes 2110, 2120 and 2130*, with the last one considered as priority habitat for protection and conservation (See Chapter 1, section 1.2). Plant communities in coastal habitats are in a delicate exchange with their surrounding environment (Del Vecchio et al., 2017) because they are the result of a dynamic equilibrium among many factors such as fluvial supply, wave motion, marine currents, and wind action (Bertoni et al., 2014).

Coastal dunes are highly dynamic systems and thus prone to changes even under natural conditions and often could drive to an advanced state of degradation, irreversible alteration, or lost (Agır et al., 2016). Coastal dune systems are also particularly fragile and several potential dangers threaten them (Carboni et al., 2009). Urbanization, agriculture and touristic development are the most important factors leading to habitat degradation, fragmentation, and species and habitat loss (Buffa et al., 2012; Pintó et al., 2014). Ecosystems that feature high ecological diversity, hosting a striking number of habitats considered to be relevant to international conservation goals (Janssen et al., 2016).

Coastal dune vegetation it is also vulnerable due to its high specialization. These species are adapted to live in a narrow range of limiting environmental conditions (Wilson and Sykes, 1999). However, in this habitat we also find generalist species, which have higher environmental tolerances and can grow in more diverse sites (Büchi and Vuilleumier, 2014). Disturbances as habitat degradation and destruction could force competition between generalist and specialists, which could produce the extinction of specialists (Clavel et al., 2011). This process could lead to biotic homogenization, which is the replacement of local species by other more widespread species. If we know the processes that influence the settlement of specialist and generalist species, we could take better conservation measures.

Understanding how environmental factors influence the vegetation is crucial in dealing with the effects of human disturbance (Fenu et al., 2013). Many authors have focused on the relationships between plant communities and soil factors in coastal dunes. Isermann (2005) studied the connection between pH and species diversity, Lee et al., (2007) showed how communities arranged with soil particle size, Angiolini et al. (2013) worked on soil factors as pH, NaCl or $CaCO_3$ to see its relation with coastal vegetation. Also some studies have shown the relation of coastal dunes with climate in situations of disturbance or future climatic change (Miller et al., 2009; Ranasinghe, 2016).

The aim of this study is to explore the species relationship with environmental factors (soil, climate) and spatial variables in coastal dunes of southwest of Europe in a biogeographic gradient, represented by four biogeographical sectors, which belong to the Cantabrian Atlantic subprovince (Rivas-Martínez et al., 2017b). We expect changes in soil chemical variables between the three vegetation types and between the biogeographical sectors, as they span up to 750 km (H1). We also analyze the relationship between species composition (total species and generalist and specialists) and three group of variables: climate, spatial distribution of plots and soil factors. As climate is relatively homogeneous in the same site and along the study area, temperate oceanic bioclimate sensu (Rivas-Martínez et al., 2017a), we expect so the most explaining factors would be spatial allocation of the plots, both in the ecological gradient and along the coast, and soil variables (H2).

6.2. Material and methods

6.2.1. Study area and sampling

The study area was set in the Atlantic coast of north Spain and south France, which belongs to the Cantabrian Atlantic biogeographical subprovince. Inside four sectors are recognized: Galicia and North Portugal (GP), North Galicia and Asturias (GA), Cantabrian and Basque (CB) and Aquitaine-Landes (AL) (Rivas-Martínez, 1982; Rivas-Martínez et al., 2017b). Western sectors show temperate hyperoceanic submediterranean conditions, while in the eastern sectors a temperate oceanic bioclimate is dominant (Rivas-Martínez et al., 2017a). Three sites were sampled for each biogeographical sector. In each site three vegetation types were distinguished: embryo, mobile and fixed dunes, representing the local ecological gradient that occurs in dune ecosystems (from sea to inland). In each vegetation type four 100 m^2 (10 x 10 m) plots were set. In each 100 m^2 plot, species were recorded by presence/absence. In order to split the vascular plants in generalist and specialist species, we checked the plant habitat preferences and distribution in floras and guides (Castroviejo, 1986; Aizpuru et al., 2007). Species which live only in coastal dunes were regarded as specialists. In contrast, those that inhabit in a greater range of habitats were considered generalist species .

To analyze the possible effect of abiotic factors on observed diversity patterns, we collected surface soil samples, approximately 0.5 kg at 10-15 cm depth, in the middle of each plot. Sampling took place during the months of June and July of 2014 and 2015. Eight soil parameters and soil texture, expressed in percentage of grain size, were measured. Soil properties assayed included pH, organic matter (%), Kjeldahl Nitrogen (%), P (mg/l), Na (mg/l), K (mg/l), Mg (mg/l), Ca (mg/l) and soil texture (%) (Table 6.1). All analyses were conducted on Laboratorio Agroambiental Fraisoro in Gipuzkoa (Basque Country, Spain).

To analyze the influence of climate, a climatic table was created from the data retrieved from WorldClim with 30 seconds resolution (Fick and Hijmans, 2017). We used the coordinates of the 100 m^2 plots with *raster* and *sp* R (R Core Team, 2015) packages and *getData* function. Nine bioclimatic variables were considered: annual mean temperature (°C), mean diurnal range (°C), isothermality (%), temperature seasonality (standard deviation * 100), temperature annual range (°C), mean temperature of the warmest quarter (°C), annual precipitation (mm), precipitation of the driest month (mm) and precipitation of the warmest quarter (mm) (Table 6.1). These bioclimatic variables have been used in studies of coastal dunes relating climate change scenarios, ecological niche modelling or conservation issues (Mendoza-González et al., 2013, 2016; Prisco et al., 2013). In our case we will use them to explain community composition patterns.

Table 6.1: Summary of the soil, bioclimatic and spatial variables.

Variable type	Variable name	Unit	Variable type
Soil	pH	-	Lab measure
	Organic matter	%	Lab measure
	Kjeldahl Nitrogen	%	Lab measure
	pH	mg/l	Lab measure
	Na	mg/l	Lab measure
	K	mg/l	Lab measure
	Ca	mg/l	Lab measure
	Soil texture		
	-Silt and clay (0.063 mm)	%	Lab measure
	-Fine sand (0.063-0.25 mm)	%	Lab measure
	-Coarse sand (0.25-2 mm)	%	Lab measure
	-Gravel(2-4mm)	%	Lab measure
Bioclimatic	BIO1 Annual Mean Temperature	ºC	Wordclim
	BIO2 Mean Diurnal Range (Mean of monthly (max temp - min temp))	ºC	Wordclim
	BIO3 Isothermality (BIO2/BIO7) (* 100)	-	Wordclim
	BIO4 Temperature Seasonality (standard deviation *100)	-	Wordclim
	BIO7 Temperature Annual Range (BIO5-BIO6)	ºC	Wordclim
	BIO10 Mean Temperature of Warmest Quarter	ºC	Wordclim
	BIO12 Annual Precipitation	mm	Wordclim
	BIO14 Precipitation of Driest Month	mm	Wordclim
	BIO18 Precipitation of Warmest Quarter	mm	Wordclim
Spatial	Spatial coordinates	Decimal degrees	Field measure

6.2.2. Data analysis

Firstly, mean and standard deviation of chemical properties of the soil for each dune habitat and biogeographical sector were calculated. Then, soil texture percentages were represented for each dune habitat and sector. Before analysis, as the soil properties were expressed in different units, they were standardized (the interval 0-1) by first subtracting the minimum observed for each variable and then dividing by the range, method of ranging proposed by Sneath and Sokal (1973). This method allows for the simultaneous adjustment of the magnitude and the variability of the descriptors. In addition, multicollinearity of soil properties was assessed with the Pearson correlation coefficient. If two variables had a correlation coefficient of 0.9, the one less correlated with the response variable was removed from further analysis. This preliminary approach was not applied to soil texture. Climatic variables were also standardized with the same method as in the soil variables. Then correlation was assessed. We used ANOVA and Tukey post-hoc analysis to test differences between biogeographical sectors for soil chemical variables and texture.

Secondly, Canonical Correspondence Analysis (CCA; ter Braak, 1986), was used to study the relationship between species composition and environmental factors (Fenu et al., 2013). CCA is a multivariate statistical analysis that looks for principal axes in a constrained, or restricted, part of the space (Greenacre, 2007). CCA is useful to document the influence of soil conditions on the spatial distribution of plant species (Kim and Yu, 2009). Stepwise model selection was applied to extract the more significant soil and climatic variables. CCA and other calculations were performed with the Vegan package (Oksanen et al., 2016) of R. Before conducting each analysis variable correlation was assessed in order to remove shared correlation between variables. If correlation was higher than 0.9, one of the variables of the correlated pair was removed (Angiolini et al., 2018). Overall, removed variables, although not all in each analysis, were the following ones: BIO2, BIO4, BIO7, BIO14, Coarse sand.

Vegan package with the function *varpart* was also used to calculate the variation partitioning (adjusted R^2) between three group of variables: space, climate and soil. The analysis included a matrix with species composition and three response matrices: the geographical coordinates for space, the chemical and grain-size variables for soil and the bioclimatic variables for climate for each 100 m^2 plot. For this analysis species were considered in total and separated by specialists and generalists.

6.3. Results

The species pool of vascular plants consisted of 120 species, 49 of embryo dunes, 85 of mobile dunes and 105 of fixed dunes. This pattern of increasing species richness along the ecological gradient is also present when data are divided by biogeographical sectors (Table 6.2). The comparison between generalist and habitat specialist species showed that specialists were usually more abundant both in number and cover in the three plant dune communities, with few exceptions. In fixed dunes generalists showed a cover ranging from 5% to 12%, while specialists had a cover from 29% to 51%. Mosses were only present in mobile and fixed dunes, lichens only in fixed dunes. Non-vascular cover was very low, excepting mosses in North Galicia and Asturias (GA), (38%), and Cantabrian and Basque (CB), (22%) sectors.

6.3.1. Comparative data of soil and climate

In the Table 6.3, that presents the descriptive data of soil parameters with mean and standard deviation for each vegetation type and sector, we can observe significant differences between biogeographical sectors for each vegetation type. pH, Ca and Na decrease from embryo to fixed dunes, while organic matter, phosphorus, and potassium increased. Nitrogen did not show any trend and Mg had a mixed pattern, which increased for Galicia and North Portugal (GP) and Aquitaine-Landes (AL) sectors and it decreased in North Galicia and Asturias (GA) and Cantabrian and Basque sectors (CB). About changes between sectors it could be highlighted phosphorus with the highest value in GP and the lowest in AL for the three habitats. Sodium showed the same pattern in embryo and fixed dune. Magnesium showed the highest value in GA and the lowest in AL. In general French localities presented lower values of minerals, which made to present most of the significant differences with the other biogeographical sectors.

For soil texture (Figure 6.1) the highest percentage of grain size was coarse sand in the three vegetation types. This coincided for AL, GA and GP sectors, while for CB sector the highest value was for fine sand in the three habitats. Then, sand tended to be a little bit finer in the CB sector. On the high range of texture, in the AL sector for embryo dune gravel was present around 5%, while for other sectors and habitats was zero. On the low range of texture, for silt and clay there was almost not record in any habitat. Table 6.4 presents the significant differences between biogeographical sectors for each vegetation type. In general, most of the differences were set in the range of fine sand, in particular in CB sector (Table 6.4).

Table 6.2: Descriptive values of number of species and cover for vascular and non-vascular species.

			Embryo					Mobile					Fixed				
				Species		Cover %			Species		Cover %			Species		Cover %	
			Total	Mean	SD	Mean	SD	Total	Mean	SD	Mean	SD	Total	Mean	SD	Mean	SD
GP	Vascular	Generalists	10	1.67	2.06	0.89	1.63	12	2.42	2.02	0.8	1.37	25	7.92	3.09	10.41	8
		Specialists	19	7.16	3.79	33.59	21.68	24	11	3.49	44.68	19.4	23	11.92	1.88	37.34	23.94
	Non-Vascular	Mosses	-	-	-	-	-	-	-	-	-	-	7	1.88	0.85	16.46	23.15
		Lichens	-	-	-	-	-	-	-	-	-	-	4	0.33	0.7	0.13	0.51
GA	Vascular	Generalists	6	1.08	1.08	1.07	2.43	20	5.42	2.78	1.43	2.08	18	7.67	1.83	7.08	3.05
		Specialists	12	6.17	1.4	37.83	23.64	19	8.67	2.02	40.09	21.22	25	11.33	1.67	28.85	16.61
	Non-Vascular	Mosses	-	-	-	-	-	4	0.25	0.9	0.25	0.9	7	1.63	0.82	37.61	35.03
		Lichens	-	-	-	-	-	-	-	-	-	-	2	0.25	0.53	0.23	0.7
CB	Vascular	Generalists	6	1.16	1.85	0.98	2.22	19	3.83	2.44	2.11	2.36	23	5.75	1.82	4.67	3.5
		Specialists	11	5	1.41	31.36	23.64	22	8.16	1.75	53.64	25.81	23	8.83	1.47	35.66	25.85
	Non-Vascular	Mosses	-	-	-	-	-	5	0.7	1.04	0.07	0.1	7	1.5	1.02	22.42	33.12
		Lichens	-	-	-	-	-	-	-	-	-	-	1	0.04	0.2	0.004	0.02
AL	Vascular	Generalists	4	0.58	0.67	0.43	0.95	17	3.17	2.44	2.57	3.37	24	6.33	3.03	12.4	13.78
		Specialists	15	5.92	2.11	41.6	22.25	25	10.83	4.34	55.28	18.62	29	10.17	4.06	50.82	27.27
	Non-Vascular	Mosses	-	-	-	-	-	3	0.21	0.59	0.02	0.06	5	0.46	0.88	2.79	8.36
		Lichens	-	-	-	-	-	-	-	-	-	-	2	0.21	0.59	0.94	3.67

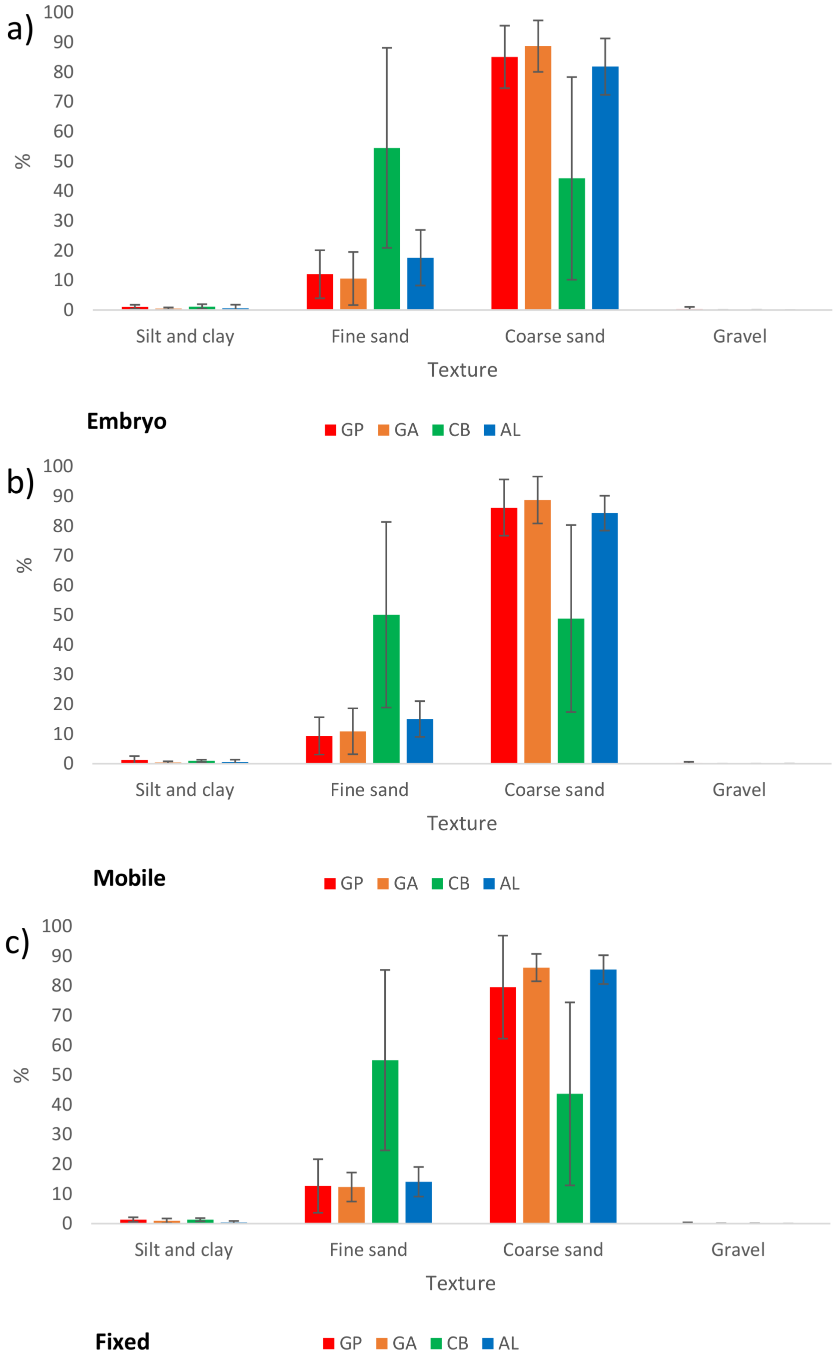

Figure 6.1: Distribution of soil particle sizes in percentage for each dune habitat: embryo dunes (a), mobile dunes (b) and fixed dunes (c). Bars are for standard deviation. Silt and clay <0.063 mm, fine sand 0.063-0.25 mm, coarse sand 0.25-2 mm, gravel 2-4 mm.

In relation to climate variables, Table 6.5 includes a summary of the climatic variables for each site. Annual mean temperature ranged from 13.6°C in the most eastern site to 14.9°C in the most western site. Annual precipitation ranged between 991 mm in western biogeographical sectors and 1336 mm in eastern sectors. The sites with the highest annual precipitation were those in France. Nevertheless, there were bigger differences for the precipitation of the driest month and of the warmest quarter, which showed a clear decrease from east to west.

6.3.2. Abiotic factors explaining species composition by CCA

Soil parameters and texture were analyzed by vegetation type with CCA (Canonical Correspondence Analysis) (Figure 6.2). Ordination shows that plots clustered by biogeographical sector, in particular in fixed dunes, where western sectors, Galicia and North Portugal (GP) and North Galicia and Asturias (GA), and eastern ones, Cantabrian and Basque (CB) and Aquitaine-Landes (AL), showed separated. CB plots were related to fine sand variable in the three cases. All models were significant and explained variation was 39% for embryo dunes, 37% for mobile dunes and 45% for fixed dunes. Climatic variables were analyzed also by vegetation type (Figure 6.3). Plots again clustered by biogeographical sector, in particular in mobile and fixed dunes. Most of CB plots showed no relation with climatic variables and western sectors (GP, GA) were related to BIO1. Models were significant and explained variation of 29% for embryo dunes, 31% for mobile dunes and 32% for fixed dunes. If we consider at the same time the three group of variables (space, climate and soil) model explanation was higher: 54% for embryo dunes, 54% for mobile dunes and 60% for fixed dunes (Table 6.6).

Table 6.3: Descriptive data of soil parameters with mean and standard deviation (SD) for the three dune habitats. pH, organic matter (%), Kjeldahl Nitrogen (%), P (mg/l), Na (mg/l), K (mg/l), Mg (mg/l), Ca (mg/l). OM = Organic Matter. In bold pairs of letters indicate significant differences p>0.05.

						Embryo			
		pH	OM	N	P	Na	K	Mg	Ca
GP	Mean	9.42 a	0.1	0.02	**4.42 ac**	**65.58 a**	**6.17 b**	**83.50 a**	**4209.17 a**
	SD	0.22	0.01	0.02	1.98	17.76	2.95	43.87	764.86
GA	Mean	**9.43 b**	**0.11 ab**	**0.04**	**4.00 b**	**71.75 b**	7.67	**105.17 b**	**4502.50 b**
	SD	0.16	0.02	0.02	2	33.63	2.27	39.61	569.47
CB	Mean	**9.44 c**	**0.10 b**	**0.02**	**2.58 c**	55.75	**8.92 ab**	**91.41 c**	**4458.33 c**
	SD	0.14	0	0.02	1	27.39	2.19	10.87	255.62
AL	Mean	**9.23 abc**	**0.10 a**	**0.02**	**1.83 ab**	**33.75 ab**	**6.42 a**	**16.42 abc**	**1253.67 abc**
	SD	0.13	0	0.02	0.72	17.05	1.88	4.54	878.08

						Mobile			
		pH	OM	N	P	Na	K	Mg	Ca
GP	Mean	9.38	0.11	0.02	**4.67 ad**	**53.83 a**	**5.5 c**	**81.42 a**	**4166.67 a**
	SD	0.22	0.02	0.02	1.87	9.77	2.35	43.65	800.86
GA	Mean	9.37	**0.13 a**	0.04	**3.42 b**	**68.58 bc**	**7.41 b**	**96.42 b**	**4358.33 b**
	SD	0.17	0.05	0.02	1.24	40.68	2.57	31.81	477.99
CB	Mean	9.14	0.11	0.04	**3.00 cd**	**35.33 c**	**8.08 ac**	**85.00 c**	**4100.83 c**
	SD	0.34	0.02	0.02	1.21	3.11	2.11	8.43	299.41
AL	Mean	9.18	**0.10 a**	0.02	**1.42 abc**	**17.67 ab**	**4.83 ab**	**12.42 abc**	**1365.17 abc**
	SD	0.11	0	0.02	0.67	7.89	0.72	3	819.35

						Fixed			
		pH	OM	N	P	Na	K	Mg	Ca
GP	Mean	**8.90 a**	0.29	0.02	**5.00 ab**	**51.08 ae**	**9.42 a**	**85.33 a**	**3902.50 a**
	SD	0.3	0.23	0.02	1.76	9.51	3.06	39.03	663.48
GA	Mean	**9.06 b**	0.23	0.04	3.75	**45.67 bd**	8.25	**98.25 b**	**4040.83 b**
	SD	0.29	0.15	0.02	1.42	8.08	2.38	28.8	539.47
CB	Mean	**8.90 c**	0.3	0.04	**3.25 b**	**34.58 cde**	9.08	**84.75 c**	**3756.67 c**
	SD	0.29	0.28	0.02	1.66	6.54	2.27	15.94	270.77
AL	Mean	**8.12 abc**	0.27	0.02	**2.17 a**	**18.75 abc**	**6.42 a**	**21.92 abc**	**849.50 abc**
	SD	0.99	0.26	0.02	1.53	8.28	1.73	10.35	808.21

Table 6.4: Significant differences in sand grain size between biogeographical sectors for each vegetation type. In bold pairs of letters indicate significant differences p>0.05.

Embryo									
		Silt and clay		Fine sand		Coarse sand		Gravel	
	mm	0.063		0.063-0.25		0.25-2		2	
GP	Mean	1.08		**12.03**	**c**	**85.09**	**c**	0.36	
	SD	0.68		8.08		10.51		0.69	
GA	Mean	0.53		**10.59**	**b**	**88.71**	**b**	0.01	
	SD	0.37		8.92		8.65		0.02	
CB	Mean	1.18		**54.52**	**abc**	**44.26**	**abc**	0.02	
	SD	0.79		33.62		34.05		0.03	
AL	Mean	0.58		**17.59**	**a**	**81.82**	**a**	0	
	SD	1.22		9.33		9.48		0	
Mobile									
		Silt and clay		Fine sand		Coarse sand		Gravel	
	mm	0.063		0.063-0.25		0.25-2		2	
GP	Mean	1.28		**9.36**	**c**	**86.21**	**c**	0.24	a
	SD	1.26		6.28		9.47		0.41	
GA	Mean	0.44		**10.9**	**b**	**88.77**	**b**	**0.01**	**a**
	SD	0.36		7.73		7.89		0.03	
CB	Mean	0.95		**50.14**	**abc**	**48.87**	**abc**	0.02	
	SD	0.41		31.23		31.46		0.03	
AL	Mean	0.57		**15.03**	**a**	**84.33**	**a**	0.02	
	SD	0.81		6		5.87		0.05	
Fixed									
		Silt and clay		Fine sand		Coarse sand		Gravel	
	mm	0.063		0.063-0.25		0.25-2		2	
GP	Mean	**1.34**	**a**	**12.66**	**c**	**79.58**	**c**	**0.16**	**a**
	SD	0.78		9.01		17.33		0.23	
GA	Mean	0.92		**12.3**	**b**	**86.15**	**b**	0.03	
	SD	0.79		4.88		4.62		0.05	
CB	Mean	1.31		**54.99**	**abc**	**43.65**	**abc**	0.03	
	SD	0.54		30.37		30.8		0.05	
AL	Mean	**0.43**	**a**	**14.07**	**a**	**85.46**	**a**	**0**	**a**
	SD	0.45		4.99		4.84		0	

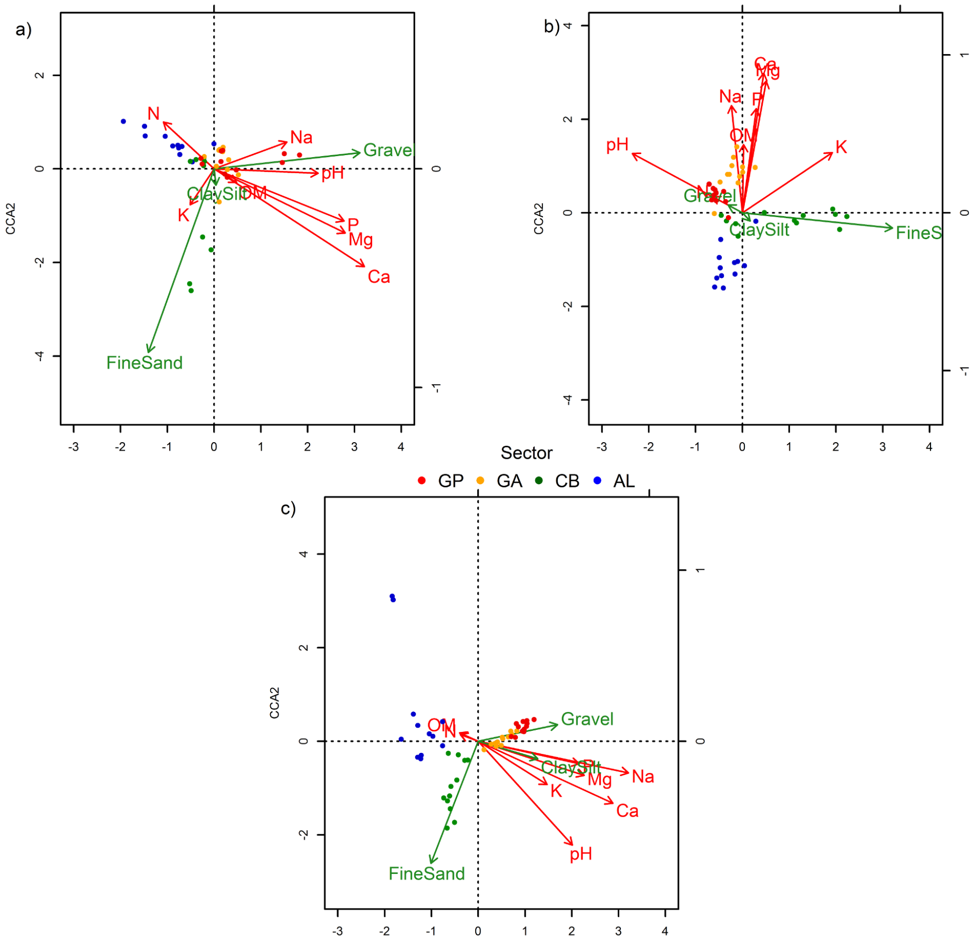

Figure 6.2: DCCA of soil parameters (red) and texture (green) by vegetation type: embryo dune (a), mobile dune (b) and fixed dune (c). Galicia and North Portugal (GP), North Galicia and Asturias (GA), Cantabrian and Basque (CB) and Aquitaine-Landes (AL). Abbreviations for variables can be seen in Table 1.

Table 6.5: Summary of climatic variables for each site, from the data obtained from Worldclim. See Table 1 for description of the variables (BIO1-BIO18).

	BIO 1	BIO 2	BIO 3	BIO 4	BIO 7	BIO 10	BIO 12	BIO 14	BIO 18
Lanzada	14.9	5.9	39	340.2	15.1	19.3	1216	26	132
As Furnas	14.4	6.6	4.2	322.9	15.7	18.7	1036	29	141
Carnota	14.8	5.9	38	323.6	15.2	19.1	1007	25	132
Barrañán	14.4	6.6	42	322.9	15.7	18.7	1036	29	141
San Xurxo	14.2	6.8	43	319.6	15.7	18.6	1001	30	141
Valdoviño	14.2	6.9	43	327.1	15.9	18.7	991	31	143
Oyambre	14.3	6.8	38	384.3	17.5	19.4	872	38	171
Liencres	14.2	6.1	37	368	16.3	19.2	1006	42	199
Noja	14.1	5.8	36	366.6	15.9	19	1122	45	218
Tarnos	13.9	8.1	40	443.9	20.1	19.6	1336	69	286
Casernes	13.7	8.4	40	450.2	20.7	19.4	1323	66	281
Messanges	13.6	8.5	40	455.3	20.8	19.4	1306	65	278

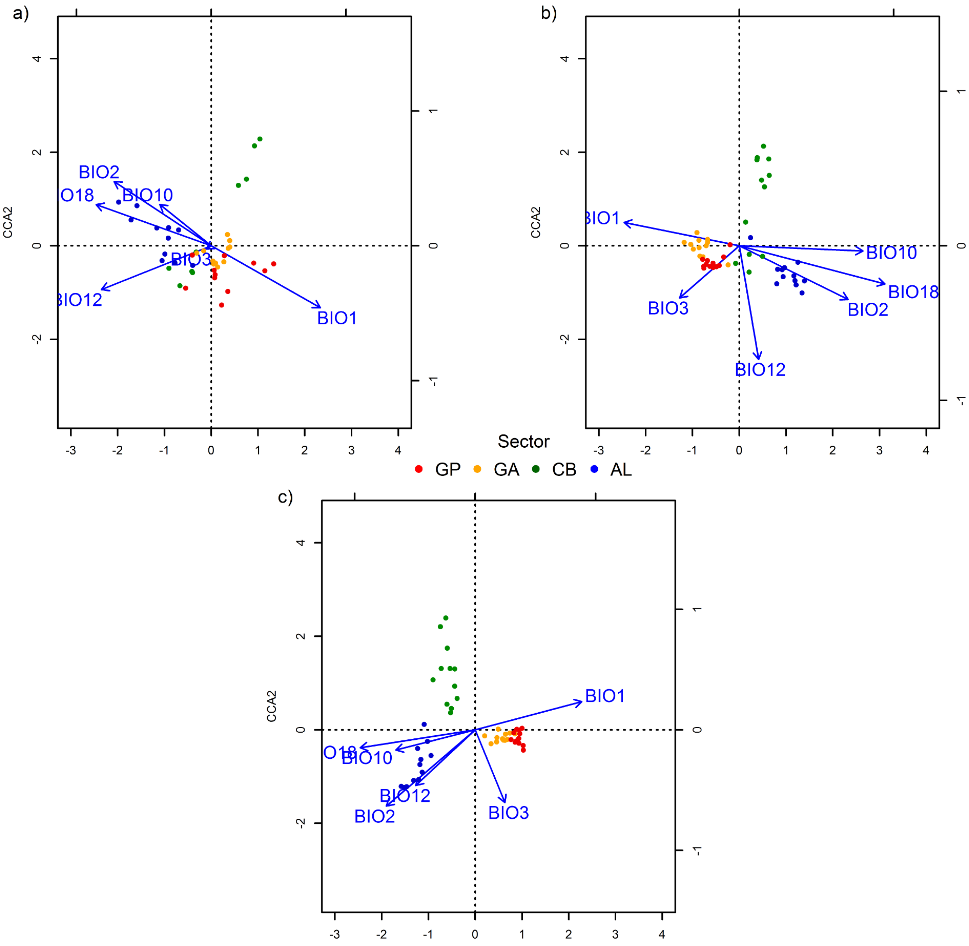

Figure 6.3: CCA of climatic variables by vegetation type: embryo dune (a), mobile dune (b) and fixed dune (c). Galicia and North Portugal (GP), North Galicia and Asturias (GA), Cantabrian and Basque (CB) and Aquitaine-Landes (AL).

Table 6.6: Explained variation of the models derived from CCA analysis and removed variables.

Model 1: only climatic variables		
	Explained (%)	Removed variables
Embryo dunes	29	BIO 4,7,14
Mobile dunes	31	BIO 4,7,14
Fixed dunes	32	BIO 4,7,14
Model 2: Texture and soil chemical variables		
	Explained (%)	Removed variables
Embryo dunes	39	Coarse Sand
Mobile dunes	37	Coarse Sand
Fixed dunes	45	Coarse Sand
Model 3: Climatic, texture and soil chemical variables		
	Explained (%)	Removed variables
Embryo dunes	54	BIO 4,7,14, Coarse Sand
Mobile dunes	54	BIO 4,7,14, Coarse Sand
Fixed dunes	60	BIO 4,7,14, Coarse Sand

6.3.3. Variation partitioning of plant dune communities

Variation partitioning of plant dune communities was analyzed for embryo, mobile and fixed dunes considering species composition by total, generalist and habitat specialist (Figure 6.4). The group of variables that explained most of the variation in all cases was climate, followed by soil in most of the situations. Just in embryo dune for generalists and specialists spatial coordinates explained higher variation than soil. In all models we found that fixed dunes explained more variation than mobile and embryo dunes. There were no big differences in the total variation explained considering total species, generalists and specialists.

Figure 6.4: Variation partitioning for embryo, mobile, and fixed dunes, and each for total species, specialists and generalists for climate (in blue), soil chemical variables (in light red) and spatial coordinates (in green). Figure 4d with no data due to half of the plots with no species. Values > 0 not shown

6.4. Discussion

6.4.1. Comparative data of soil and climate

We found a decrease on pH and an increase of organic matter in the ecological gradient studied, i.e., from embryo to fixed dunes. This trend is supported by recent studies in coastal dunes such as Ruocco et al. (2014); Abdelaal et al. (2019); Agır et al. (2019). pH decrease could be related to a reduction of the marine aerosol and to the production of organic acid by vegetation (Maun, 2009; Angiolini et al., 2013). We could also link this patterns to an older successional stage of the soil in the areas further from the coast (Lane et al., 2008). In plant communities towards inland, in most of the sites, there was a non-vascular species cover. This, added to a relative slowness of the processes of mineralization of organic substances resulted in a higher organic matter content (Rao and Pathak, 1996; Álvarez-Rogel et al., 2007).

Phosphorous (P) increased from the coast to inland, which was consistent with the findings of Lammerts and Grootjans (1997). Çakan and Karataş (2006) found no significant changes in P along the sea-inland gradient. The presence of P could be related to the fixation because of the presence of endomycorrhizae (Hesp, 1991). For Potassium (K) we found a decrease from embryo to mobiles dunes and then an increase in fixed dunes. (Agır et al., 2019) showed a continuous decrease of K from coast to land. Potassium plays an important role in osmotic regulation in plants (Marschner, 2011) so species nearer to sea, and those exposed to salt spray, could store higher amounts of K in their tissues as it occurs in salt-marshes (Gorham et al., 1980). Then, the litter and the organic matter of these potassium accumulators could explain the high presence of K in embryo dune soils and the decrease inland. In general, there is a decrease of exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}) from coastline to inland due to the aeolian processes that transport salt spray (Kim and Yu, 2009). If we compare the biogeographical sectors the most remarkable result is the low values of minerals in Aquitaine-Landes (France). In French fixed dunes, maybe this could be related to a lower moss cover (2.79%, Table 6.2) and consequently less retention of minerals.

Some authors have showed that grain size has big influence of the composition of coastal plant communities (Bertoni et al., 2014), with grain size decreasing toward inland dunes (Fenu et al., 2012). We found almost no changes in grain size from embryo to fixed dunes, with a peak in the three habitats in coarse sand. In our case plots were set next to the coastline and there was short distance among them, because of the small extension of many of the dunes studied. Then, wind speed would not change so much and we would not expect a change in grain size along the environmental gradient studied. Finally, the similarity found of soil texture between sectors, excepting CB which showed significant lower values, could be related to the different composition of the dominant substrate as we find granite in Galicia (GA, GP) and limestone in Cantabria (CB) (Flor and Flor-Blanco, 2014; Vidal-Romaní et al., 2014).

6.4.2. Abiotic factors explaining species composition by CCA

In the CCA we found an opposite correlation between minerals as Ca and Mg and species composition of French sites, excepting N in embryo dunes. This Nitrogen correlation is in accordance with the high amount of atmospheric nitrogen deposition found in Atlantic coasts of south France (Forey et al., 2008). The correlation of fine sand and plot composition of CB sites (Fig. 6.2) agrees with the higher proportion of sand of this size found in CB sector (Fig. 6.1). This fine sand-species plot composition correlation is higher than the correlation found in climatic variables. However, we found that BIO1 (Annual Mean Temperature) correlated with plot composition of western sectors (GA, GP), which agrees with the higher temperature in this sites (Table 6.5). BIO2 (Mean Diurnal Range) showed a relation with AL plots. This could be related to the warmer temperatures in western sectors in contrast with those located in the east (AL). The higher variation explained by the models when all variables were included, in comparison with the splitting between soil and climate, means that climate adds explained variation to soil variables. This result agrees with the idea that coastal dune species are linked to suitable climates (Brunbjerg et al., 2014).

6.4.3. Variation partitioning of plant dune communities

Soil is important for plant growth and is a function of climate, organisms, topography and time (Jafari et al., 2004). Wisz et al. (2013) showed that plant distribution was related such as edaphic conditions, climate and biotic interactions. Abdelaal et al. (2019) studied the variation partitioning in coastal dunes between topographic, regional climatic, soil and anthropogenic factors. In the study of Abdelaal et al. (2019), taking into account the pure effect of variables, soil factors was the variable explaining most of the pure variation (0.08), while climate was the less explaining variable (0.01), although the interaction with soil was one of the highest (0.09). Jiménez-Alfaro et al. (2015) found a higher influence of climate in fixed dunes than in embryo and mobile dunes, where main driver was space. In another azonal vegetation such as floodplain forest in the Iberian Peninsula, Biurrun et al. (2016) concluded that climate variables were the most important in composition and distribution of species. Our results in all models showed a higher contribution of the pure effect of climate compared to the pure effect of the soil and space (Fig. 4). Variation explained by climate was indeed higher when the shared effect of soil was taken into account. Surprisingly, this contrast with our expectations of a higher influence of soil factors alone (H2), although, according to some authors (Heikkinen et al., 2006), climatic variables when measured over gradients could override the effect of edaphic variables in distribution models. Our results agree with the studies of Biurrun et al. (2016) and Jiménez-Alfaro et al. (2015). In Abdelaal et al. (2019), study area was smaller, less than 500 km along the coast of Egypt. In our case the study area spanned around 750 km and it was next to the border of the Mediterranean Region, which could lead to a greater climate influence.

We also found an increasing total variation explained from sea to inland, which in accordance with Jiménez-Alfaro et al. (2015), who found an increasing explained variation by climate in fixed dunes. Fixed dunes are less exposed environments and waves and wind play a minor role in comparison to embryo dunes, so in fixed dunes would arise the influence of variables as climate and soil. There are more habitat specialist species in fixed dunes (Table 6.2) maybe because specialists are supposed to perform better in relatively homogeneous habitats (Futuyma and Moreno, 1988; Östergård and Ehrlén, 2005). Specialists, which are well adapted to their habitat, would be more affected by changes in the environmental conditions (Büchi and Vuilleumier, 2014). Then, generalists would be more independent than specialist to environmental changes as they can grow in a higher range of habitats. This agrees with the lower total variation explained by generalist for climate and soil variables. Vegetation can be regarded as a good indicator of overall biodiversity and in particular of ecosystem integrity of coastal dunes (Araújo et al., 2002; Lopez and Fennessy, 2002). Therefore, specialist species are a suitable to be monitored in order to follow impacts in the habitat as they reflect better the environmental changes.

Conclusions

In this study we analyzed the abiotic factors that can explain community composition in coastal dunes. These factors were climate, soil variables and spatial coordinates. Comparative values of soil variables showed a decrease of pH and Sodium from embryo to fixed dunes and an increase of organic matter and Phosphorus. This is related to the reduction of the influence of marine aerosol and the presence of more species inland, including a cover of non-vascular plants. We did not detect a decrease on sand grain sand towards land due to the small distance from sea to land considered. In the study area in Cantabrian and Basque sector sand was finer maybe because of different origin material, which was limestone. We also found a link between community composition and climate, which was greater than the relation with soil or space. Besides variables explained community patterns more in fixed dunes and for specialist species. Specialist are well adapted to the habitats they grow in and they have a narrow tolerance range. Then they reflect better the environmental changes than generalists, which have a wider tolerance range and can grow in more habitats. Therefore, dune specialist species, some of them endangered species, would be a suitable target for monitoring biodiversity changes in coastal dunes.

References

Abdelaal, M., Ahmed, D., Fois, M., Fenu, G., Bacchetta, G., 2019. Floristic patterns and ecological drivers of sand dune ecosystem along the Mediterranean coast of Egypt. Arid Land Res. Manag. 0, 1–24. https://doi.org/10.1080/15324982.2018.1564147

Agır, S.U., Kutbay, H.G., Surmen, B., 2016. Plant diversity along coastal dunes of the Black Sea (North of Turkey). Rendiconti Lincei 27, 443–453. https://doi.org/10.1007/s12210-015-0497-z

Agır, S.U., Surmen, B., Kutbay, H.G., 2019. The relationships among some chemical and physical soil traits and coastal dune plant species in Central Black Sea Region of Turkey. Rendiconti Lincei Sci. Fis. E Nat. 30, 207–222. https://doi.org/10.1007/s12210-019-00780-1

Aizpuru, I., Aseginolaza, C., Uribe-Echebarría, P.M., Urrutia, P., Zorrakin, I., Garín, P., Hermosilla, C.E., Lizaur, X., Patino, S., Pérez Dacosta, J.M., Renobales, G., Valencia, J., 2007. Claves ilustradas de la flora del País Vasco y territorios limítrofes. Publication Service of The Basque Country Government, Vitoria-Gasteiz.

Álvarez-Rogel, J., Carrasco, L., Marín, C.M., Martínez-Sánchez, J.J., 2007. Soils of a dune coastal salt marsh system in relation to groundwater level, micro-topography and vegetation under a semiarid Mediterranean climate in SE Spain. CATENA 69, 111–121. https://doi.org/10.1016/j.catena.2006.04.024

Angiolini, C., Bonari, G., Landi, M., 2018. Focal plant species and soil factors in Mediterranean coastal dunes: An undisclosed liaison? Estuar. Coast. Shelf Sci. 31, 248–258. https://doi.org/10.1016/j.ecss.2017.06.001

Angiolini, C., Landi, M., Pieroni, G., Frignani, F., Finoia, M.G., Gaggi, C., 2013. Soil chemical features as key predictors of plant community occurrence in a Mediterranean coastal ecosystem. Estuar. Coast. Shelf Sci. 119, 91–100. https://doi.org/10.1016/j.ecss.2012.12.019

Araújo, R., Honrado, J., Granja, H.M., De Pinho, S.N., Caldas, F.B., 2002. Vegetation complexes of coastal sand dunes as an evaluation instrument of geomorphologic changes in the coastline., in: Littoral 2002. The Changing Coast. EUROCOAST/EUCC. Porto, Portugal, pp. 337–339.

Barbour, M.G., DeJong, T.M., 1977. Response of west coast beach taxa to salt spray, seawater inundation, and soil salinity. Bull. Torrey Bot. Club 104, 29–34. https://doi.org/10.2307/2484662

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bertoni, D., Biagioni, C., Sarti, G., Ciccarelli, D., Ruocco, M., 2014. The role of sediment grain-size, mineralogy, and beach morphology on plant communities of two Mediterranean coastal dune systems. Ital. J. Geosci. 133, 271–281. https://doi.org/10.3301/IJG.2014.09

Biurrun, I., Campos, J.A., García-Mijangos, I., Herrera, M., Loidi, J., 2016. Floodplain forests of the Iberian Peninsula: Vegetation classification and climatic features. Appl. Veg. Sci. 19, 336–354. https://doi.org/10.1111/avsc.12219

Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., Ejrnaes, R., Aarssen, L.W., Buckley, H.L., Forey, E., Jansen, F., Kattge, J., Lane, C., Lubke, R.A., Moles, A.T., Monserrat, A.L., Peet, R.K., Roncal, J., Wootton, L., Svenning, J.-C., 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. J. Plant Ecol. 7, 101–114. https://doi.org/10.1093/jpe/rtt069

Büchi, L., Vuilleumier, S., 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. Am. Nat. 183, 612–624. https://doi.org/10.1086/675756

Buffa, G., Fantinato, E., Pizzo, L., 2012. Effects of disturbance on sandy coastal ecosystems of N-Adriatic coasts (Italy), in: Lameed, G.A. (Ed.), Biodiversity Enrichment in a Diverse World. InTech, Rijeka, HR, pp. 339–372. https://doi.org/10.5772/48473

Çakan, H., Karataş, Ç., 2006. Interactions between mycorrhizal colonization and plant life forms along the successional gradient of coastal sand dunes in the eastern Mediterranean, Turkey. Ecol. Res. 21, 301–310. https://doi.org/10.1007/s11284-005-0134-x

Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112, 143–149. https://doi.org/10.1007/s004420050293

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349. https://doi.org/10.1007/BF02912621

Carboni, M., Carranza, M.L., Acosta, A., 2009. Assessing conservation status on coastal dunes: A multiscale approach. Landsc. Urban Plan. 91, 17–25. https://doi.org/10.1016/j.landurbplan.2008.11.004

Castillo, S.A., Moreno-Casasola, P., 1996. Coastal sand dune vegetation: An extreme case of species invasion. J. Coast. Conserv. 2, 13–22. https://doi.org/10.1007/BF02743033

Castroviejo, S. (coord. gen.). 1986-2012. Flora iberica 1-8, 10-15, 17-18, 21. Real Jardín Botánico, CSIC, Madrid.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228. https://doi.org/10.1890/080216

Costa, C.S.B., Cordazzo, C.V., Seeliger, U., 1996. Shore Disturbance and Dune Plant Distribution. J. Coast. Res. 12, 133–140.

Currie, D.J., 1991. Energy and large-scale patterns of animal- and plant-species richness. Am. Nat. 137, 27–49.

Daubenmire, R., 1968. Plant communities. A textbook of plant synecology. Plant Communities Textb. Plant Synecology.

Del Vecchio, S., Jucker, T., Carboni, M., Acosta, A.T.R., 2017. Linking plant communities on land and at sea: The effects of Posidonia oceanica wrack on the structure of dune vegetation. Estuar. Coast. Shelf Sci. 184, 30–36. https://doi.org/10.1016/j.ecss.2016.10.041

Fenu, G., Carboni, M., Acosta, A.T.R., Bacchetta, G., 2013. Environmental factors influencing coastal vegetation pattern: new insights from the Mediterranean basin. Folia Geobot. 48, 493–508. https://doi.org/10.1007/s12224-012-9141-1

Fenu, G., Cogoni, D., Ferrara, C., Pinna, M.S., Bacchetta, G., 2012. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 146, 586–602. https://doi.org/10.1080/11263504.2012.656727

Fick, S., Hijmans, R., 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. https://doi.org/10.1002/joc.5086

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Turner, J.R.G., 2009. Spatial species-richness gradients across scales: a meta-analysis. J. Biogeogr. 36, 132–147. https://doi.org/10.1111/j.1365-2699.2008.01963.x

Flor, G., Flor-Blanco, G., 2014. Raised Beaches in the Cantabrian Coast, in: Gutiérrez, F., Gutiérrez, M. (Eds.), Landscapes and landforms of Spain, world geomorphological landscapes. Springer Netherlands, Dordrecht, pp. 239–248. https://doi.org/10.1007/978-94-017-8628-7_20

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. J. Veg. Sci. 19, 493–502. https://doi.org/10.3170/2008-8-18392

Frederiksen, L., Kollmann, J., Vestergaard, P., Bruun, H.H., 2006. A multivariate approach to plant community distribution in the coastal dune zonation of NW Denmark. Phytocoenologia 36, 321–342. https://doi.org/10.1127/0340-269X/2006/0036-0321

Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 19, 207–233. https://doi.org/10.1146/annurev.es.19.110188.001231

Goldberg, D.E., 1990. Components of resource competition in plant communities., in: Grace, J., Tilman, D. (Eds.), Perspectives on Plant Competition. New York, pp. 27–49.

Gorham, J., Hughes, L., Jones, R.G.W., 1980. Chemical composition of salt-marsh plants from Ynys Môn (Anglesey): the concept of physiotypes. Plant Cell Environ. 3, 309–318. https://doi.org/10.1111/1365-3040.ep11581858

Greenacre, M., 2007. Correspondence analysis in practice, Second Edition. Chapman and Hall/CRC, London. https://doi.org/10.1201/9781420011234

Grime, J.P., 1979. Plant strategies and vegetation processes. John Wiley & Sons, Toronto.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, Water, and Broad-Scale Geographic Patterns of Species Richness. Ecology 84, 3105–3117. https://doi.org/10.1890/03-8006

Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog. Phys. Geogr. Earth Environ. 30, 751–777. https://doi.org/10.1177/0309133306071957

Hesp, P.A., 1991. Ecological processes and plant adaptations on coastal dunes. J. Arid Environ.

Humboldt, A.V., Bonpland, A., 1805. Essai sur la geographie des plantes. Chez Levrault, Schoell, Paris.

Isermann, M., 2005. Soil pH and species diversity in coastal dunes. Plant Ecol. 178, 111–120. https://doi.org/10.1007/s11258-004-2558-8

Jafari, M., Chahouki, M.A.Z., Tavili, A., Azarnivand, H., Amiri, Gh.Z., 2004. Effective environmental factors in the distribution of vegetation types in Poshtkouh rangelands of Yazd Province (Iran). J. Arid Environ. 56, 627–641. `https://doi.org/10.1016/S0140-1963(03)00077-6`

Janssen, J.A.M., Rodwell, J.S., Criado, M.G., Gubbay, S., Haynes, T., Nieto, A., Sanders, N., Landucci, F., Loidi, J., Ssymank, A., Tahvanainen, T., Valderrabano, M., Acosta, A., Aronsson, M., Arts, G., Attorre, F., Bergmeier, E., Biurrun, I., Calix, M., Capelo, J., Čarni, A., Chytrý, M., Dengler, J., Dimopoulos, P., Essl, F., Gardfjell, H., Gigante, D., Hájek, M., Jansen, F., Jansen, J., Kapfer, J., Mickolajczak, A., Molina, J.A., Molnár, Z., Paternoster, D., Piernik, A., Poulin, B., Renaux, B., Schaminée, J.H.J., Šumberová, K., Toivonen, H., Tonteri, T., Tsiripidis, I., Tzonev, R., Valachovič, M., 2016. European Red List of Habitats. Part 2. Terrestrial and freshwater habitats. Eur. Union 44.

Jiménez-Alfaro, B., Marcenò, C., Guarino, R., Chytrý, M., 2015. Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages. J. Biogeogr. 42, 452–462. `https://doi.org/10.1111/jbi.12437`

Kim, C.-S., Ihm, B.-S., 1988. Studies on the vegetation of the salt marsh in the southwestern coast of Korea. Korean J. Ecol. 11, 175–192.

Kim, D., Yu, K.B., 2009. A conceptual model of coastal dune ecology synthesizing spatial gradients of vegetation, soil, and geomorphology. Plant Ecol. 202, 135. `https://doi.org/10.1007/s11258-008-9456-4`

Kreft, H., Jetz, W., 2007. Global patterns and determinants of vascular plant diversity. Proc. Natl. Acad. Sci. 104, 5925–5930. `https://doi.org/10.1073/pnas.0608361104`

Lammerts, E.J., Grootjans, A.P., 1997. Nutrient deficiency in dune slack pioneer vegetation: a review. J. Coast. Conserv. 3, 87. `https://doi.org/10.1007/BF02908183`

Lane, C., Wright, S.J., Roncal, J., Maschinski, J., 2008. Characterizing environmental gradients and their influence on vegetation zonation in a subtropical coastal sand dune system. J. Coast. Res. 4, 213–224. `https://doi.org/10.2112/07-0853.1`

Lee, J.-S., Ihm, B.-S., Cho, D.S., Son, D.-Y., Kim, J.-W., 2007. Soil particle sizes and plant communities on coastal dunes. J. Plant Biol. 50, 475. `https://doi.org/10.1007/BF03030685`

Lopez, R.D., Fennessy, M.S., 2002. Testing the floristic quality assessment index as an indicator of wetland condition. Ecological Applications 12, 487–497. `https://doi.org/10.1890/1051-0761(2002)012[0487:TTFQAI]2.0.CO;2`

Marschner, H., 2011. Marschner's mineral nutrition of higher plants. Academic Press.

Maun, M.A., 2009. The biology of coastal sand dunes. Oxford University Press, New York.

Maun, M.A., 2008. Burial of plants as a selective force in sand dunes, in: coastal dunes, ecological studies. Springer, Berlin, Heidelberg, pp. 119–135. https://doi.org/10.1007/978-3-540-74002-5_8

Mendoza-González, G., Martínez, M.L., Rojas-Soto, O., Téllez-Valdés, O., Arias-Del Razo, I., 2016. Priority areas for conservation of beach and dune vegetation of the Mexican Atlantic coast. J. Nat. Conserv. 33, 25–34. https://doi.org/10.1016/j.jnc.2016.04.007

Mendoza-González, G., Martínez, M.L., Rojas-Soto, O.R., Vázquez, G., Gallego-Fernández, J.B., 2013. Ecological niche modeling of coastal dune plants and future potential distribution in response to climate change and sea level rise. Glob. Change Biol. 19, 2524–2535. https://doi.org/10.1111/gcb.12236

Miller, T.E., Gornish, E.S., Buckley, H.L., 2009. Climate and coastal dune vegetation: disturbance, recovery, and succession. Plant Ecol. 206, 97. https://doi.org/10.1007/s11258-009-9626-z

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2.3-5.

Oosting, H.J., Billings, W.D., 1942. Factors affecting Vegetational Zonation on Coastal Dunes. Ecology 23, 131–142. https://doi.org/10.2307/1931081

Östergård, H., Ehrlén, J., 2005. Among population variation in specialist and generalist seed predation – the importance of host plant distribution, alternative hosts and environmental variation. Oikos 111, 39–46. https://doi.org/10.1111/j.0030-1299.2005.13902.x

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Pintó, J., Martí, C., Fraguell, R.M., 2014. Assessing current conditions of coastal dune systems of Mediterranean developed shores. J. Coast. Res. 832–842. https://doi.org/10.2112/JCOASTRES-D-13-00116.1

Prisco, I., Carboni, M., Acosta, A.T.R., 2013. The fate of threatened coastal dune habitats in Italy under climate change scenarios. PLOS ONE 8, e68850. https://doi.org/10.1371/journal.pone.0068850

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/, Vienna, Austria.

Ranasinghe, R., 2016. Assessing climate change impacts on open sandy coasts: A review. Earth-Sci. Rev. 160, 320–332. https://doi.org/10.1016/j.earscirev.2016.07.011

Rao, D.L.N., Pathak, H., 1996. Ameliorative influence of organic matter on biological activity of salt-affected soils. Arid Land Res. Manag. - ARID LAND RES MANAG 10, 311–319. https://doi.org/10.1080/15324989609381446

Rivas-Martínez, S., 1982. Series de vegetación de la región Eurosiberiana de la Península Ibérica. Lazaroa 4, 155–166.

Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T.E., Rivas-Sáenz, S., 2017a. Bioclimatology of the Iberian Peninsula and the Balearic Islands, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 29–80. https://doi.org/10.1007/978-3-319-54784-8_2

Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Cantó, P., del Río, S., Costa, J.C., Herrero, L., Molero, J., 2017b. Biogeographic units of the Iberian Peninsula and Balearic Islands to district level. A concise synopsis, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula: Volume 1, Plant and Vegetation. Springer International Publishing, Cham, pp. 131–188. https://doi.org/10.1007/978-3-319-54784-8_5

Ruocco, M., Bertoni, D., Sarti, G., Ciccarelli, D., 2014. Mediterranean coastal dune systems: Which abiotic factors have the most influence on plant communities? Estuar. Coast. Shelf Sci. 149, 213–222. https://doi.org/10.1016/j.ecss.2014.08.019

Schimper, A.F.W., 1903. Plant Geography Upon a Physiological Basis. Clarendon Press, Oxford.

Schimper, A.F.W., 1898. Pflanzen-geographie auf physiologischer grundlage. G. Fischer, Jena.

Sneath, P.H.A., Sokal, R.R., 1973. Numerical taxonomy. The principles and practice of numerical classification. Numer. Taxon. Princ. Pract. Numer. Classif.

ter Braak, C.J.F., 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179. https://doi.org/10.2307/1938672

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. U. S. A. 102, 8245–8250. https://doi.org/10.1073/pnas.0409902102

Tilman, D., 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press.

Vidal-Romaní, J.R., Vaqueiro, M., Sanjurjo, J., 2014. Granite Landforms in Galicia, in: Gutiérrez, F., Gutiérrez, M. (Eds.), Landscapes and landforms of Spain, world geomorphological landscapes. Springer Netherlands, Dordrecht, pp. 63–69. https://doi.org/10.1007/978-94-017-8628-7_4

Whittaker, R.H., 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26, 2–80. https://doi.org/10.2307/1943577

Wilson, Sykes, 1999. Is zonation on coastal sand dunes determined primarily by sand burial or by salt spray? A test in New Zealand dunes. Ecol. Lett. 2, 233–236. https://doi.org/10.1046/j.1461-0248.1999.00084.x

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol. Rev. Camb. Philos. Soc. 88, 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

Chapter 7

General conclusions

This doctoral thesis provides an insight in the community assembly patterns of coastal dunes in northern Spain and southwest France. Two main gradients were analyzed: one ecological at local scale from sea to inland and another biogeographical at broader scale from west to east in the study area. It also assesses the changes in functional and phylogenetic diversity both for alpha and beta diversity. These changes were also studied in the context of nested increasing sampling area from 1 cm^2 to 100 m^2. Finally, we looked for the drivers behind the community patterns and we analyzed soil chemistry, texture and climatic variables effect in dune specialist and generalist species.

Alpha biodiversity changes along the sea-inland gradient

We analyzed the species composition in embryo, mobile and fixed dunes, representing the ecological gradient, at alpha diversity level. We found an increase of taxonomic and functional diversity from plant communities nearer to sea, embryo dunes, to those more inland, fixed dunes. Phylogenetic diversity followed the opposite pattern. This results could be related to the harsh conditions in exposed sites near to the beach, so due to environmental filtering only species well adapted could survive. This sieve would filter some traits leading to a functional homogenization regardless of the family or genus, which agrees with the higher phylogenetic overdispersion found in embryo dunes.

Across the biogeographical gradient we found no differences for any dune habitat concerning taxonomic, functional and phylogenetic diversity. This finding was surprising because of the species composition change detected. It means that despite the species replacement phylogenetic structure and functional diversity were conserved in the biogeographical gradient in alpha diversity.

Beta diversity analysis along the coast

In this case taxonomic, functional and phylogenetic indices were analyzed in the three vegetation types with the variable distance along the coast to assess how beta diversity changed along the study area. This approach is a proxy of the biogeographical gradient. We found and increasing beta diversity from embryo to fixed dunes, which could be related to the increasing richness in the sea-inland gradient. Indeed, vegetation type explained a higher proportion of beta diversity, regardless of which index was considered, than distance along the coast. Then, the ecological gradient played a major role in species composition patterns.

Plot distribution in the spatial ordination were mainly explained by the spatial variable in fixed dunes for all biodiversity indices applied, while in embryo dunes it was only taxonomic diversity. This means that embryo dunes present a more similar functional and phylogenetic diversity while taxonomic diversity differs. This exception could be related to the presence of some particular and less abundant species besides the more common and abundant ones. Again we found the action of environmental filtering selecting species and traits in the more exposed communities. In more protected plant communities, the effects of winds and waves would be lower and biotic factors as competition would arise. This situation would lead to a higher species replacement followed by a change on phylogenetic structure and functional diversity.

Diversity area relationships

We analyzed the changes in species richness, functional diversity and phylogenetic diversity with increasing sampling scale for total, generalist and habitat specialist species. Specialist species have a narrow distribution, while generalists present a broader distribution among different habitats. There were higher z-values in fixed dunes for total, generalist and specialist species. This means that there are more species in fixed dunes, which is according to the increasing species richness found in other analysis. This increase in species is followed by increase in functional and phylogenetic diversity, so the more species the more traits and families found. Then, it is not surprising that results showed significant differences considering the different sampling size. Generalists were almost no present at smaller scales, so the pattern was attributed to the well adapted habitat specialist plants. This trend of specialists reflecting all species patterns was repeated through size-steps in the three vegetation types, so specialist species drive the biodiversity structure in the coastal dunes studied. We found a correlation at the biggest scale (100 m^2) between specialists and generalists. It seems that only when there is enough area there is a significant correlation. Functional diversity did not show differences between vegetation types, maybe because traits were analyzed globally and not individually, where different trends could have aroused.

Climate, soil and space can explain community composition

In this chapter we analyzed the abiotic factors that can explain community composition in coastal dunes. These factors were climate, soil variables and spatial coordinates. Soil variables as organic matter and Phosphorus, which were higher in fixed dunes, showed a clear relation with vegetation communities. In fixed dunes there were more species and more decomposition processes. Sodium and pH decreased from embryo to fixed dunes, maybe due to reduction of the influence of marine aerosol. Although sand grain is expected to decline towards land, we did no find such reduction maybe due to the small distance between embryo and fixed dune communities in the most of the studied dunes. In the study area in Cantabrian and Basque (CB) sector sand was finer maybe because of different origin material, which was limestone. Variation explained by variables (soil, climate, space) was higher from embryo to fixed dunes and it presented higher values for habitat specialist species.

Climate was the main driver of community composition. Specialists are well adapted to the habitats they grow in and they have a narrow tolerance range. Then they reflect better the environmental changes than generalists, which have a wider tolerance range and can grow in more habitats.

Integration

Overall results show an environmental gradient from sea to inland. This gradient is the most remarkable one, which affects the zonation of plant communities and the species composition. In embryo dunes, the community most exposed to wind and waves, there is a selection of well adapted species. In this community generalists are almost absent and specialists are the dominant ones. This specialization brings a homogenization of functional traits, which leads to low values of functional diversity in comparison with other vegetation types. This trait selection takes place in different genera and families.

The species selection with their traits is present along the studied coast. However, some particular species in some sites, specially in the borders of the study area, resulted in a significant relation between taxonomic diversity and the biogeographical variable. This relation did not appear for functional and phylogenetic diversity, which were homogeneous.

Mobile dunes are transition communities between embryo and fixed dunes. They have more species richness and higher values of functional and phylogenetic diversity. In mobile dunes *Ammophila arenaria* subsp. *australis* is the most dominant species, whose attributes are reflected in the community values as in plant height. This community was the most variable one along the study area. In France the presence of *Ammophila* was from little up to completely absent in one site. In the remaining sites *Ammophila* was found in patches.

Fixed dunes are located more inland and as a consequence the effect of wind and waves is lower. Then, there are more generalist species from ruderal environments, which are built behind the coastal dunes. These could be car parks or promenades next to sea. As this community is more sheltered more species can grow, which results in higher values of species richness. This increase in species richness is followed by an increase in functional diversity. Phylogenetic diversity is lower than in embryo dunes, although an index more related to richness showed higher values of phylogenetic diversity. Moreover there is an increase in the genera and species inside the most abundant families such as *Poaceae* and *Asteraceae*.

These changes in fixed dunes in the ecological gradient result in changes along the coast. The species composition is divided in two main groups. First, western biogeograhical sectors, North Galicia and Asturias and Galicia and North Portugal and second, eastern biogeographical sectors, Cantabrian and Basque and Aquitaine-Landes. This division is also present in functional and phylogenetic diversity, although in some cases genera of the same family, or even species of the same genus, were replace from one site to other one. For example the replacement of *Helichrysum stoechas* by *Helichrysum picardii.* This change could be based on the climatic transition along the study area.

The eastern area with Cantabria and France showed lower temperatures and higher precipitation during the year. In the western area, Galicia, temperatures were milder and summers were drier. This allow the growth of Mediterranean species. As there are more Mediterranean species, there would be a change in taxonomic and functional diversity. Soil variables showed that texture was constant among sites, which agrees with the short distance from sea, hundreds of meters inland, of the communities. This location would not lead to a significant decrease of grain size more inland. However, there was finer sand in Cantabrian sites, which could be related to limestone source in contrast to granitic source in Galicia.

Furthermore, results showed an increase of species richness with sampling area. This increase was followed by functional and phylogenetic diversity increase. The slope of this increase was stepper in fixed dunes than in embryo dunes, which agrees with the increase in species richness in the ecological gradient. Related to the increase in the diversity components, there was a dominant pattern of dune specialist species. This is in accordance with the low presence of generalists in embryo dunes and the low cover in the remaining communities.

To sum up, we can conclude that environmental conditions at local level are the most important ones regarding the species distribution in coastal dunes. In communities nearer to sea environmental conditions are more selective due to the action of wind and waves. This situation leads to a more homogeneous vegetation in embryo dunes along all the study area and a higher differentiation in fixed dunes. This phenomenon applies to species composition, followed by functional and phylogenetic diversity. The biogeographical differentiation could be led by climatic transitions between regions with an Atlantic influence in the East and more Mediterranean influence in the West.

Brief conclusions

1. Taxonomic, functional and phylogenetic patterns across the sea-inland gradient are not the same, phylogenetic diversity decrease while the other two components increase. This patterns could be explained by environmental filtering in embryo dunes and competition between species in fixed dunes.

2. Despite species composition changes there were no changes in taxonomic, functional and phylogenetic diversity between biogeographical sectors. This agrees with the idea of a unique biogeographical Subprovince, which coincides with the limits of the study area.

3. The ecological sea-inland gradient has a greater influence in species composition patterns than the biogeographical gradient, distance along the coast. Then, the influence of waves and wind in embryo dunes and its harsh conditions compared to the more protected ones in fixed dunes plays a major role in community composition.

4. In embryo dunes distance along the coast did not explain beta functional and phylogenetic diversity, while in fixed dunes it explained the three diversity components. The environmental filtering could select some specialized species which are common to studied sites, while in fixed dunes there would be a greater species differentiation.

5. The higher values of z-values for species-area relationship in fixed dunes for taxonomic diversity is followed by functional and phylogenetic diversity. More protected vegetation types allow the growth of more species, and more species in this case means more functional and phylogenetic diversity.

6. Generalist species are almost no present at smaller scales and specialists drive the community composition trends. At the scale of 100 m^2 there was a correlation between generalists and specialists, so the bigger the area the more generalists found.

7. Soil parameters present different trends along the sea-inland gradient. Phosphorous and organic matter increased while sodium and pH decreased. Soil texture was homogeneous for the three vegeation types and finer in Cantabrian and Basque biogeographical sector.

8. Climate explained better species composition patterns than spatial coordinates or soil parameters for the vegetation types. The explained variation was higher in fixed dunes and for specialist species, which means that specialist reflect better the environmental changes than generalists.

Appendix A

Data appendix

The data of this chapter are part of chapter 3, which were published on a separated paper of Data in Brief.

Table A.1: PERMANOVA results for community assemblage at scales of plot, location and sector for each dune habitat. df = degrees of freedom, MS = mean squares, ns = no significant. VC = Variance Component. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Habitat		df	MS	Pseudo-F		VC
Embryo	Sector = Se	3	5901.8	0.96	ns	0
	Local = Lo(Se)	8	6128.9	3.91	***	562.9
	Plot = Pl(Lo(Se))	36	1565.7	2.23	***	431.7
	Residual	48	702.2			702.2
	Total	95				
Mobile	Sector = Se	3	12958	2.23	**	297.9
	Local = Lo(Se)	8	5808.9	3.791	***	534.6
	Plot = Pl(Lo(Se))	36	1532.3	2.069	***	395.8
	Residual	48	740.7			740.7
	Total	95				
Fixed	Sector = Se	3	42095	3.69	***	1279.1
	Local = Lo(Se)	8	11396	6.24	***	1196.1
	Plot = Pl(Lo(Se))	36	1827.1	3.38	***	643.7
	Residual	48	539.8			539.8
	Total	95				

Table A.2: PERMANOVA results for Taxonomic Diversity (Shannon Index and Species richness), Phylogenetic Diversity (NRI and NTI) and Functional Diversity (RaoQ and CWM). df = degrees of freedom, MS = mean squares, ns = no significant. VC = Variance Component. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Taxonomic Diversity		df	Shannon				Richness			
			MS	Pseudo-F		VC	MS	Pseudo-F		VC
Embryo	Sector = Se	3	0.252	0.169	ns	0	12.372	0.486	ns	0
	Location = Lo(Se)	8	1.49	5.15	***	0.1	25.469	3.818	**	1.903
	Plot = Pl(Lo(Se))	36	0.29	16.078	ns	0.055	6.67	1.699	*	1.372
	Residual	48	0.18			0.18	3.927			3.927
	Total	95								
Mobile	Sector = Se	3	1.301	2.1	ns	0.028	21.361	0.616	ns	0
	Location = Lo(Se)	8	0.619	2.469	*	0.046	34.688	4.078	**	2.818
	Plot = Pl(Lo(Se))	36	0.251	1.641	ns	0.049	8.507	2.49	**	2.545
	Residual	48	0.153			0.153	3.417			3.417
	Total	95								
Fixed	Sector = Se	3	1.254	4.102	ns	0.038	99.038	2.82	ns	2.664
	Location = Lo(Se)	8	0.306	0.988	ns	0	35.115	3.518	**	3.142
	Plot = Pl(Lo(Se))	36	0.309	2.818	***	0.027	9.983	2.183	**	2.705
	Residual	48	0.11			0.184	4.573			4.573
	Total	95								

Phylogenetic Diversity		df	NRI				NTI			
			MS	Pseudo-F		VC	MS	Pseudo-F		VC
Embryo	Sector = Se	3	0.54	0.901	ns	0	2.532	1.255	ns	0.021
	Location = Lo(Se)	8	0.599	1.911	ns	0.034	2.018	3.59	**	0.182
	Plot = Pl(Lo(Se))	36	0.313	2.776	**	0.1	0.562	2.52	**	0.169
	Residual	48	0.113			0.113	0.223			0.223
	Total	95								
Mobile	Sector = Se	3	0.18	0.443	ns	0	0.985	0.656	ns	0
	Location = Lo(Se)	8	0.406	2.056	ns	0.018	1.501	1.645	ns	0.06
	Plot = Pl(Lo(Se))	36	0.198	1.246	ns	0.02	0.912	1.847	*	0.209
	Residual	48	0.159			0.159	0.494			0.494
	Total	95								
Fixed	Sector = Se	3	2.506	2.413	ns	0.061	0.527	0.473	ns	0
	Location = Lo(Se)	8	1.038	1.456	ns	0.041	1.113	1.313	ns	0.031
	Plot = Pl(Lo(Se))	36	0.713	2.892	**	0.233	0.848	2.184	**	0.23
	Residual	48	0.247			0.247	0.388			0.388
	Total	95								

Functional Diversity		df	RaoQ				CWM			
			MS	Pseudo-F		VC	MS	Pseudo-F		VC
Embryo	Sector = Se	3	0.008	0.06	ns	0	874.5	0.675	ns	0
	Location = Lo(Se)	8	0.133	5.387	***	0.009	1295.1	4.909	***	114.6
	Plot = Pl(Lo(Se))	36	0.025	1.703	*	0.005	263.8	2.771	***	84.3
	Residual	48	0.014			0.014	95.2			95.2
	Total	95								
Mobile	Sector = Se	3	0.101	2.289	ns	0.002	2674.4	0.687	ns	0
	Location = Lo(Se)	8	0.044	2.428	*	0.003	3891.8	4.946	***	346.6
	Plot = Pl(Lo(Se))	36	0.018	1.36	ns	0.002	786.9	1.142	ns	48.8
	Residual	48	0.013			0.013	689.2			689.2
	Total	95								
Fixed	Sector = Se	3	0.033	1.381	ns	0	11932	2.511	ns	299.1
	Location = Lo(Se)	8	0.024	1.393	ns	0.001	4752.6	6.232	***	498.2
	Plot = Pl(Lo(Se))	36	0.017	2.858	***	0.006	762.5	0.99	ns	0
	Residual	48	0.006			0.006	770.1			766.9
	Total	95								

List of species sampled. First name is what was used in the study, between parentheses the name accepted in 2020 when is different.

Aira praecox L.
Allium sphaerocephalon L.
Ammophila arenaria subsp. ***australis*** (Mabille) Hayek (***Ammophila arenaria*** subsp. ***arundinacea*** (Host) H. Lindb.)
Anagallis arvensis L.
Andryala integrifolia L.
Anthyllis vulneraria subsp. ***iberica*** (W. Becker) Cullen
Artemisia campestris subsp. ***maritima*** (DC.) Arcang.
Asperula cynanchica subsp. ***occidentalis*** (Rouy) Stace
Asterolinon linum-stellatum (L.) Duby
Astragalus baionensis Loisel.
Bellardia trixago (L.) All.
Briza minor L.
Bromus ferronii Mabille (***Bromus hordeaceus*** subsp. ***pseudothominei*** (P. M. Sm.) H. Scholz)
Bromus hordeaceus L. subsp. ***hordeaceus***
Cakile maritima subsp. ***integrifolia*** (Hornem.) Greuter & Burdet
Calystegia soldanella (L.) Roem. & Schult.
Carex arenaria L.
Carpobrotus edulis (L.) N. E. Br.
Catapodium marinum (L.) C. E. Hubb.
Catapodium rigidum (L.) C. E. Hubb. subsp. ***rigidum***
Centaurium chloodes (Brot.) Samp.
Centranthus calcitrapae (L.) Dufr. subsp. ***calcitrapae***
Cerastium diffusum Pers. subsp. ***diffusum***
Cerastium glomeratum Thuill.
Cerastium pumilum Curtis
Cistus salviifolius L.
Clematis vitalba L.
Coincya monensis (L.) Greuter & Burdet (***Coincya monensis*** (L.) Greuter & Burdet subsp. ***monensis***)
Corynephorus canescens (L.) P. Beauv.
Crepis capillaris (L.) Wallr.
Crithmum maritimum L.
Crucianella maritima L.
Cuscuta campestris Yunck.
Cutandia maritima (L.) Benth.
Cynodon dactylon (L.) Pers.
Cyperus capitatus Vand.
Daucus carota L. (***Daucus carota*** L. subsp. ***carota***)
Dianthus hyssopifolius subsp. ***gallicus*** (Pers.) M. Laínz & Muñoz Garm.

Echium vulgare L. (***Echium vulgare*** L. subsp. ***vulgare***)
Elytrigia juncea subsp. ***boreoatlantica*** (Simonet & Guin.) Hyl.
Erica cinerea L.
Erigeron bilbaoanus (J. Rémy) Cabrera
Erigeron sumatrensis Retz.
Erodium cicutarium (L.) L'Hér.
Eryngium maritimum L.
Euphorbia paralias L.
Euphorbia peplis L.
Euphorbia polygonifolia L.
Euphorbia portlandica L.
Euphorbia terracina L.
Festuca juncifolia Chaub.
Festuca arenaria Osbeck
Festuca vasconcensis (Markgr.-Dann.) Auquier & Kerguélen
Galium arenarium Loisel.
Helichrysum italicum subsp. ***picardii*** (Boiss. & Reut.) Franco
Helichrysum stoechas (L.) Moench subsp. ***stoechas***
Herniaria ciliolata subsp. ***robusta*** Chaudhri
Hieracium eriophorum St.-Amans
Hypochaeris radicata L.
Iberis procumbens Lange (***Iberis procumbens*** Lange subsp. ***procumbens***)
Jasione maritima (Duby) Merino
Jasione montana L.
Koeleria albescens DC.
Lagurus ovatus L. (***Lagurus ovatus*** L. subsp. ***ovatus***)
Leontodon taraxacoides (Vill.) Mérat (***Leontodon saxatilis*** Lam.)
Linaria arenaria DC.
Linaria polygalifolia Hoffmanns. & Link
Linaria supina subsp. ***maritima*** (Lam. & DC.) M. Laínz
Linaria thymifolia (Vahl) DC.
Lolium perenne L.
Lotus corniculatus L. subsp. ***corniculatus***
Malcolmia littorea (L.) W. T. Aiton
Matthiola sinuata (L.) W. T. Aiton
Medicago italica (Mill.) Fiori (***Medicago tornata*** subsp. ***helix*** (Willd.) Ooststr. & Reichg.)
Medicago littoralis Loisel.
Medicago marina L.
Mibora minima (L.) Desv.
Minuartia hybrida (Vill.) Schischk.(***Minuartia hybrida*** (Vill.) Schischk. subsp. ***hybrida***)
Oenothera affinis Cambess.
Oenothera x fallax Renner
Ononis diffusa Ten.
Ononis natrix subsp. ***ramosissima*** (Desf.) Batt.
Ononis reclinata L. (***Ononis reclinata*** L. subsp. ***reclinata***)

Ononis spinosa L. subsp. ***maritima***
Orobanche minor Sm.
Otanthus maritimus (L.) Hoffmanns. & Link (***Achillea maritima*** (L.) Ehrend. & Y. P. Guo)
Pancratium maritimum L.
Parapholis strigosa (Dumort.) C. E. Hubb.
Parietaria judaica L. (***Parietaria judaica*** L. subsp. ***judaica***)
Phleum arenarium L. (***Phleum arenarium*** L. subsp. ***arenarium***
Plantago arenaria Waldst. & Kit. (***Plantago arenaria*** Waldst. & Kit. subsp. ***arenaria***)
Plantago coronopus L.
Plantago lanceolata L.
Polycarpon tetraphyllum (L.) L.
Polygala vulgaris L. (***Polygala vulgaris*** L. subsp. ***vulgaris***)
Polygonum maritimum L.
Pseudorlaya pumila (L.) Grande
Reichardia gaditana (Willk.) Samp.
Rubia peregrina L. (***Rubia peregrina*** L. subsp. ***peregrina***)
Rumex bucephalophorus subsp. ***hispanicus*** (Steinh.) Rech. f.
Salsola kali L.
Scabiosa atropurpurea L. (***Sixalix atropurpurea*** (L.) Greuter & Burdet)
Scolymus hispanicus L.
Scrophularia canina L. (***Scrophularia canina*** subsp. ***frutescens*** (L.) O. Bolòs & Vigo)
Sedum acre L.
Sedum album L.
Seseli tortuosum L.
Silene portensis L. (***Silene portensis*** L. subsp. ***portensis***)
Silene scabriflora subsp. ***gallaecica*** Talavera
Silene uniflora subsp. ***thorei*** (Dufour) Jalas
Solidago virgaurea subsp. ***macrorrhiza*** (Lange) Nyman
Sonchus oleraceus L.
Stenotaphrum secundatum (Walter) Kuntze
Thesium humifusum DC.
Thymus praecox subsp. ***ligusticus*** (Briq.) Paiva & Salgueiro
Verbascum pulverulentum Vill.
Vulpia alopecuros (Schousb.) Dumort.
Vulpia fasciculata (Forssk.) R. M. Fritsch
Vulpia membranacea (L.) Dumort.
Xolantha guttata (L.) Raf. (***Tuberaria guttata*** (L.) Fourr.)

Table A.3: Table of species present in 10 m^2 of embryo dunes expressed as percentage of cover

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Aira praecox	0	0	0	0	0	0	0	0	0	0	0	0
Allium sphaerocephalon	0	0	0	0	0	0	0	0	0	0	0	0
Ammophila arenaria subsp. *australis*	2	0	1	3	1	0	0	1	7	0	5	1
Anagallis arvensis	0	0	0	0	0	0	0	0	0	0	0	0
Andryala integrifolia	0	0	0	0	0	0	0	0	0	0	0	0
Anthyllis vulneraria subsp. *iberica*	0	0	0	0	0	0	0	0	0	0	0	0
Artemisia campestris subsp. *maritima*	1	0	0	0	0	0	0	0	0	0	0	0
Asperula cynanchica	0	0	0	0	0	0	0	0	0	0	0	0
Astragalus baionensis	0	0	0	0	0	0	0	0	0	0	0	5
Bellardia trixago	0	0	0	0	0	0	0	0	0	0	0	0
Briza minor	0	0	0	0	0	0	0	0	0	0	0	0
Bromus ferronii	0	0	0	0	0	0	0	0	0	0	0	0
Bromus hordeaceus	0	0	0	0	0	0	0	0	0	0	0	0
Cakile maritima subsp. *integrifolia*	1	0	0	0	0	0	0	0	3	0	0	0
Calystegia soldanella	6	3	2	2	3	2	2	9	2	5	5	4
Carex arenaria	0	0	0	0	0	0	1	0	0	0	0	0
Catapodium marinum	0	0	0	0	0	0	0	0	0	0	0	0
Catapodium rigidum subsp. *rigidum*	0	0	0	0	0	0	0	0	0	0	0	0
Centaurium chloodes	0	0	0	0	0	0	0	0	0	0	0	0
Centranthus calcitrapae subsp. *calcitrapae*	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium diffusum subsp. *diffusum*	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium glomeratum	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium pumilum	0	0	0	0	0	0	0	0	0	0	0	0
Cistus salviifolius	0	0	0	0	0	0	0	0	0	0	0	0
Coincya monensis	0	0	0	0	0	0	0	0	0	0	0	0
Corynephorus canescens	0	0	0	0	0	0	0	0	0	0	0	0
Crepis capillaris	0	0	0	0	0	0	0	0	0	0	0	0
Crithmum maritimum	0	0	0	0	0	0	0	0	0	0	0	0
Crucianella maritima	0	0	0	10	1	1	0	0	0	0	0	0
Cuscuta campestris	0	0	0	0	0	0	0	0	0	0	0	0

Continued on next page

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Cutandia maritima	0	0	0	0	0	0	1	0	0	0	0	0
Cynodon dactylon	1	0	0	0	0	0	0	0	0	0	0	0
Cyperus capitatus	0	0	0	0	0	0	0	0	0	0	0	0
Daucus carota	0	0	0	0	0	0	0	0	0	0	0	0
Dianthus hyssopifolius subsp. *gallicus*	0	0	0	0	0	0	0	0	0	0	0	0
Echium vulgare	0	0	0	0	0	0	0	0	0	0	0	0
Elytrigia juncea subsp. *boreoatlantica*	39	21	12	3	44	20	3	44	13	18	10	34
Erica cinerea	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron bilbaoanus	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron sumatrensis	0	0	0	0	0	0	0	0	0	0	0	0
Erodium cicutarium	0	0	0	0	0	0	0	0	0	0	0	0
Eryngium maritimum	1	1	2	3	0	3	2	1	1	14	5	2
Euphorbia paralias	1	1	1	3	2	4	4	0	1	0	5	2
Euphorbia polygonifolia	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia portlandica	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia terracina	0	0	0	0	0	0	0	0	0	0	0	0
Festuca juncifolia	0	0	0	0	0	0	0	0	0	0	0	1
Festuca arenaria	0	0	0	0	0	0	0	0	0	0	0	0
Festuca vasconcensis	0	0	0	0	0	0	0	0	0	0	0	0
Galium arenarium	0	0	0	0	0	0	0	0	0	0	3	6
Helichrysum italicum subsp. *picardii*	0	0	0	0	0	0	0	0	0	0	0	0
Helichrysum stoechas subsp. *stoechas*	0	0	0	0	0	0	0	0	0	0	0	0
Herniaria ciliolata subsp. *robusta*	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium eriophorum	0	0	0	0	0	0	0	0	0	0	1	2
Hypochaeris radicata	0	0	0	0	0	1	1	0	0	0	0	0
Iberis procumbens	0	0	0	0	0	0	0	0	0	0	0	0
Jasione maritima	0	0	0	0	0	0	0	0	0	0	0	0
Jasione montana	0	0	0	0	0	0	0	0	0	0	0	0
Koeleria albescens	0	0	0	0	0	0	0	0	0	0	0	0
Lagurus ovatus	0	0	0	0	0	0	0	0	0	0	0	0
Leontodon taraxacoides	1	0	0	0	1	1	0	0	0	0	0	0
Linaria polygalifolia	0	0	0	0	0	0	0	0	0	0	0	0
Linaria supina subsp. *maritima*	0	0	0	0	0	0	0	0	0	0	0	0
Linaria thymifolia	0	0	0	0	0	0	0	0	0	0	0	0

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Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Lolium perenne	0	0	0	0	0	0	0	0	0	0	0	0
Lotus corniculatus subsp. *corniculatus*	0	0	0	0	0	0	0	0	0	0	0	0
Malcolmia littorea	0	0	0	0	0	1	0	0	0	0	0	0
Matthiola sinuata	0	0	0	0	0	0	0	0	0	0	0	0
Medicago italica	0	0	0	0	0	0	0	0	0	0	0	0
Medicago littoralis	0	0	0	3	0	0	0	0	0	0	0	0
Medicago marina	0	0	0	0	0	0	0	0	0	0	0	0
Mibora minima	0	0	0	0	0	0	0	0	0	0	0	0
Oenothera x fallax	0	0	0	0	0	0	0	0	0	0	0	0
Ononis diffusa	0	0	0	0	0	0	0	0	0	0	0	0
Ononis natrix subsp. *ramosissima*	0	0	0	0	0	0	0	0	0	0	0	0
Ononis reclinata	0	0	0	0	0	0	0	0	0	0	0	0
Ononis spinosa subsp. *maritima*	0	0	0	0	0	0	0	0	0	0	0	0
Orobanche minor	0	0	0	0	0	0	0	0	0	0	0	0
Otanthus maritimus	0	1	0	0	0	0	0	0	0	0	0	0
Pancratium maritimum	1	0	1	2	0	2	0	0	0	0	0	0
Parapholis strigosa	0	0	0	0	0	0	0	0	0	0	0	0
Parietaria judaica	0	0	0	0	0	0	0	0	0	0	0	0
Phleum arenarium	0	0	0	0	0	0	0	0	0	0	0	0
Plantago arenaria	0	0	0	0	0	0	0	0	0	0	0	0
Plantago coronopus	0	0	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	1	0	0	0	0	0
Polycarpon tetraphyllum	0	0	0	0	0	0	0	0	0	0	0	0
Polygala vulgaris	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum maritimum	0	0	0	0	0	0	0	0	0	0	0	0
Pseudorlaya pumila	0	0	0	0	0	0	0	0	0	0	0	0
Rubia peregrina	0	0	0	0	0	0	0	0	0	0	0	0
Rumex bucephalophorus subsp. *hispanicus*	0	0	0	0	0	0	0	0	0	0	0	0
Salsola kali	0	0	0	0	0	0	0	0	0	0	0	0
Scabiosa atropurpurea	0	0	0	0	0	0	0	0	0	0	0	0
Scolymus hispanicus	0	0	0	0	0	0	0	0	0	0	0	0
Scrophularia canina	0	0	0	0	0	0	0	0	0	0	0	0
Sedum acre	0	0	0	0	0	0	0	0	0	0	0	0
Sedum album	0	0	0	0	0	0	0	0	0	0	0	0
Seseli tortuosum	0	0	0	0	0	0	0	0	0	0	0	0

Continued on next page

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Silene portensis	0	0	0	0	0	0	0	0	0	0	0	0
Silene scabriflora subsp. *gallaecica*	0	0	0	0	0	0	0	0	0	0	0	0
Silene uniflora subsp. *thorei*	0	0	0	0	0	0	0	0	0	0	0	1
Solidago virgaurea subsp. *macrorrhiza*	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus oleraceus	0	0	0	0	0	0	0	0	0	0	0	0
Thesium humifusum	0	0	0	0	0	0	0	0	0	0	0	0
Thymus praecox subsp. *ligusticus*	0	0	0	0	0	0	0	0	0	0	0	0
Vulpia alopecuros	0	0	0	0	0	0	0	0	0	0	0	0
Vulpia fasciculata	0	0	0	0	0	0	0	0	0	0	0	0
Vulpia membranacea	0	0	0	0	0	0	0	0	0	0	0	0
Xolantha guttata	0	0	0	0	0	0	0	0	0	0	0	0

Table A.4: Table of species present in 10 m^2 of mobile dunes expressed as percentage of cover

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Aira praecox	0	0	0	0	0	0	0	0	0	0	0	0
Allium sphaerocephalon	0	0	0	0	0	0	0	0	0	0	0	0
Ammophila arenaria subsp. *australis*	18	29	29	39	18	12	56	22	53	1	36	22
Anagallis arvensis	0	0	0	0	0	0	0	0	0	0	0	0
Andryala integrifolia	0	0	0	0	0	0	0	0	0	0	0	0
Anthyllis vulneraria subsp. *iberica*	0	0	0	0	0	0	0	0	0	0	0	0
Artemisia campestris subsp. *maritima*	4	0	1	0	0	0	0	0	0	0	0	0
Asperula cynanchica	0	0	0	0	0	0	0	0	0	0	0	0
Astragalus baionensis	0	0	0	0	0	0	0	0	0	0	0	0
Bellardia trixago	0	0	0	0	0	0	0	0	0	0	0	0
Briza minor	0	0	0	0	0	0	0	0	0	0	0	0
Bromus ferronii	0	0	0	0	0	0	0	0	0	0	0	0
Bromus hordeaceus	0	0	0	0	0	0	0	0	0	0	0	0
Cakile maritima subsp. *integrifolia*	2	0	0	0	0	0	0	0	0	0	0	0
Calystegia soldanella	4	3	1	4	2	1	3	8	2	3	4	4
Carex arenaria	0	0	0	0	0	0	0	1	0	5	0	1
Catapodium marinum	0	0	0	0	0	0	0	0	0	0	0	0
Catapodium rigidum subsp. *rigidum*	0	0	0	0	0	0	0	0	0	0	0	0
Centaurium chloodes	0	0	0	0	0	0	0	0	0	0	0	0
Centranthus calcitrapae subsp. *calcitrapae*	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium diffusum subsp. *diffusum*	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium glomeratum	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium pumilum	0	0	0	0	0	0	0	0	0	0	0	0
Cistus salviifolius	0	0	0	0	0	0	0	0	0	0	0	0
Coincya monensis	0	0	0	0	0	0	0	0	0	0	0	0
Corynephorus canescens	0	0	0	0	1	0	0	0	0	0	0	0
Crepis capillaris	0	0	0	0	0	0	0	0	1	0	0	0
Crithmum maritimum	0	0	0	0	0	0	0	0	0	0	0	0
Crucianella maritima	0	10	1	3	14	1	0	3	0	0	0	0
Cuscuta campestris	0	0	0	0	0	0	0	0	0	0	0	0

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Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Cutandia maritima	0	0	0	0	0	0	0	0	0	0	0	0
Cynodon dactylon	0	0	0	0	0	0	0	0	0	0	0	0
Cyperus capitatus	0	0	0	0	0	0	0	0	0	0	0	0
Daucus carota	0	0	0	0	0	0	0	0	0	0	0	0
Dianthus hyssopifolius subsp. *gallicus*	0	0	0	0	0	0	0	0	0	0	0	0
Echium vulgare	0	0	0	0	0	0	0	0	0	0	0	0
Elytrigia juncea subsp. *boreoatlantica*	8	0	1	0	1	3	0	0	0	20	0	6
Erica cinerea	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron bilbaoanus	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron sumatrensis	0	0	0	0	0	0	0	0	0	0	0	0
Erodium cicutarium	0	0	0	0	0	0	0	0	0	0	0	0
Eryngium maritimum	1	1	3	2	1	2	0	2	2	6	4	3
Euphorbia paralias	2	2	0	2	2	2	0	0	2	2	1	3
Euphorbia polygonifolia	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia portlandica	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia terracina	0	0	0	0	0	0	0	0	0	0	0	0
Festuca juncifolia	0	0	0	0	1	0	0	0	1	1	0	2
Festuca arenaria	0	0	0	0	2	0	0	0	0	0	0	0
Festuca vasconcensis	0	0	0	0	0	0	0	0	0	0	0	0
Galium arenarium	0	0	0	0	0	0	0	0	0	4	3	13
Helichrysum italicum subsp. *picardii*	0	0	0	0	1	0	0	0	0	0	0	0
Helichrysum stoechas subsp. *stoechas*	0	0	0	0	0	0	1	0	0	0	1	0
Herniaria ciliolata subsp. *robusta*	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium eriophorum	0	0	0	0	0	0	0	0	0	6	1	2
Hypochaeris radicata	0	1	0	0	0	0	0	0	0	3	0	0
Iberis procumbens	0	0	0	0	0	0	0	0	0	0	0	0
Jasione maritima	0	0	0	0	0	0	0	0	0	0	0	0
Jasione montana	0	0	0	0	0	0	0	0	0	0	0	0
Koeleria albescens	0	0	0	0	0	0	1	0	1	0	0	0
Lagurus ovatus	0	0	0	0	0	1	3	0	0	0	0	0
Leontodon taraxacoides	1	1	0	0	1	0	1	0	1	1	0	0
Linaria polygalifolia	0	0	0	0	0	0	0	0	0	0	0	0
Linaria supina subsp. *maritima*	0	0	0	0	0	0	0	0	0	0	0	0
Linaria thymifolia	0	0	0	0	0	0	0	0	0	1	0	0

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Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Lolium perenne	0	0	0	0	0	0	0	0	0	0	0	0
Lotus corniculatus subsp. *corniculatus*	0	0	0	0	0	0	0	0	0	0	0	2
Malcolmia littorea	0	0	0	0	1	2	0	0	0	0	0	0
Matthiola sinuata	1	0	0	0	0	0	0	0	0	0	0	0
Medicago italica	0	0	0	0	0	0	0	0	0	0	0	0
Medicago littoralis	1	0	0	0	0	0	0	0	0	0	0	0
Medicago marina	0	0	0	0	2	0	0	0	0	0	0	0
Mibora minima	0	0	0	0	0	0	0	0	0	0	0	0
Oenothera x fallax	0	0	0	0	0	0	0	0	0	0	0	0
Ononis diffusa	0	0	0	0	0	0	0	0	0	0	0	0
Ononis natrix subsp. *ramosissima*	0	0	0	0	0	0	0	0	0	0	0	0
Ononis reclinata	0	0	0	0	0	0	0	0	0	0	0	0
Ononis spinosa subsp. *maritima*	0	0	0	0	0	0	0	0	0	6	0	2
Orobanche minor	0	0	0	0	0	0	0	0	0	0	0	0
Otanthus maritimus	0	1	0	0	0	0	0	0	0	1	0	0
Pancratium maritimum	2	3	1	1	0	1	0	0	0	1	0	0
Parapholis strigosa	0	0	0	0	0	0	0	0	0	0	0	0
Parietaria judaica	0	0	0	0	0	0	0	0	0	0	0	0
Phleum arenarium	0	0	0	0	0	0	0	0	0	0	0	0
Plantago arenaria	0	0	0	0	0	0	0	0	0	0	0	0
Plantago coronopus	0	0	0	0	1	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0	0	0
Polycarpon tetraphyllum	0	0	0	0	0	0	0	0	0	0	0	0
Polygala vulgaris	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum maritimum	0	0	0	0	0	0	0	0	0	0	0	0
Pseudorlaya pumila	0	0	0	0	0	0	0	0	0	0	0	0
Rubia peregrina	0	0	0	0	0	0	0	0	0	0	0	0
Rumex bucephalophorus subsp. *hispanicus*	0	0	0	0	0	0	2	0	0	0	0	0
Salsola kali	0	0	0	0	0	0	0	0	0	0	0	0
Scabiosa atropurpurea	0	0	0	0	0	0	0	0	0	0	0	0
Scolymus hispanicus	0	0	0	0	0	0	0	0	0	0	0	0
Scrophularia canina	0	0	0	0	0	0	0	0	0	0	0	0
Sedum acre	0	0	0	0	0	0	0	0	0	0	0	0
Sedum album	0	0	0	0	0	0	0	0	0	0	0	0
Seseli tortuosum	1	0	0	0	0	0	0	0	0	0	0	0

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Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Silene portensis	0	0	0	0	0	0	0	0	0	0	0	0
Silene scabriflora subsp. *gallaecica*	0	0	0	0	0	0	0	0	0	0	0	0
Silene uniflora subsp. *thorei*	0	0	0	0	0	0	0	0	0	0	0	0
Solidago virgaurea subsp. *macrorrhiza*	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus oleraceus	0	0	0	0	0	0	0	0	0	0	0	0
Thesium humifusum	0	0	0	0	0	0	0	0	0	1	0	0
Thymus praecox subsp. *ligusticus*	0	0	0	0	0	0	0	0	0	0	0	0
Vulpia alopecuros	6	0	0	0	0	0	0	0	0	0	0	0
Vulpia fasciculata	0	0	0	0	0	0	0	0	0	0	0	0
Vulpia membranacea	0	0	0	0	0	0	0	0	0	0	0	0
Xolantha guttata	0	0	0	0	0	0	0	0	0	0	0	0

Table A.5: Table of species present in 10 m^2 of fixed dunes expressed as percentage of cover

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Aira praecox	0	0	0	0	0	0	0	0	0	0	0	1
Allium sphaerocephalon	0	0	0	0	0	0	0	0	0	0	0	0
Ammophila arenaria subsp. *australis*	1	2	1	0	1	2	0	0	0	0	2	0
Anagallis arvensis	1	0	0	0	0	0	0	0	0	0	0	0
Andryala integrifolia	2	0	0	0	1	0	0	0	0	0	0	0
Anthyllis vulneraria subsp. *iberica*	1	0	2	0	0	0	0	0	0	0	0	0
Artemisia campestris subsp. *maritima*	8	0	12	0	3	0	0	0	0	1	0	0
Asperula cynanchica	0	0	0	0	0	0	0	0	0	0	0	0
Astragalus baionensis	0	0	0	0	0	0	0	0	0	0	0	0
Bellardia trixago	0	0	0	0	0	0	0	0	0	0	0	0
Briza minor	0	0	0	0	0	0	0	0	0	0	0	0
Bromus ferronii	0	0	0	0	0	0	0	0	0	0	0	0
Bromus hordeaceus	0	0	0	0	0	0	0	0	0	1	0	0
Cakile maritima subsp. *integrifolia*	0	0	0	0	0	0	0	0	0	0	0	0
Calystegia soldanella	0	1	0	0	0	1	2	0	1	1	1	0
Carex arenaria	0	0	0	0	0	0	2	1	1	10	0	1
Catapodium marinum	0	0	0	0	0	0	0	0	0	0	0	0
Catapodium rigidum subsp. *rigidum*	0	0	0	0	0	0	0	0	0	1	0	0
Centaurium chloodes	1	0	0	0	0	0	0	0	0	0	0	0
Centranthus calcitrapae subsp. *calcitrapae*	0	0	1	0	0	0	0	0	0	0	0	0
Cerastium diffusum subsp. *diffusum*	0	0	0	0	0	0	0	1	0	1	0	0
Cerastium glomeratum	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium pumilum	0	0	0	0	0	0	0	0	0	0	0	0
Cistus salviifolius	0	0	0	0	0	0	0	0	0	0	0	1
Coincya monensis	0	0	0	0	0	0	0	0	0	0	0	0
Corynephorus canescens	1	0	0	0	3	1	0	0	0	0	0	5
Crepis capillaris	0	0	0	0	0	0	0	0	0	0	0	0
Crithmum maritimum	0	0	0	0	0	0	0	0	0	0	0	0
Crucianella maritima	4	10	1	5	3	8	0	8	0	0	0	0
Cuscuta campestris	0	0	0	0	0	0	0	0	0	0	0	0
Cutandia maritima	0	0	0	0	0	0	0	1	0	1	0	0

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Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Cynodon dactylon	0	0	0	0	0	0	0	0	0	1	0	0
Cyperus capitatus	0	0	0	0	0	0	0	0	0	0	0	0
Daucus carota	0	0	0	0	0	0	0	0	0	0	0	0
Dianthus hyssopifolius subsp. *gallicus*	0	0	0	0	0	0	0	0	0	7	0	0
Echium vulgare	0	0	0	0	0	0	0	0	0	0	0	0
Elytrigia juncea subsp. *boreoatlantica*	0	0	0	0	0	1	0	0	0	0	1	0
Erica cinerea	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron bilbaoanus	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron sumatrensis	0	0	0	0	0	0	0	0	0	0	0	0
Erodium cicutarium	0	0	0	0	0	0	0	0	0	0	0	0
Eryngium maritimum	0	1	0	0	1	2	1	1	0	1	0	0
Euphorbia paralias	0	0	0	0	1	1	0	0	0	0	0	0
Euphorbia polygonifolia	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia portlandica	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia terracina	0	0	0	1	0	0	0	0	0	0	0	0
Festuca juncifolia	0	0	0	0	0	1	0	0	2	0	20	0
Festuca arenaria	0	0	0	0	0	0	0	0	0	0	0	0
Festuca vasconcensis	0	0	0	0	0	0	0	0	0	1	5	2
Galium arenarium	0	0	0	0	0	0	0	0	0	1	1	0
Helichrysum italicum subsp. *picardii*	10	3	11	7	22	18	0	0	0	0	0	0
Helichrysum stoechas subsp. *stoechas*	0	0	0	0	0	0	1	30	18	31	36	25
Herniaria ciliolata subsp. *robusta*	0	0	0	0	0	0	1	2	0	0	0	0
Hieracium eriophorum	0	0	0	0	0	0	0	0	0	0	1	1
Hypochaeris radicata	0	0	0	0	0	0	0	0	0	1	0	0
Iberis procumbens	0	2	1	0	0	0	0	0	0	0	0	0
Jasione maritima	3	7	1	0	0	0	0	0	0	0	0	0
Jasione montana	0	0	0	0	0	0	0	0	0	0	0	1
Koeleria albescens	0	0	0	0	0	0	1	16	1	0	0	0
Lagurus ovatus	0	0	0	0	1	0	1	0	1	0	0	0
Leontodon taraxacoides	0	0	0	0	0	0	0	1	0	0	1	1
Linaria polygalifolia	0	0	0	0	0	0	0	0	0	0	0	0
Linaria supina subsp. *maritima*	0	0	0	0	0	0	0	0	0	0	0	0
Linaria thymifolia	0	0	0	0	0	0	0	0	0	0	0	0
Lolium perenne	0	0	0	0	0	0	0	0	0	0	0	0

Continued on next page

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Lotus corniculatus subsp. *corniculatus*	0	0	0	0	0	0	0	0	0	0	2	1
Malcolmia littorea	2	0	0	0	1	2	0	0	0	0	0	0
Matthiola sinuata	0	0	0	0	0	0	0	0	0	0	0	0
Medicago italica	0	0	0	0	0	0	1	0	0	0	0	0
Medicago littoralis	1	0	0	1	0	0	0	0	0	1	0	0
Medicago marina	0	0	0	0	0	0	0	0	0	0	0	0
Mibora minima	0	2	2	3	0	0	0	0	0	0	0	0
Oenothera x fallax	0	0	0	0	0	0	0	0	0	0	0	0
Ononis diffusa	0	0	0	0	0	0	0	0	0	0	0	0
Ononis natrix subsp. *ramosissima*	0	0	0	0	0	0	0	0	16	0	0	0
Ononis reclinata	0	0	0	0	0	0	0	0	0	0	0	0
Ononis spinosa subsp. *maritima*	0	0	0	0	0	0	0	0	0	0	1	0
Orobanche minor	0	0	0	0	0	0	0	0	0	0	0	0
Otanthus maritimus	0	0	0	0	0	0	0	0	0	0	0	0
Pancratium maritimum	2	1	1	1	0	2	0	0	0	2	0	0
Parapholis strigosa	0	0	0	0	0	0	0	0	0	0	0	0
Parietaria judaica	0	0	0	0	0	0	0	0	0	0	0	0
Phleum arenarium	0	0	0	0	0	0	0	0	1	2	1	0
Plantago arenaria	0	0	0	0	0	0	0	0	0	0	0	0
Plantago coronopus	0	0	0	0	0	0	1	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	2	0	0	0	0	0
Polycarpon tetraphyllum	0	0	0	0	0	0	0	1	0	0	0	0
Polygala vulgaris	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum maritimum	0	0	0	0	0	0	0	0	0	0	0	0
Pseudorlaya pumila	0	0	0	1	0	0	0	0	0	0	0	0
Rubia peregrina	0	0	0	0	0	0	0	0	0	0	0	0
Rumex bucephalophorus subsp. *hispanicus*	1	0	1	1	1	0	3	0	3	0	0	1
Salsola kali	0	0	0	0	0	0	0	0	0	0	0	0
Scabiosa atropurpurea	1	0	0	0	0	0	0	0	0	0	0	0
Scolymus hispanicus	0	0	0	0	0	0	0	0	0	0	0	0
Scrophularia canina	0	5	0	0	0	0	0	0	0	0	0	0
Sedum acre	0	1	3	1	0	0	0	0	0	0	0	0
Sedum album	5	1	3	3	3	3	0	0	2	1	0	0
Seseli tortuosum	1	0	0	0	0	0	0	0	0	0	0	0
Silene portensis	0	0	0	0	0	0	0	0	0	0	0	0

Continued on next page

Species	La Lanzada	As Furnas	Carnota	Barrañán	San Xurxo	Valdoviño	Oyambre	Liencres	Noja	Tarnos	Casernes	Messanges
Silene scabriflora subsp. *gallaecica*	0	2	0	0	0	0	0	0	0	0	0	0
Silene uniflora subsp. *thorei*	0	0	0	0	0	0	0	0	0	0	0	0
Solidago virgaurea subsp. *macrorrhiza*	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus oleraceus	0	0	0	0	0	0	0	0	0	0	0	0
Thesium humifusum	0	0	0	0	0	0	0	0	0	0	0	0
Thymus praecox subsp. *ligusticus*	0	0	0	0	0	0	0	0	0	5	0	2
Vulpia alopecuros	22	0	0	0	0	0	0	0	0	0	0	0
Vulpia fasciculata	0	0	0	1	0	0	1	1	0	0	1	0
Vulpia membranacea	1	0	1	0	1	1	2	0	0	4	0	0
Xolantha guttata	0	0	0	0	0	0	0	0	0	0	0	1

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Publications

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Changes in plant diversity patterns along dune zonation in south Atlantic European coasts

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A R T I C L E I N F O

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A B S T R A C T

Coastal dunes are valuable and threatened habitats. They present a sea-land environmental gradient and different vegetation types are found in a very short space: embryo, mobile and fixed dunes. The aims were to study changes in taxonomic diversity and species richness along the ecological gradient and if they were followed by changes in functional or phylogenetic diversity. This study took place along a 750 km coastal stretch, belonging to four biogeographic sectors, in the southwest of France and northwest of Spain. Twelve locations were selected, where coastal dune habitats were explored. In each location and for each vegetation type four 10 × 10 m plots were sampled. In each plot abundances of vascular plants were recorded. Taxonomic, functional and phylogenetic diversity at the alpha level were measured. NMDS analysis, PERMANOVA and linear mixed effects models were used to explore differences between biogeographic sectors and habitats for species composition and each derived taxonomic, functional and phylogenetic index. We found different species composition in each vegetation type: in embryo dunes it was constant along biogeographic sectors, while it changed in mobile and fixed dunes. Taxonomic diversity, functional diversity and phylogenetic diversity indices did not show changes at biogeographic sector level despite the species difference in mobile and fixed dunes. An increase in taxonomic diversity from embryo to fixed dunes was also found, followed by an increase in functional divergence. Phylogenetic diversity decreased from embryo to fixed dunes. Therefore, in habitats more exposed to sea, wind and waves, as embryo dunes, environmental filtering selects some traits of non-related species. On more sheltered habitats such as fixed dunes, biotic interactions like competitive exclusion leads to a divergence in functionality. In conclusion, coastal dunes showed different biodiversity patterns along a sea-land gradient; despite a difference in species, functional and phylogenetic diversity remained without changes along a geographical gradient.

1. Introduction

Coastal dunes are present all over the world under a wide range of climatic and geologic conditions (Maun, 2009). They make up 20% of the world's coastlines and they are transitional ecosystems between land and sea (Van Der Maarel, 2003). Moreover, these azonal ecosystems present unique characteristics with a highly specialized fauna and flora (McLachlan and Brown, 2006). With regard to humans, coastal dunes offer protection against winds and tides as well as being used as places for recreation and landscape aesthetics (Ciccarelli, 2014; Del Vecchio et al., 2017; Martínez et al., 2017). However, coastal dune systems are also particularly fragile environments and threatened by several potential dangers (Carboni et al., 2009; Drius et al., 2013), for example, loss of habitat by urbanization (Malavasi et al., 2018). About conservation status of coastal habitats, more than 75% of the habitats reported had an unfavourable assessment (EEA, 2015). By the mid-1980s Europe had already lost almost three-quarters of its coastal sand dunes and heaths because of land-use change, infrastructure development, pollution and urban expansion (The European Commission, 2015). Due to increasing urbanization about the 70% of the dune systems in European coasts has disappeared (Brown and McLachlan, 2002), and as a consequence of the loss of vegetation, dunes and beaches are more prone to wind and water erosion (Gómez-Pina et al., 2002).

Looking at environmental changes conditions, coastal dunes are characterized by a sea-to-inland gradient responsible for the coexistence of different plant communities (Wiedemann and Pickart, 2004; Frederiksen et al., 2006). Coastal dunes present environmental heterogeneity and spatial variability along the sea inland transect gradient which result in a high ecological diversity (Acosta et al., 2009). Biotic

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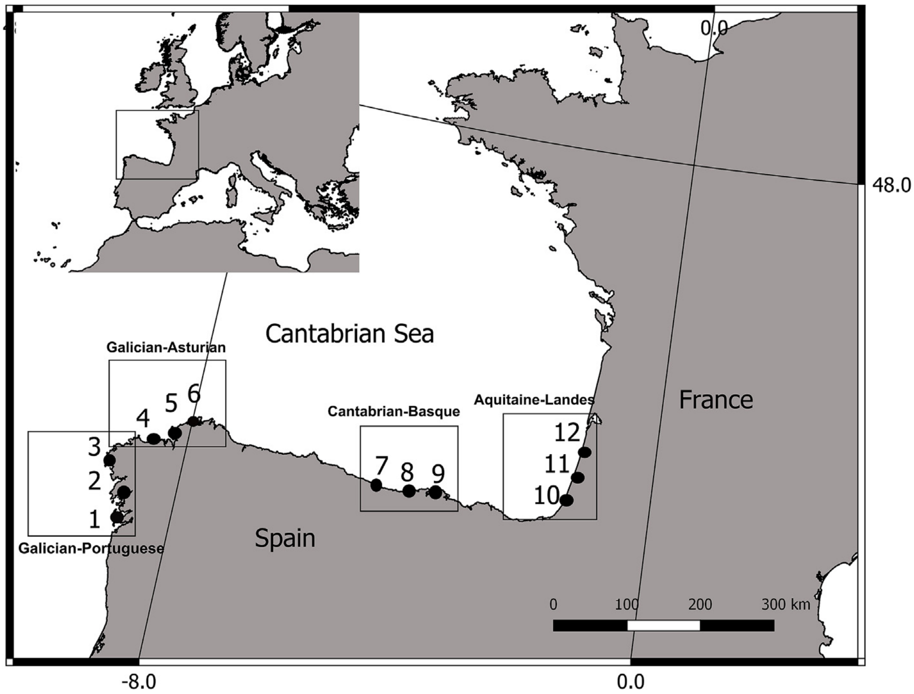

Fig. 1. Study area. Twelve locations sampled from Galicia (Spain) to France grouped by biogeographic sectors. Galician-Portuguese: 1. La Lanzada 2. As Furnas 3. Carnota Galician-Asturian: 4. Barrañán 5. San Xurxo 6. Valdoviño Cantabrian-Basque: 7. Oyambre 8. Liencres 9. Noja Aquitaine-Landes 10. Tarnos 11. Casernes 12. Messanges.

and abiotic factors interact, thus leading to a characteristic zonation that represents the succession from embryo to fixed dunes (Ruocco et al., 2014). As a consequence, environmental conditions of coastal plant communities are very specific and the position of plant communities in the sequence tends to be fixed (Carboni et al., 2009; Bazzichetto et al., 2016). In this sense, we speak about vegetation zones with different plant communities: beach, embryo, mobile, fixed or grey dunes. Upper beach and embryo dune vegetation are closer to the sea and more exposed to salt spray, winds and sand burial, while mobile dunes and especially fixed dunes (also named backed dunes or grey dunes in North Atlantic areas) become progressively less exposed to these harsh environmental constraints (Carboni et al., 2009; Fenu et al., 2012; Ciccarelli, 2014; Ruocco et al., 2014). These vegetation zones also represented are typical for three different habitats recognized in the Habitat Directive (92/43/CEE Directive): 2110 Embryonic shifting dunes, 2120 Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes) and 2130 *Fixed coastal dunes with herbaceous vegetation (grey dunes). The last one is classified as a Priority Conservation habitat (The European Commission, 2013).

Biodiversity is a multifaceted concept which goes further than simply counting the number of species present in a given place (Villéger et al., 2013). Variation can be assessed at different levels: alpha refers to local diversity, beta to spatial differentiation and gamma to regional diversity (Cardoso et al., 2014). Alpha diversity takes into account how diversified the species are within a site, while beta diversity focuses on how diversified the sites are in species composition within a region (Legendre and De Cáceres, 2013). Patterns and processes determining species diversity change across spatial scales (Turner, 1989; Whittaker, 1998; Ricklefs, 2005). Three magnitudes could be taken into account: global scale, regional scale and local scale (Isermann, 2010). In our study we considered local and regional scales.

This study measures taxonomic diversity, functional diversity and phylogenetic diversity at alpha level as phylogenetic and functional components add valuable information to species richness (Ahrendsen et al., 2016). Using taxonomic, functional and phylogenetic diversity together allows us to test predictions about the different effects of competition and environmental filtering on phylogenetic and functional diversity (Arnan et al., 2016). Indeed, phylogenetic diversity and functional diversity are less often quantified, but these forgotten dimensions may be equally or more important (Swenson, 2011). Also, alpha diversity is useful to identify the mechanism underlying local-scale co-occurrence (Swenson et al., 2012). Functional and phylogenetic components of diversity are related to environment and biotic interactions. Environmental filtering which filters species on the basis of their tolerance to abiotic conditions (Weiher and Keddy, 1995). Competitive interactions among species playing a role in their long-term coexistence (Leibold, 1998).

In relation to phylogeny, phylogenetic clustering takes place when closely related species tend to co-occur as a consequence of environmental filtering. In contrast, under competitive exclusion, closely related species compete leading to phylogenetic overdispersion (Cavender-Bares et al., 2006). Species from the same lineage are more likely to compete, leading to trait differentiation or exclusion in the same lineage. This could result in patterns of high trait dispersion and low phylogenetic dispersion (Prinzing et al., 2008). Finally, neutral processes, which lead to randomly assembled communities, give less importance to the niches assuming that all taxa are demographically and ecologically equivalent and that dispersal limitation plays a role in structuring of communities (Hubbell, 2001).

This study took place along a 750 km coastal stretch in northern Spain and southwestern France. Abundances of vascular plants were recorded. We expected a change in species composition along the ecological gradient from sea-to-inland. Then, we investigated if this change was followed by changes in phylogenetic and functional diversity or if species richness was affected.

2. Material and methods

2.1. Study area

The present study was conducted along 750 km of the Atlantic coast of north Spain and southwest France (Fig. 1). From a biogeographic point of view the study area is included in the Atlantic European Province, Cantabroatlantic subprovince. The French area belongs to the Aquitaine-Landes (AL) biogeographic sector. The Spanish area includes three different biogeographic sectors: Cantabrian-Basque (CB), Galician-Asturian (GA) and Galician-Portuguese (GP) (Rivas-Martínez, 1982, 2007). A detailed bioclimatic characterization of each sector is presented onTable 3 in Torca et al., in press.

Concerning the main vegetation types, different plant formations were identified along the sea-inland gradient and most of them are changing because different human and environmental pressures. Specifically the following syntaxa are present: on embryo dunes (Habitat Directive code 2110), to date, *Euphorbio paraliae-Agropyretum junceiformis* is the only association present with no important changes along the study area (Rivas-Martínez et al., 2011). Embryo dunes are exposed to wind and waves, which makes it a very stressful system. This dune vegetation is characterized by anual specialized species and some perennial ones creating some grasslands dominated by *Elytrigia juncea* (Gracia et al., 2009). On mobile dunes (Habitat Directive code 2120), the associations *Otantho maritimi-Ammophiletum australis* in Spain and *Sileno thorei-Ammophiletum arenariae* and *Galio arenarii-Hieracietum eriophori* in France have been mentioned (Demartini, 2016). Mobile dunes begin to accumulate sand by wind deposition due to the stoloniferous stems of plant species and because the wind speed is lower than in embryo dunes. The dominant species is *Ammophila arenaria* (Gracia, 2009). On fixed dunes (Habitat Directive code 2130), two different orders are recognized in the study area: *Crucianelletalia maritimae* including the *Helichrysion picardii* alliance and *Artemisio lloydii-Koelerietalia albescentis* order including *Euphorbio portlandicae-Helichrysion stoechadis* alliance (Mucina et al., 2016. Marcenò et al., 2018). On fixed dunes wind intensity decreases and allows soil stability and accumulation of organic matter. This habitat is colonized by herbaceous species and little shrubs (Gracia and Muñoz, 2009).

2.2. Sampling

Vegetation sampling was performed on a set of representative tracts of the Atlantic coasts distributed along the four biogeographic sectors and in which the three main dune vegetation types were present (Fig. 1). Deeply disturbed locations were avoided. Sites ranged from 180 to 7000 m of longitude and from 20 to 500 m of width. In France there was a continuum of beach and dunes along the coast.

In each location, and for each different coastal dune vegetation type, four 100 m^2 (10 × 10 m) plots were sampled. In every plot, two 10 m^2 subplots were set in the corners following Dengler (2009). In each 10 m^2 subplot the total list of the vascular plant species encountered was registered. Mosses and lichens were listed but not taken into account for this study. The extended Braun-Blanquet scale (Westhoff and Van Der Maarel, 1978) was used, in which value r = rare + = sparse, 1 = < 4%, 2 is divided in 2 m = 5%, 2a = 5–12% and 2b = 12–25%, 3 = 25–49%, 4 = 50–74%, 5 = 75–100%. Sampling took place during the months of June and July of 2014 and 2015.

2.3. Traits

Ten different traits were taken into account (Table 1). Traits were selected under the hypothesis of a change from Atlantic to Mediterranean conditions in both the ecological and biogegraphical gradients. This include the adaptations to more Mediterranean conditions.

For the LHS (leaf-height-seed) framework (Westoby, 1998) specific leaf area (SLA), plant height and seed mass of the most abundant species were measured. Height was directly recorded in the field, while SLA and seed mass were measured *a posteriori* in the laboratory following Pérez-Harguindeguy et al. (2013). For less abundant species and other traits data were collected from online databases (see bibliographic references in Torca et al., in press) and regional and national floras (Castroviejo, 1986; Aizpuru et al., 2007). Value of the traits measured or gathered from databases are given on Table S1 in Torca et al., in press.

2.4. Diversity indices

Taxonomic, functional and phylogenetic diversity were studied at the alpha level. For taxonomic diversity we calculated species richness (number of species per subplot) and Shannon's Index, which is a common index to measure species diversity in many habitats, included coastal dunes (Carboni et al., 2009; Honrado et al., 2009; Malavasi et al., 2018).

In order to measure phylogenetic diversity two indices were calculated: NRI (Net Relatedness Index) and NTI (Nearest Taxon Index). NRI and NTI values were multiplied by −1 so positive values indicate phylogenetic clustering while negative values overdispersion. To measure NRI and NTI a phylogenetic tree was constructed using the species list and the *Brrranching* package of R (R Core Team, 2015). To calculate the random distributions the null model used was *taxa.label* from the R-package *Picante* (Kembel et al., 2010). In this model names are randomly swapped 999 times across the phylogenetic tree, holding species richness of plots and species turnover among them constant (Brunbjerg et al., 2015). This null model has been frequently used in studies of alpha dispersion (Swenson et al., 2012).

Other studies have measured functional traits in coastal dunes taking into account the relationship between phylogenetic and functional diversity of plant communities (Ricotta et al., 2012; Carboni et al., 2013; Brunbjerg et al., 2014; Marcantonio et al., 2014). In our study two indices were calculated to estimate functional diversity: CWM (Community Weighted Mean) (Garnier et al., 2004) and RaoQ (Pavoine and Dolédec, 2005; Leps et al., 2006).

2.5. Data analysis

First, in order to explore if species composition changes along the ecological gradient, NMDS was performed using package *Vegan* (Oksanen et al., 2016). Braun-Blanquet cover values were back-transformed to percentages according to Van Der Maarel (1979) in the following way: r = 0.02, + = 0.1, 1 = 2.5, 2 m = 5, 2a = 8.75, 2b = 18.75, 3 = 37.5, 4 = 62.5 and 5 = 87.5. Then, square-root transformation was applied in order to balance the highest and lowest

Table 1
List of traits analysed with decomposition in categories for discrete ones.

Trait	Description	Data Type	Attribute
Life form	Raunkiaer life form	Nominal	Chamaephyte, Geophyte, Hemicryptophyte, Phanerophyte, Therophyte
Geographical distribution	Geographical range	Nominal	Eurosiberian, Mediterranean, Non-European, Pluriregional
Flowering onset	Beginning of flowering	Quantitative	1–12
Flowering span	Flowering duration	Quantitative	1–12
Pollination	Pollination vector	Nominal	Animals, Selfing, Wind
Fruit type	Fruit type	Nominal	Capsule, Caryopsis, Follicle, Legume, Nut, Schizocarp, Siliqua
Seed dispersal	Seed dispersal vector	Nominal	Anemochorous, Autochorous, Barochorous, Hydrochorous, Without Adaptations, Zoochorous
SLA	Specific Leaf Area (Leaf area/dry weight)	Quantitative	cm^2/g
Plant height	Plant height at maturity	Quantitative	m
Seed mass	Weight of dried dispersules	Quantitative	g

cover values. The dissimilarity matrix was constructed using Bray-Curtis distance.

The differences in floristic composition of biogeographic sectors were tested by nested permutational multivariate analyses of variance (PERMANOVA) (Anderson, 2001) using PERMANOVA + for Primer software (Clarke and Gorley, 2006). This was also applied to calculated diversity indices: Shannon, species richness, NRI, NTI, RaoQ and CWM. Then, to detect characteristic or indicator species for each coastal dune vegetation type, IndVal, Indicator Value (Dufrene and Legendre, 1997), was calculated. The IndVal coefficient combines the relative abundance of the species and its relative frequency of occurrence in a group of replicates. For IndVal analyses *indicspecies* R package (Cáceres and Legendre, 2009) was used. Species were sorted by IndVal value.

For functional diversity a detailed analysis was conducted and every trait was analysed separately for CWM and RaoQ indices. Moreover, for CWM, discrete traits were decomposed in their different categories establishing the percentage of contribution of each category to the CWM. Then, for an overall estimation of the functional diversity an integrated value of RaoQ was calculated using *SYNCSA R* package (Debastiani and Pillar, 2012). Gower distance was used in order to include both continuous and discrete traits. Gower's formula can be applied to a mixture of different measurement scales and it allows the inclusion of ordinal variables (Ricotta and Burrascano, 2008).

In the case of phylogenetic diversity NRI and NTI indices were applied using *Picante* R package (Kembel et al., 2010). NRI and NTI were calculated for each site in order to detect any pattern along the biogeographic gradient. Then, the number of plots with significant patterns of clustering or overdispersion were calculated and compared.

In order to make comparisons for each index, linear mixed effects models were applied as they are useful when taking into account the nested design of plots and locations (Zuur et al., 2009). Coastal dune vegetation type was considered as a fixed factor while 10 m^2 subplots nested in 100 m^2 plots and these nested in locations were set for the random factor. To construct the models, in particular for the categorical decomposition of traits in CWM, analysis was performed only when at least 75% of the plots had a CWM percentage or RaoQ value higher than zero. Also, square root or log transformation were applied to response variables in some cases to meet model assumptions. Models were calculated with *lme4* R package (Bates et al., 2015). Finally, to test differences between coastal dune vegetation types, pairwise comparisons were conducted using R package *lmeans* (Lenth, 2016).

3. Results

Overall, 110 vascular plant taxa were identified in this study. The most widely represented family was *Poaceae* with a total of 25 taxa, followed by *Asteraceae* with 13 and *Fabaceae* with 10. Most genera presented one or two taxa with the exception of *Euphorbia* and *Ononis* with 4 taxa and *Cerastium*, *Festuca*, *Linaria*, *Medicago*, *Plantago*, *Silene* and *Vulpia* with 3 taxa each. Herbaceous species dominated with 40 therophytes, 39 hemicryptophytes and 6 geophytes. Woody species had almost no presence in embryo and mobile dune, while they appeared more frequently in fixed dunes. No ferns were found in this study.

3.1. Changes in species composition

The ordination analysis (NMDS) (Fig. 2) showed a clear difference in floristic composition of the three vegetation types of coastal dune zonation (NMDS1), with fixed dunes that also differed according with their biogeographic characteristics (NMDS2). For fixed dunes two groups were differentiated, eastern (AL, CB) and western (GA, GP) biogeographic sectors.

PERMANOVA results (Table 1 in Torca et al., in press) showed no differences in species composition of the embryo dunes between different biogeographic regions. But differences in species composition in mobile dunes and are most visible in fixed dunes. There was 1 indicator species in embryo dunes, 4 in mobile dunes and 34 in fixed dunes (Table 2 in Torca et al., in press).

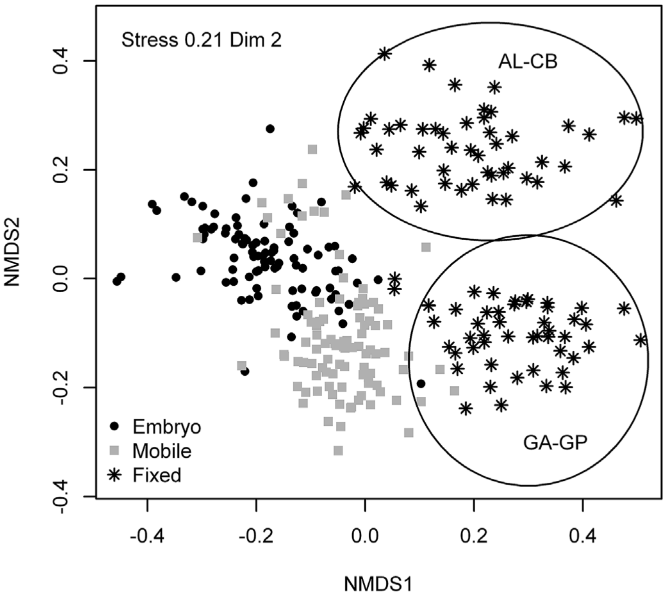

Fig. 2. NMDS ordination of species composition using square root of abundances and Bray-Curtis distance for embryo, mobile and fixed dunes. Circles show eastern and western biogeographic sector plots grouping in fixed dunes. AL = Aquitaine-Landes, CB = Cantabrian-Basque, GA = Galician-Asturian and GP = Galician-Portuguese.

3.2. Overall taxonomic, functional and phylogenetic diversities

The PERMANOVA results showed no differences at biogeographic sector level for any dune habitat in any diversity index (Table 3 in Torca et al., in press). Data about taxonomic diversity measured by the Shannon index showed higher values on fixed dunes than in mobile and embryo dunes. Overall functional diversity calculated with RaoQ presented the same trend from embryo to fixed dunes. There were differences between fixed dunes and embryo and mobile dunes for the Shannon Index and RaoQ. Relative to phylogenetic diversity calculated with NRI and NTI, there were differences between fixed and embryo dunes and between fixed and mobile dunes (Fig. 3). In summary, in all cases there were not differences between embryo and mobile dunes, while there were between fixed dunes and the other two vegetation types. From ecological point of view, it means that a higher values on taxonomic diversity for fixed dunes is followed by higher values of trait divergence; so the more diversity in species, the more diverse in traits.

Analysis of the percentage of significant phylogenetic patterns showed higher values of overdispersion in mobile dunes and the lowest values in fixed dunes. NTI differences between embryo and mobile dunes and fixed dunes were significant (post hoc $p < 0.02$ mobile dune; $p < 0.03$ embryo dune). For NRI, there were significant differences between mobile and fixed dunes ($p < 0.018$) (Fig. 4). This means that species would tend to be more phylogenetically related in fixed dunes than in embryo and mobile dunes.

3.3. Functional diversity in detail

CWM of discrete traits were split into their categories. Only trait categories used in the model comparison analysis were reported (Tables 2 and 3).

With reference to plant biotype, percentage of contribution of chamaephytes to CWM was higher in fixe dunes, while geophytes decreased along the sea-inland gradient. Therophytes showed higher values in fixed dunes. Looking at the geographical origin, in proportion,

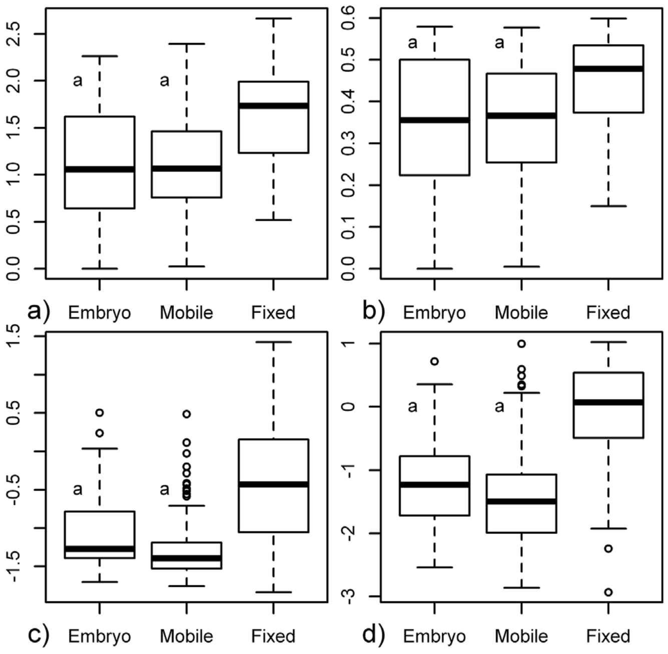

Fig. 3. Distribution of Shannon index (a), RaoQ (b), NRI (c) and NTI (d) for the three dune vegetation types. Letters indicate no significant differences ($p < 0.05$) after pairwise comparison of the factor dune vegetation types in the linear mixed models.

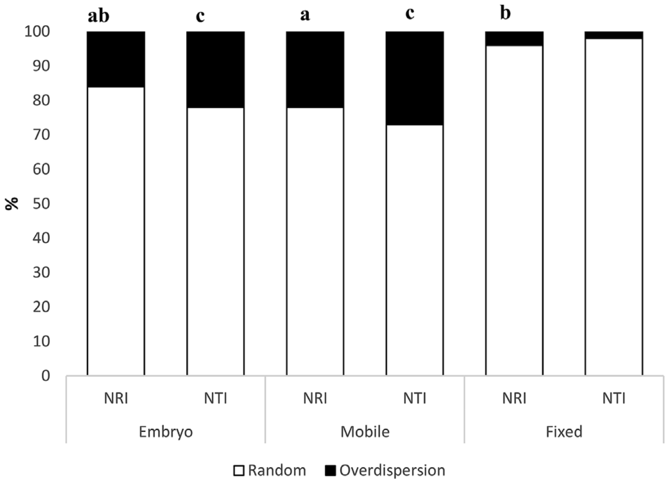

Fig. 4. Percentages of significantly phylogenetic patterns (overdispersion, random) for NRI and NTI for each dune vegetation type. Letters indicate no significant differences ($p < 0.05$) for overdispersion.

the most abundant species in embryo dunes were species of Eurosiberian origin, while in mobile and fixed dunes were Mediterranean species most abundant. Pollination by wind presented lower values from embryo to fixed dunes and in contrast zoophily showed higher values on fixed dunes. Regarding fruit type, the most characteristic types were caryopsis in embryo and mobile dunes and nuts in fixed dunes. Then, dispersion by wind was more frequent in fixed dunes, followed by embryo dunes. Dispersion without adaptations was higher on mobile dunes. Flowering onset was about late April and early May in the three vegetation types, and flowering span lasted for about four months. Relating LHS scheme, SLA was almost equal in embryo and mobile dune vegetation types and showed a higher value in fixed dunes. The highest growth height was recorded in mobile dunes. Seed mass remained almost the same in embryo and mobile dunes and it increased significant in fixed dunes.

Table 2
Mean values of functional diversity for CWM for each dune vegetation type. Discrete traits decomposed in categories (sd = standard deviation). Letters indicate no significant differences ($p < 0.05$) after pairwise comparison of the factor dune vegetation type in the linear mixed models.

	Embryo		Mobile		Fixed	
	Mean	sd	Mean	sd	Mean	sd
Life form chamephyte	0.14	0.18^a	0.14	0.19^a	0.58	0.24
Life form geophyte	0.71	0.28	0.21	0.20	0.06	0.08
Life form terophyte	0.04	0.11^a	0.00	0.01	0.15	0.15^a
Mediterranean	0.08	0.11	0.69	0.29^a	0.65	0.20^a
Pluriregional	0.23	0.20^a	0.17	0.15^a	0.21	0.15^a
Eurosiberian	0.54	0.33	0.14	0.23^a	0.14	0.18^a
Flowering onset	5.01	0.38^a	4.97	0.29^a	4.93	0.44^a
Flowering span	4.17	0.69	3.67	0.66	4.60	0.63
Pollination wind	0.56	0.29^a	0.37	0.26^a	0.27	0.18
Pollination zoophily	0.44	0.29^a	0.63	0.26^a	0.72	0.19
Fruit nut	0.04	0.09^a	0.07	0.12^a	0.46	0.23
Fruit capsule	0.26	0.22	0.19	0.20^a	0.18	0.19^a
Fruit caryopsis	0.55	0.29^a	0.61	0.27^a	0.21	0.15
Dispersal anemochorous	0.28	0.23^a	0.25	0.20^a	0.53	0.22
Dispersal without adaptations	0.08	0.16^a	0.60	0.28	0.20	0.20^a
Dispersal zoochorous	0.03	0.08^a	0.04	0.08^a	0.24	0.17
SLA	104.21	16.83^a	101.73	32.57^a	133.97	38.42
Plant height	0.44	0.10	0.71	0.24	0.31	0.06
Seed mass	0.05	0.06^a	0.05	0.09^a	0.08	0.09

Table 3
Mean values of functional diversity for RaoQ for each dune vegetation type. Discrete traits decomposed in categories (sd = standard deviation). Letters indicate no significant differences ($p < 0.05$) after pairwise comparison of the factor dune vegetation type in the linear mixed models.

	Embryo		Mobile		Fixed	
	Mean	sd	Mean	sd	Mean	sd
Life form	0.08	0.06^a	0.08	0.04^a	0.10	0.03
Geographical range	0.08	0.05^a	0.08	0.04^a	0.10	0.04
Flowering onset	0.23	0.29^a	0.16	0.17^a	0.79	1.01
Flowering span	0.25	0.42^a	0.28	0.36^a	0.51	0.33
Pollination	0.11	0.05^a	0.11	0.04^a	0.11	0.05^a
Fruit type	0.06	0.03^a	0.06	0.03^a	0.08	0.03
Dispersal	0.08	0.04^a	0.08	0.04^a	0.08	0.02^a
Plant height	1.11	1.12^a	3.20	1.73	0.65	0.73^a
Seed mass	0.26	0.51^a	0.33	0.68^{ab}	0.43	0.73^b
SLA	0.14	0.20^a	0.27	0.24^a	0.73	0.42

Analysis of traits using RaoQ (taking into account that RaoQ measures the dispersion or divergence of the trait while CWM measures the mean) showed higher values on fixed dunes in life form, geographical range, fruit type, flowering span and onset, seed mass and SLA. The rest of traits presented a mixed pattern with higher values on embryo and mobile dunes or equal values between dune vegetation types.

4. Discussion

We expected differences in species composition across dune vegetation types in correspondence with strong environmental gradient from sea-to-inland (Van Der Maarel, 2003). Indeed, different phytosociological associations have been traditionally recognized (Feola et al., 2011; Frederiksen et al., 2006). Then we proposed that this change could be followed by a change in functional and phylogenetic diversity

(Carboni et al., 2009; Malavasi et al., 2018). In this study we analysed the patterns of taxonomic, functional and phylogenetic diversity and if there were related in some way in the coastal dune ecosystems of northwest Spain and southwest France.

4.1. Exploration of changes in species composition

Species composition of dune vegetation types in embryo dunes presented one group, which matches with the unique phytosociological association described for the Cantabro Atlantic sector: *Euphorbio paraliae-Agropyretum junceiformis*. These communities are dominated by *Elytrigia juncea* subsp. *boreoatlantica, Calystegia soldanella* and *Eryngium maritimum,* species of broad coastal distribution in Europe (Kadereit and Westberg, 2007). Also, the habitat is exposed to stress, as it occurs in the case of embryo dunes, the more its vegetation is habitat-related and independent from the biogeographic region in which it is located (Wiedemann and Pickart, 2004; Feola et al., 2011; Mahdavi et al., 2017).

With regard to mobile dunes, our results confirm the differences between biogeographic sectors. This is in accordance with the two different associations accepted in the French sector for mobile dunes: *Sileno thorei-Ammophiletum arenariae* and *Galio arenarii-Hieracietum eriophori* (Demartini, 2016). These associations are characterized by species as *Silene uniflora* subsp. *thorei*, *Galium arenarium*, *Hieracium eriophorum* and *Linaria thymifolia* (Table 2 in Torca et al., in press), which are not present along the northern Atlantic coast of Spain. Along the other Iberian biogeographic sectors, the communities of mobile dunes were floristically and structurally very similar among them (Fig. 2) and were included in the *Otantho maritimi-Ammophiletum australis* association, well characterized by *Ammophila arenaria* subsp. *australis*. This characteristic species agrees with stated in Marceno et al. (2018)

On fixed dune vegetation two main groups were evident corresponding one to Galician-Portuguese and Galician-Asturian and the other to Cantabrian-Basque and Aquitaine-Landes biogeographic sectors (Fig. 2). This is in accordance with the two phytosociological alliances recognized: the *Helichrysion picardii* in the western areas and *Euphorbio portlandicae-Helichrysion stoechadis* in the eastern ones (Marcenò et al., 2018). Some indicator species, such as *Helichrysum stoechas subsp. maritimum*, *Koeleria albescens* or *Phleum arenarium,* were only present in eastern biogeographic sectors; while other species, such as *Andryala integrifolia, Helichrysum italicum* subsp. *picardii, Iberis procumbens* or *Mibora minima,* were only in western biogeographic sectors (Table 2 in Torca et al., in press). There were also some western endemic species as *Silene scabriflora* subsp. *gallaecica.*

The presence of a unique association in embryo dunes and the homogeneus composition along the coast in the study could be related to azonality. The vegetation of communities next to sea could be considered azonal; while in inner, more stable dunes species composition would be more related to local climatic conditions (Buffa et al., 2012). Indeed, Jiménez-Alfaro et al. (2015) found climatic variables to be more important in fixed dunes for the Iberian peninsula.

4.2. Taxonomic, functional and phylogenetic diversity overall

Coastal dunes show a sea-land gradient where environmental conditions change from more exposed to more sheltered ones (Carboni et al., 2011; Bazzichetto et al., 2016). Some studies have found a change (generally an increase) in species richness along this environmental gradient, with a peak at the intermediate position (Fenu et al., 2012), sometimes depending on the shoreline stability or accretion trend (Prisco et al., 2016). In our study we found that taxonomic diversity increased from embryo to fixed dunes. This agrees with the results found by Isermann (2005) and Acosta et al. (2009). Moreover, the number of specialist indicator species increased from 1 in embryo dunes to 34 in fixed dunes.

Overall functional diversity showed an increase along the sea-inland gradient through different coastal dune vegetation types as Ricotta et al. (2012) also reported. Embryo dunes present specific plant species well adapted to this extreme environment (Maun, 1994). In our study the most frequent species in embryo dunes were *Calystegia soldanella, Elytrigia juncea, Eryngium maritimum and Euphorbia paralias*. Carboni et al. (2016) found that vegetation types closer to the sea, such as embryo dunes, showed a higher proportion of specialist species and higher average specialization levels. They listed five most specialized species *(Chamaesyce peplis, Cutandia maritima, Eryngium maritimum, Polygonum maritimum* and *Salsola kali),* typical of beaches and dunes. Four of them were also present in our vegetation plots. Nevertheless, in dunes vegetation is formed by a reduced set of specialized species (Angiolini et al., 2018). This specialization is congruent with the lower trait divergence (low value of RaoQ) found in our embryo dunes, and environmental filtering is suggested to increase functional similarity among species site (Kembel and Hubbell, 2006). For fixed dunes, trait divergence was higher than in embryo dunes (Fig. 3). Competition for resources results in trait divergence and encourages coexistence between organisms in relation to limiting similarity (Pacala and Tilman, 1994). Moreover, trait divergence is assumed to originate from biotic filters and it is expected under low environmental stress (Conti et al., 2017), which would be the case for fixed dunes.

When looking at phylogenetic diversity, there was a general increase of values from embryo to fixed dunes, with fixed dunes being significantly different from the other two coastal dune vegetation types. Phylogenetic diversity presented decreasing overdispersion values from embryo to fixed dunes (Fig. 4). Embryo dunes showed a mean species/family ratio of close to 1 while in fixed dunes it was 1.64 (Table S2 in Torca et al., in press). Then, although fixed dunes have more absolute species diversity, this diversity tends to be clustered around main families. There are more species, but also more closely related, which would be in accordance with the lower overdispersed values of phylogenetic diversity, both NRI and NTI, and the lower percentage of significant overdispersed plots (Fig. 4).

Our results showed trait convergence and phylogenetic overdispersion on embryo dunes. When adaptations are evolutionary convergent environmental filtering could cause phylogenetic overdispersion (Webb, 2000; Webb et al., 2002). Distantly related species may be found in communities with similar environmental conditions due to evolutionary convergence of the traits (Ackerly et al., 2006; Davies, 2006). In our case the similar environmental conditions would be the strong winds and waves that communities next to sea are exposed to. For fixed dunes we found a pattern of trait divergence and phylogenetic less overdispersion. This agrees with Brunbjerg et al. (2012), who found in general a clustered phylogenetic community structure on stable dunes. Phylogenetic clustering and phenotypic overdispersion would take place when co-ocurring close relative species differ in one or more important traits (Kawano, 2002).

Dune ecosystems are harsh environments and the stressful conditions constrain the range of plant physiological responses as result of a process of environmental filtering (Meinzer, 2003). Only species with particular adaptations can survive in these ecosystems (Maun, 2009). This would apply to embryo dunes in particular as the most exposed habitat to wind and waves. Under the environmental filtering paradigm, environmental conditions at a site are assumed to drive the optimal trait values or within limits (Swenson et al., 2012). This species assemblage would lead to high phylogenetic diversity, while trait convergence is related to environmental filtering. Also at a local scale, when disturbance tolerance requires specific traits, the process of environmental filtering leads to convergent trait composition (Weiher and Keddy, 1995).

In fixed dunes we found the opposite pattern: higher trait divergence and more phylogenetic clustering. This could be explained by negative ecological interactions leading to the competitive exclusion of similar species or by past negative interactions responsible for trait divergence (Prinzing et al., 2008). Negative biotic interactions would result in co-occurring species that are dissimilar in traits relating to competition (Swenson et al., 2012). Competitive exclusion could lead to divergence of relevant traits (Bello et al., 2013; Carboni et al., 2013). Therefore, we found different plant communities, which could be the response to different ecological processes. This could be related to a hierarchical model of community assembly where species sequentially pass through historical, abiotic, and biotic filters to result in the local assemblage observed (Webb et al., 2002, 2008).

With reference to the diversity indices and biogeographic sectors, we found no differences at regional scale (Table 3 in Torca et al., in press), despite the species composition change between mobile and fixed dunes. This agrees with Mahdavi et al. (2017), who found changes in species pools and vegetation types in four different regions and functionally analogous species in coastal ecosystems including dune habitats.

4.3. Functional diversity

We found a change from Eurosiberian distribution range in embryo dunes to a Mediterranean in fixed dunes. The Eurosiberian distribution could be related to azonality, as this habitat presented an homogeneus species composition along the study area. Wind strategies (wind pollination) were higher in embryo dunes while animal strategies (animal pollination) characterized fixed dunes (Table 2). Mahdavi and Bergmeier (2016) reported entomophilous species to be found more frequently in fixed dunes. We found that the most abundant species in mobile dunes were taller than species in other coastal dune vegetation types. Phenological phases are prone to be related to local climate following mild temperatures and precipitations. In our study the onset of flowering was set about May extending during 3 or 4 months. There were not differences along the sea-inland gradient.

Height is an indirect characteristic of the ability to compete for light (Westoby et al., 2002). It was minimum in fixed dunes and maximum in mobile dunes, maybe due to the height of *Ammophila arenaria* subsp. *australis*, which is the tallest and most dominant species in mobile dunes. Taller plants compete more effectively for light (Cavender Bares et al., 2004)) and this would be the strategy of *Ammophila arenaria* subsp. *australis*. Smaller plants in embryo dunes could be explained since they are more resilient under high disturbance (Westoby, 1998). In embryo dunes taller plants such as *Elytrigia juncea* subsp. *boreoatlantica* coexisted with smaller ones such as *Calystegia soldanella* or *Eryngium maritimum*. This would be another case where smaller and taller species tend to coexist more frequently indicating differences in light acquisition strategies (de Bello et al., 2011). Seed mass could be used to represent the trade-off between the number and size of seeds produced (Moles and Westoby, 2006). We found lighter seeds in embryo dunes and heavier on fixed dunes. A reduced seed mass would have a positive effect on competitive ability and a negative effect on colonisation or dispersal ability (Kisdi and Geritz, 2003). Embryo dune species often have a strategy based on high capacity of long distance dispersal. SLA could be used to represent the leaf economics spectrum such as structural investment, long leaf life spans, and low photosynthetic rates (Wright et al., 2004). Also it is a good surrogate for the plant ability to use light efficiently (Westoby et al., 2002). We found the highest values of SLA in fixed dunes and the lowest in mobile dunes.

5. Conclusions

We found different species composition for each coastal dune vegetation types. In embryo dunes species assemblage was constant along biogeographic sectors, while it changed in mobile and fixed dunes. Taxonomic, functional and phylogenetic diversity indices did not show changes at biogeographic sector level despite the species change in mobile and fixed dunes. We also found an increase in taxonomic diversity from embryo to fixed dunes followed by an increase in functional divergence. In habitats more exposed to sea, wind and waves, such as embryo dunes, few species phylogenetically dispersed were selected by their traits leading to functional convergence. This could be due to environmental filtering. Some traits would be selected regardless of the family so that could explain the more phylogenetic overdispersion found. Fixed dunes, a more sheltered habitat, showed higher taxonomic diversity and trait divergence, which could be related to competitive exclusion of similar functional species. In conclusion, on the one hand coastal dunes showed different biodiversity patterns along a sea-land gradient at small scale, and on the other hand, despite a change in species, functional and phylogenetic diversity remained without changes at larger scale along a geographical gradient.

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Abbreviations

CWM	community weighted mean
FD	functional diversity
NMDS	non-metric multidimensional scaling
NRI	net relatedness index
NTI	nearest taxon index
PD	phylogenetic diversity
SLA	specific leaf area
TD	taxonomic diversity

References

Ackerly, D.D., Schwilk, D.W., Webb, C.O., 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology 87, S50–S61.

Acosta, A., Carranza, M.L., Izzi, C.F., 2009. Are there habitats that contribute best to plant species diversity in coastal dunes? Biodivers. Conserv. 18, 1087–1098. https://doi.org/10.1007/s10531-008-9454-9.

Ahrendsen, D.L., Aust, S.K., Roxanne Kellar, P., 2016. Biodiversity assessment using next-generation sequencing: comparison of phylogenetic and functional diversity between Nebraska grasslands. Plant Systemat. Evol. 302, 89–108. https://doi.org/10.1007/s00606-015-1246-6.

Aizpuru, I., Aseginolaza, C., Uribe-Echebarría, P.M., Urrutia, P., Zorrakin, I., 2007. Claves ilustradas de la flora del País Vasco. Servicio de publicaciones del Gobierno Vasco, Vitoria-Gasteiz 831pp.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Angiolini, C., Bonari, G., Landi, M., 2018. Focal plant species and soil factors in Mediterranean coastal dunes: an undisclosed liaison? Estuar. Coast Shelf Sci. 31, 248–258. Available on-line. https://doi.org/10.1016/j.ecss.2017.06.001.

Arnan, X., Cerdá, X., Retana, J., 2016. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40, 448–457. https://doi.org/10.1111/ecog.01938.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. ýJ. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01.

Bazzichetto, M., Malavasi, M., Acosta, A., Carranza, M., 2016. How does dune morphology shape coastal EC habitats occurrence? A remote sensing approach using airborne LiDAR on the Mediterranean coast. Ecol. Indicat. 71, 618–626. https://doi.org/10.1016/j.ecolind.2016.07.044.

Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š., Lepš, J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity: intraspecific variability in functional diversity. Methods Ecol. Evol. 2, 163–174. https://doi.org/10.1111/j.2041-210X.2010.00071.x.

Bello, F. de, Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F., Thuiller, W., 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography 36, 393–402. https://doi.org/10.1111/j.1600-0587.2012.07438.x.

Brown, A.C., McLachlan, A., 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environ. Conserv. 29, 62–77. https://doi.org/10.1017/S037689290200005X.

Brunbjerg, A.K., Borchsenius, F., Eiserhardt, W.L., Ejrnaes, R., Svenning, J.-C., 2012.

Disturbance drives phylogenetic community structure in coastal dune vegetation. J. Veg. Sci. 23, 1082–1094. https://doi.org/10.1111/j.1654-1103.2012.01433.x.

Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., Ejrnaes, R., Aarssen, L.W., Buckley, H.L., Forey, E., Jansen, F., Kattge, J., Lane, C., Lubke, R.A., Moles, A.T., Monserrat, A.L., Peet, R.K., Roncal, J., Wootton, L., Svenning, J.-C., 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. J. Plant Ecol. 7, 101–114. https://doi.org/10.1093/jpe/rtt069.

Brunbjerg, A.K., Jørgensen, G.P., Nielsen, K.M., Pedersen, M.L., Svenning, J.-C., Ejrnæs, R., 2015. Disturbance in dry coastal dunes in Denmark promotes diversity of plants and arthropods. Biol. Conserv. 182, 243–253. https://doi.org/10.1016/j.biocon.2014.12.013.

Buffa, G., Fantinato, E., Pizzo, L., 2012. Effects of disturbance on sandy coastal ecosystems of N-Adriatic coasts (Italy). In: Lameed, G.A. (Ed.), Biodiversity Enrichment in a Diverse World. InTech, pp. 338–372. https://doi.org/10.5772/47480.

Cáceres, M.D., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1.

Carboni, M., Carranza, M.L., Acosta, A.T.R., 2009. Assessing conservation status on coastal dunes: a multiscale approach. Landsc. Urban Plann. 91, 17–25. https://doi.org/10.1016/j.landurbplan.2008.11.004.

Carboni, M., Santoro, R., Acosta, A.T.R., 2011. Dealing with scarce data to understand how environmental gradients and propagule pressure shape fine-scale alien distribution patterns on coastal dunes: drivers of alien patterns on coastal dunes. J. Veg. Sci. 22, 751–765. https://doi.org/10.1111/j.1654-1103.2011.01303.x.

Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? J. Veg. Sci. 24, 932–941. https://doi.org/10.1111/jvs.12095.

Carboni, M., Zelený, D., Acosta, A.T.R., 2016. Measuring ecological specialization along a natural stress gradient using a set of complementary niche breadth indices. J. Veg. Sci. 27, 892–903. https://doi.org/10.1111/jvs.12413.

Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius, M., Borges, P.A.V., Podani, J., Schmera, D., 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. J. Biogeogr. 41, 749–761. https://doi.org/10.1111/jbi.12239.

Castroviejo, S. (Ed.), 1986. Flora Iberica. Real Jardín Botánico, CSIC, Madrid.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A., Bazzaz, F.A., 2004. Phylogenetic overdispersion in Floridian oak communities. Am. Nat. 163, 823–843. https://doi.org/10.1086/386375.

Cavender Bares, J., Keen, A., Miles, B., 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87, S109–S122. https://doi.org/10.1890/0012-9658(2006)87[109:PSOFPC]2.0.CO;2.

Ciccarelli, D., 2014. Mediterranean coastal sand dune vegetation: influence of natural and anthropogenic factors. Environ. Manag. 54, 194–204. https://doi.org/10.1007/s00267-014-0290-2.

Clarke, K., Gorley, R., 2006. PRIMER V6: User Manual/Tutorial, vol. 192 PRIMER-E. Plymouth.

Conti, L., de Bello, F., Lepš, J., Acosta, A.T.R., Carboni, M., 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. J. Veg. Sci. 28, 762–773. https://doi.org/10.1111/jvs.12533.

Davies, T.J., 2006. Evolutionary ecology: when relatives cannot live together. Curr. Biol. 16, 645–647.

Debastiani, V.J., Pillar, V.D., 2012. SYNCSA—R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28, 2067–2068. https://doi.org/10.1093/bioinformatics/bts325.

Del Vecchio, S., Jucker, T., Carboni, M., Acosta, A.T.R., 2017. Linking plant communities on land and at sea: the effects of Posidonia oceanica wrack on the structure of dune vegetation. Estuar. Coast Shelf Sci. 184, 30–36. https://doi.org/10.1016/j.ecss.2016.10.041.

Demartini, C., 2016. Les végétations des côtes Manche-Atlantique françaises: essai de typologie et de cartographie dynamic-caténales. Université de Bretagne Occidentale 675pp.

Dengler, J., 2009. A flexible multi-scale approach for standardised recording of plant species richness patterns. Ecol. Indicat. 9, 1169–1178. https://doi.org/10.1016/j.ecolind.2009.02.002.

Drius, M., Malavasi, M., Acosta, A.T.R., Ricotta, C., Carranza, M.L., 2013. Boundary-based analysis for the assessment of coastal dune landscape integrity over time. Appl. Geogr. 45, 41–48. https://doi.org/10.1016/j.apgeog.2013.08.003.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.2307/2963459.

EEA, 2015. State of Nature in the EU Results from Reporting under the Nature Directives 2007–2012. Publications Office of the European Union, Luxembourg 173 pp. https://doi.org/10.2800/603862.

Fenu, G., Cogoni, D., Ferrara, C., Pinna, M.S., Bacchetta, G., 2012. Relationships between coastal sand dune properties and plant community distribution: the case of Is Arenas (Sardinia). Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 146, 586–602. https://doi.org/10.1080/11263504.2012.656727.

Feola, S., Carranza, M.L., Schaminée, J.H.J., Janssen, J. a. M., Acosta, A.T.R., 2011. EU habitats of interest: an insight into Atlantic and Mediterranean beach and foredunes. Biodivers. Conserv. 20, 1457–1468. https://doi.org/10.1007/s10531-011-0037-9.

Frederiksen, L., Kollmann, J., Vestergaard, P., Bruun, H.H., 2006. A multivariate approach to plant community distribution in the coastal dune zonation of NW Denmark. Phytocoenologia 36, 321–342. https://doi.org/10.1127/0340-269X/2006/0036-0321.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., others, 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637. https://doi.org/10.1890/03-0799.

Gómez-Pina, G., Muñoz-Pérez, J.J., Ramírez, J.L., Ley, C., 2002. Sand dune management problems and techniques, Spain. J. Coast Res. 36, 325–332. https://doi.org/10.2112/1551-5036-36.sp1.325.

Gracia, F., 2009. 2120 Dunas móviles de litoral con Ammophila arenaria (dunas blancas). In: VVAA., Bases Ecológicas Preliminares Para La Conservación de Los Tipos de Hábitat de Interés Comunitario En España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, pp. 48.

Gracia, F., Muñoz, J.C., 2009. 2130 Dunas costeras fijas con vegetación herbácea (dunas grises). In: VVAA., Bases Ecológicas Preliminares Para La Conservación de Los Tipos de Hábitat de Interés Comunitario En España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, pp. 40.

Gracia, F., Hernández, L., Hernández, A.I., San Jaume, E., Flor, G., 2009. 2110 Dunas móviles embrionarias. In: VVAA., Bases Ecológicas Preliminares Para La Conservación de Los Tipos de Hábitat de Interés Comunitario En España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, pp. 54.

Honrado, J., Vicente, J., Lomba, A., Alves, P., Macedo, J.A., Henriques, R., Granja, H., Caldas, F.B., 2009. Fine-scale patterns of vegetation assembly in the monitoring of changes in coastal sand-dune landscapes. Web Ecol. 10, 1–14. https://doi.org/10.5194/we-10-1-2010.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press 392 pp.

Isermann, M., 2005. Soil pH and species diversity in coastal dunes. Plant Ecol. 178, 111–120. https://doi.org/10.1007/s11258-004-2558-8.

Isermann, M., 2010. Phytodiversity in Relation to Scale. Habilitation-manuscript to Gain the Venia Legendi in the Field of Ecology. Bremen. 140 pp. http://elib.suub.uni-bremen.de/edocs/00101844-1.pdf.

Jiménez-Alfaro, B., Marcenò, C., Guarino, R., Chytrý, M., 2015. Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages. J. Biogeogr. 42, 452–462. https://doi.org/10.1111/jbi.12437.

Kadereit, J.W., Westberg, E., 2007. Determinants of phylogeographic structure: a comparative study of seven coastal flowering plant species across their European range. Watsonia 26, 229–238.

Kawano, K., 2002. Character displacement in giant rhinoceros beetles. Am. Nat. 159, 255–271. https://doi.org/10.1086/338512.

Kembel, S.W., Hubbell, S.P., 2006. The phylogenetic structure of a neotropical forest tree community. Ecology 87, S86–S99. https://doi.org/10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.

Kisdi, E., Geritz, S.A.H., 2003. On the coexistence of perennial plants by the competition-colonization trade-off. Am. Nat. 161, 350–354. https://doi.org/10.1086/345855.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. https://doi.org/10.1111/ele.12141.

Leibold, M.A., 1998. Similarity and local co-existence of species in regional biotas. Evol. Ecol. 12, 95–110. https://doi.org/10.1023/A:1006511124428.

Lenth, R.V., 2016. Least-squares means: the R package lsmeans. J. Stat. Software 69, 1–33. https://doi.org/10.18637/jss.v069.i01.

Leps, J., De Bello, F., Lavorel, S., Berman, S., 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. Preslia 78, 481–501.

Mahdavi, P., Bergmeier, E., 2016. Plant functional traits and diversity in sand dune ecosystems across different biogeographic regions. Acta Oecol. 74, 37–45. https://doi.org/10.1016/j.actao.2016.06.003.

Mahdavi, P., Isermann, M., Bergmeier, E., 2017. Sand habitats across biogeographical regions at species, community and functional level. Phytocoenologia 139–165. https://doi.org/10.1127/phyto/2017/0127.

Malavasi, M., Bartak, V., Carranza, M.L., Simova, P., Acosta, A.T.R., 2018. Landscape pattern and plant biodiversity in Mediterranean coastal dune ecosystems: do habitat loss and fragmentation really matter? J. Biogeogr. 45, 1367–1377. https://doi.org/10.1111/jbi.13215.

Marcantonio, M., Rocchini, D., Ottaviani, G., 2014. Impact of alien species on dune systems: a multifaceted approach. Biodivers. Conserv. 23, 2645–2668. https://doi.org/10.1007/s10531-014-0742-2.

Marcenò, C., Guarino, R., Loidi, J., Herrera, M., Isermann, M., Knollová, I., Tichý, L., Tzonev, R., Acosta, A.T.R., FitzPatrick, Ú., Iakushenko, D., Janssen, J., Jiménez-Alfaro, B., Kacki, Z., Keizer-Sedláková, I., Kolomiychuk, V., Rodwell, J., Schaminée, J., Šilc, U., Chytry, M., 2018. Classification of the European and Mediterranean coastal dune vegetation. Appl. Veg. Sci. 21, 533–559. https://doi.org/10.1111/avsc.12379.

Martínez, M.L., Silva, R., Lithgow, D., Mendoza, E., Flores, P., Martínez, R., Cruz, C., 2017. Human impact on coastal resilience along the coast of Veracruz, Mexico. J. Coast Res. 77, 143–153. https://doi.org/10.2112/SI77-015.1.

Maun, M.A., 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio 111, 59–70. https://doi.org/10.1007/BF00045577.

Maun, M.A., 2009. The Biology of Coastal Sand Dunes. Oxford University Press, New York 280pp.

McLachlan, A., Brown, A., 2006. The Ecology of Sandy Shores, second ed. Academic Press, Burlington, pp. 396pp.

Meinzer, F., 2003. Functional convergence in plant responses to the environment. Oecologia 134, 1–11. https://doi.org/10.1007/s00442-002-1088-0.

Moles, A.T., Westoby, M., 2006. Seed size and plant strategy across the whole life cycle.

Oikos 113, 91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., García, R.G., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., Tichý, L., 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl. Veg. Sci. 19, 3–264. https://doi.org/10.1111/avsc.12257.

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. Vegan: Community Ecology Package. R Package Version 2. pp. 3–5.

Pacala, S.W., Tilman, D., 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. Am. Nat. 143, 222–257.

Pavoine, S., Dolédec, S., 2005. The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. Environ. Ecol. Stat. 12, 125–138. https://doi.org/10.1007/s10651-005-1037-2.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. https://doi.org/10.1071/BT12225.

Prinzing, A., Reiffers, R., Braakhekke, W.G., Hennekens, S.M., Tackenberg, O., Ozinga, W.A., Schamine, J.H.J., van Groenendael, J.M., 2008. Less lineages more trait variation: phylogenetically clustered plant communities are functionally more diverse. Ecol. Lett. 11, 809–819. https://doi.org/10.1111/j.1461-0248.2008.01189.x.

Prisco, I., Stanisci, A., Acosta, A.T.R., 2016. Mediterranean dunes on the go: evidence from a short term study on coastal herbaceous vegetation. Estuar. Coast Shelf Sci. 182, 40–46. https://doi.org/10.1016/j.ecss.2016.09.012.

R Core Team, 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ricklefs, R.E., 2005. Historical and ecological dimensions of global patterns in plant diversity. Biol. Skr. 55, 583–603.

Ricotta, C., Burrascano, S., 2008. Beta diversity for functional ecology. Preslia 80, 61–71.

Ricotta, C., Pavoine, S., Bacaro, G., Acosta, A.T.R., 2012. Functional rarefaction for species abundance data: *On functional rarefaction functions*. Methods Ecol. Evol. 3, 519–525. https://doi.org/10.1111/j.2041-210X.2011.00178.x.

Rivas-Martínez, S., 1982. Series de vegetación de la región Eurosiberiana de la Península Ibérica. Lazaroa 4, 155–166.

Rivas-Martínez, S., 2007. Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. Itinera Geobot. 17, 5–436.

Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. Rivas-Martínez, S., Díaz, T.E., Penas, A., Fernández (Eds.), Itinera Geobot. 18 (1), 5–424.

Ruocco, M., Bertoni, D., Sarti, G., Ciccarelli, D., 2014. Mediterranean coastal dune systems: which abiotic factors have the most influence on plant communities? Estuar. Coast Shelf Sci. 149, 213–222. https://doi.org/10.1016/j.ecss.2014.08.019.

Swenson, N.G., 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. Am. J. Bot. 98, 472–480. https://doi.org/10.3732/ajb.1000289.

Swenson, N.G., Erickson, D.L., Mi, X., Bourg, N.A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J.K., Liu, X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S.J., Ye, W., Zhang, J., Zimmerman, J.K., Kress, W.J., 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. Ecology 93, S112–S125. https://doi.org/10.1890/11-0402.1.

The European Comission, 2015. The State of Nature in the European Union. Report on the Status of and Trends for Habitat Types and Species Covered by the Birds and Habitats Directives for the 2007-2012 Period as Required under Article 17 of the Habitats Directive and Article 12 of the Birds Directive. Brussels. . http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:52015DC0219&from=EN.

The European Commission, 2013. Interpretation manual of European Union habitats. Eur 28. http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Systemat. 20, 171–197. https://doi.org/10.1146/annurev.es.20.110189.001131.

Torca, M., Campos, J.A., Herrera, M., in press. Synoptic and traits species tables from coastal dunes of south Atlantic Europe and other comparative data. Data in Brief.

Van Der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114.

Van Der Maarel, E., 2003. Some remarks on the functions of European coastal ecosystems. Phytocoenologia 33, 187–202. https://doi.org/10.1127/0340-269X/2003/0033-0187.

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages: decomposing functional β-diversity. Global Ecol. Biogeogr. 22, 671–681. https://doi.org/10.1111/geb.12021.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Am. Nat. 156, 145–155.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Systemat. 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Webb, C.O., Cannon, C.H., Davies, S.J., 2008. Ecological organization, biogeography, and the phylogenetic structure of tropical forest tree communities. In: Carson, P., A, W., Schnitzer, S. (Eds.), Tropical Forest Community Ecology. Wiley-Blackwell, pp. 79–97.

Weiher, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. Oikos 73, 323–335.

Westhoff, V., Van der Maarel, E., 1978. The Braun-Blanquet approach. In: Whittaker, R.H. (Ed.), Classification of Plant Communities. Dr. W. Junk Publishers, The Hague, pp. 287–399.

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729.

Westoby, M., Falster, S., Moles, A., Vesk, P., Wright, J., 2002. Plant ecological strategies: some leading dimensions of variation between species. Annu. Rev. Ecol. Evol. Syst. 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452.

Whittaker, R.J., 1998. Island Biogeography: Ecology, Evolution and Conservation. Oxford University Press, Oxford 416 pp.

Wiedemann, A.M., Pickart, A., 2004. Temperate zone coastal dunes. In: Martínez, M.L., Psuty, N.P. (Eds.), Coastal Dunes, Ecological Studies. Springer Berlin Heidelberg, pp. 53–65. https://doi.org/10.1007/978-3-540-74002-5_2.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer, New York 574pp.

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Data Article

Species composition and plant traits of south Atlantic European coastal dunes and other comparative data

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ABSTRACT

The data reported in this article relates to the research article entitled “Changes in plant diversity patterns along dune zonation in south Atlantic European coasts” (Torca et al., 2019) [1]. Data about traits of species from coastal dunes, a synoptic table and PERMANOVA comparisons are given. The information detailed in the methodology section can be used as a guide to perform analyses on taxonomic, functional and phylogenetic diversity.

Specifications table

Subject area	*Biology*
More specific subject area	*Botany, floristic studies*
Type of data	*Tables, excel file, word file*
How data was acquired	*Field measures and databases. Visual identification and cover estimation of plant species.*
Data format	*Raw and analyzed*

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Abbreviations: CWM, community weighted mean; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index

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Experimental factors	*Collected plant species were pressed before identification or measurement in the laboratory.*
Experimental features	*10 m × 10 m temporary plots in coastal dunes, where plant species composition and cover was estimated. 12 sites. A total of 244 plots.*
Data source location	*Coasts of north Spain and south west France*
Data accessibility	*Data are included in this article.*
Related research article	M. Torca, J.A. Campos, M. Herrera; 2019 Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. ⟨http://dx.doi.org/10.1016/j.ecss.2018.11.016⟩ [1]

Value of the data

- The presented data allows keeping track of the coastal dune species composition in the south-western part of Atlantic Europe.
- The raw data of traits allows the performance of further analyses for functional diversity in coastal dunes.
- The methodology section summarizes common indices for taxonomic, functional and phylogenetic diversity and can be used as a guide.

1. Data

Raw data of ten traits for 110 species from coastal dunes of southwest Atlantic Europe is provided in Table S1 of the Supplementary material. Information for traits from Table S1 was extracted from the following online databases of traits and floras:

- Biolflor [2].
- Claves ilustradas de la flora del País Vasco y territorios limítrofes [3].
- Flora Iberica [4].
- Kew Garden [5].
- LEDA [6].
- Seed Dispersal [7].
- Try [8].

Table 1
PERMANOVA results for community assemblage at scales of plot, location and sector for each dune habitat. d*f* = degrees of freedom, MS = mean squares, ns = no significant. VC = Variance Component. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Habitat		df	MS	Pseudo-F		VC
Embryo	Sector = Se	3	5901.8	0.960	ns	0.0
	Local = Lo(Se)	8	6128.9	3.910	***	562.9
	Plot = Pl(Lo(Se))	36	1565.7	2.230	***	431.7
	Residual	48	702.2			702.2
	Total	95				
Mobile	Sector = Se	3	12,958.0	2.230	**	297.9
	Local = Lo(Se)	8	5808.9	3.791	***	534.6
	Plot = Pl(Lo(Se))	36	1532.3	2.069	***	395.8
	Residual	48	740.7			740.7
	Total	95				
Fixed	Sector = Se	3	42,095.0	3.690	***	1279.1
	Local = Lo(Se)	8	11,396.0	6.240	***	1196.1
	Plot = Pl(Lo(Se))	36	1827.1	3.380	***	643.7
	Residual	48	539.8			539.8
	Total	95				

Table 2

PERMANOVA results for Taxonomic Diversity (Shannon Index and Species richness), Phylogenetic Diversity (NRI and NTI) and Functional Diversity (RaoQ and CWM). d*f* = degrees of freedom, MS = mean squares, ns = no significant. VC = Variance Component. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Taxonomic Diversity		**d*f***	**Shannon**				**Richness**			
			MS	**Pseudo-F**		**VC**	**MS**	**Pseudo-F**		**VC**
Embryo	Sector = Se	3	0.252	0.169	ns	0.000	12.372	0.486	ns	0.000
	Location = Lo(Se)	8	1.49	5.150	***	0.100	25.469	3.818	**	1.903
	Plot = Pl(Lo(Se))	36	0.290	16.078	ns	0.055	6.670	1.699	*	1.372
	Residual	48	0.180			0.180	3.927			3.927
	Total	95								
Mobile	Sector = Se	3	1.301	2.100	ns	0.028	21.361	0.616	ns	0.000
	Location = Lo(Se)	8	0.619	2.469	*	0.046	34.688	4.078	**	2.818
	Plot = Pl(Lo(Se))	36	0.251	1.641	ns	0.049	8.507	2.490	**	2.545
	Residual	48	0.153			0.153	3.417			3.417
	Total	95								
Fixed	Sector = Se	3	1.254	4.102	ns	0.038	99.038	2.820	ns	2.664
	Location = Lo(Se)	8	0.306	0.988	ns	0.000	35.115	3.518	**	3.142
	Plot = Pl(Lo(Se))	36	0.309	2.818	***	0.027	9.983	2.183	**	2.705
	Residual	48	0.110			0.184	4.573			4.573
	Total	95								
Phylogenetic Diversity		**d*f***	**NRI**				**NTI**			
			MS	**Pseudo-F**		**VC**	**MS**	**Pseudo-F**		**VC**
Embryo	Sector = Se	3	0.540	0.901	ns	0.000	2.532	1.255	ns	0.021
	Location = Lo(Se)	8	0.599	1.911	ns	0.034	2.018	3.590	**	0.182
	Plot = Pl(Lo(Se))	36	0.313	2.776	**	0.100	0.562	2.520	**	0.169
	Residual	48	0.113			0.113	0.223			0.223
	Total	95								
Mobile	Sector = Se	3	0.180	0.443	ns	0.000	0.985	0.656	ns	0.000
	Location = Lo(Se)	8	0.406	2.056	ns	0.018	1.501	1.645	ns	0.060
	Plot = Pl(Lo(Se))	36	0.198	1.246	ns	0.020	0.912	1.847	*	0.209
	Residual	48	0.159			0.159	0.494			0.494
	Total	95								
Fixed	Sector = Se	3	2.506	2.413	ns	0.061	0.527	0.473	ns	0.000
	Location = Lo(Se)	8	1.038	1.456	ns	0.041	1.113	1.313	ns	0.031
	Plot = Pl(Lo(Se))	36	0.713	2.892	**	0.233	0.848	2.184	**	0.230
	Residual	48	0.247			0.247	0.388			0.388
	Total	95								
Functional Diversity		**d*f***	**RaoQ**				**CWM**			
			MS	**Pseudo-F**		**VC**	**MS**	**Pseudo-F**		**VC**
Embryo	Sector = Se	3	0.008	0.060	ns	0.000	874.5	0.675	ns	0.0
	Location = Lo(Se)	8	0.133	5.387	***	0.009	1295.1	4.909	***	114.6
	Plot = Pl(Lo(Se))	36	0.025	1.703	*	0.005	263.8	2.771	***	84.3
	Residual	48	0.014			0.014	95.2			95.2
	Total	95								
Mobile	Sector = Se	3	0.101	2.289	ns	0.002	2674.4	0.687	ns	0.0
	Location = Lo(Se)	8	0.044	2.428	*	0.003	3891.8	4.946	***	346.6
	Plot = Pl(Lo(Se))	36	0.018	1.360	ns	0.002	786.9	1.142	ns	48.8
	Residual	48	0.013			0.013	689.2			689.2
	Total	95								
Fixed	Sector = Se	3	0.033	1.381	ns	0.000	11,932.0	2.511	ns	299.1
	Location = Lo(Se)	8	0.024	1.393	ns	0.001	4752.6	6.232	***	498.2
	Plot = Pl(Lo(Se))	36	0.017	2.858	***	0.006	762.5	0.990	ns	0.0
	Residual	48	0.006			0.006	770.1			766.9
	Total	95								

Table S2 of the Supplementary material provides a synoptic representation of the IndVal values. Finally, in Tables 1 and 2 a PERMANOVA analysis of species composition, taxonomic, functional and phylogenetic diversity is reported.

2. Experimental design, materials and methods

2.1. Study area

The research was conducted along the Atlantic coasts of north Spain and southwest of France. The Cantabrian coast lies in E-W direction with a dominant north face [9]. Galicia and Cantabria show high sedimentary deposition, while in Asturias cliffs are abundant [10]. In Galicia and Cantabria estuaries open and there sand dune fields occur in numerous localities [9]. In the south of France cliffs are less common and a continuous dune field is present. Along the western areas temperate hyper-oceanic submediterranean conditions predominate, while in the eastern areas a temperate oceanic bioclimate is dominant [11]. Climatic characterization of the studied locations is shown in Table 3.

2.2. Diversity indices

For **taxonomic diversity** Shannon index was calculated

$$H = -\sum_{i=1}^{n} p_i \, lnp_i$$

where p_i is the relative abundance of species i.

For **phylogenetic diversity**, NRI (Net Relatedness Index) and NTI (Nearest Taxon Index) were calculated:

$$NRI = -1\frac{(MPD_{obs} - MPD_{rand})}{sd\ MPD_{rand}} \quad NTI = -1\frac{(MNTD_{obs} - MNTD_{rand})}{sd\ MNTD_{rand}}$$

where MPD stands for Mean Pairwise Distance both observed (obs) and random (rand). The difference between the observed and random value is divided by the standard deviation of the random distribution. NTI is the same except that the MNTD (Mean Nearest Taxon Distance) is applied. Both NRI and NTI can be calculated using species presence-absence data but, in this study, weighed abundance was measured.

Regarding the phylogenetic tree used for distances, the reference tree selected was Phylomatic tree R20120829 for plants. As one species, *Cynodon dactylon* was not included, it was manually added. Then, polytomies were randomly resolved, as trees containing polytomies have less resolution and statistical power [13]. Finally, branch length was estimated using BLADJ (Branch Length Adjustment)

Table 3

Climatic data for biogeographical sectors. Galician-Portuguese (GP), Galician-Asturian (GA), Cantabrian-Basque (CB) and Aquitanian-Landes sector (AL). Longitude (Long), latitude (Lat), elevation (Ele, m.a.s.l.), annual mean temperature (*T*, in °C), positive annual rainfall (Pp, in mm), continentality index (Ic), ombrotermic indices of summer months (Ios_1, Ios_2, Ios_3 and Ios_4, for June, June + July, June + July + August and June + July + August + September, respectively), thermicity index (It), mediterraneity index of July (Im_1). For more information about used bioclimatic indices see [12].

Station	Sector	Long	Lat	Ele	*T*	Pp	Ic	Ios_1	Ios_2	Ios_3	Ios_4	It	Im_1
Noia	GP	8°53'W	42°47'N	104	13.8	1833	11.4	2.6	2.61	3.13	4.16	311	2.23
Padrón	GP	8°38'W	42°44'N	58	14.8	1692	11.8	1.24	1.88	2.42	3.34	334	4.71
La Coruña	GA	8°22'W	43°23'N	57	13.7	963	8.6	1.83	2.08	2.14	2.52	332	3.69
Porto do Baqueiro	GA	7°41'W	43°47'N	80	13.1	2080	8.6	2.36	3.08	4.21	5.66	317	2.41
Comillas	CB	4°17'W	43°23'N	24	13.5	1242	10.1	2.49	3.99	4.06	4.52	309	2.32
Oriñón	CB	3°19'W	43°24'N	63	13,9	1400	10.7	2.9	3.87	3.94	4.39	320	1.99
Hondarribia	AL	1°47'W	43°21'N	8	14.1	1720	12	4.34	5.08	5.16	5.9	310	1.35
Bordeaux	AL	0°42'W	44°49'N	49	12.8	1539	15.3	2.38	2.43	2.27	2.99	234	2.49

and an age file according to Wikström et al. [14] in Phylocom [15]. Having few dated nodes, the resulting phylogenetic distance can be considered as a marked improvement over using only the number of intervening nodes as phylogenetic distance [16].

For **functional diversity**, CWM (Community Weighted Mean) was used. It is a metric of functional composition and it was proposed by Garnier et al. [17] to calculate the average of trait values weighted by the relative abundances of each species [18]. It is a good indicator of the expected functional value of a trait in a random community sample [19], and can also be used to understand how environmental gradients select trait composition at local communities [20].

$$CWM = -\sum_{i=1}^{S} p_i x_i$$

where p_i is the relative abundance of species i ($i = 1, 2, \ldots, S$), and x_i is the trait value for species i.

Another functional index used was RaoQ based on Rao [21] quadratic diversity and proposed by Pavoine and Dolédec [22] and Leps et al. [23]. RaoQ is considered the expected dissimilarity between two individuals of a given species assemblage selected at random with replacement [18].

$$Q = -\sum_{i=1}^{S} d_{ij} p_i p_j$$

where d_{ij} is the dissimilarity (i.e., not necessarily a metric distance) between species i and j and p_i and p_j the relative abundance of species i and j respectively. CWM and RaoQ are complementary as CWM quantifies the weighted mean of a given functional trait within a given species assemblage, while the RaoQ is a measure of trait dispersion or divergence *sensu* Villéger et al. [24] (see [18]).

2.3. Sampling and data analysis

Plant community composition was assessed by visual identification and cover estimation of species in the plots. Details are provided in [1]. Permutational multivariate analyses of variance (PERMANOVA) [25] was performed using PERMANOVA+ for Primer software [26]. Synoptic table based on IndVal values was filled with the *multipatt* function of the *indicspecies* [27] package of R [28].

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Transparency document. Supplementary material

Transparency data associated with this article can be found in the online version at https://doi.org/10.1016/j.dib.2018.12.005.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at https://doi.org/10.1016/j.dib.2018.12.005.

References

[1] M. Torca, J.A. Campos, M. Herrera, Changes in plant diversity patterns along dune zonation in south Atlantic European coasts, Estuar. Coast. Shelf Sci. 5 (2019) 39–47, http://dx.doi.org/10.1016/j.ecss.2018.11.016.

[2] I. Kühn, W. Durka, S. Klotz, BiolFlor: a new plant-trait database as a tool for plant invasion ecology, Divers. Distrib. 10 (2004) 363–365.

[3] I. Aizpuru, C. Aseginolaza, P.M. Uribe-Echebarría, P. Urrutia, I. Zorrakin, P. Garín, C.E. Hermosilla, X. Lizaur, S. Patino, J.M. Pérez Dacosta, G. Renobales, J. Valencia, Claves ilustradas de la flora del País Vasco y territorios limítrofes, Publication Service of The Basque Country Goverment, Vitoria-Gasteiz, 2007.

[4] S. Castroviejo (Ed.), Flora Iberica, Real Jardín Botánico, CSIC, Madrid, 1986.

[5] Royal Botanic Gardens Kew, Seed Information Database (SID). Version 7.1. Available from: 〈http://data.kew.org/sid/〉, (Accesed on 01-07-2015).

[6] M. Kleyer, R.M. Bekker, I.C. Knevel, J.P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J.M. van Groenendael, L. Klimeš, J. Klimešová, S. Klotz, G.M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J.G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W.A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H.J. Steendam, O. Tackenberg, B. Wilmann, J.H.C. Cornelissen, O. Eriksson, E. Garnier, B. Peco, The LEDA Traitbase: a database of life-history traits of the Northwest European flora, J. Ecol. 96 (2008) 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x.

[7] C. Hintze, F. Heydel, C. Hoppe, S. Cunze, A. König, O. Tackenberg, D3: the dispersal and diaspore database – baseline data and statistics on seed dispersal, Perspect. Plant Ecol. Evol. Syst. 15 (2013) 180–192. https://doi.org/10.1016/j.ppees.2013.02.001.

[8] J. Kattge, S. Díaz, S. Lavorel, I.C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, P.B. Reich, I.J. Wright, J.H. C. Cornelissen, C. Violle, S.P. Harrison, P.M. Van Bodegom, M. Reichstein, B.J. Enquist, N.A. Soudzilovskaia, D.D. Ackerly, M. Anand, O. Atkin, M. Bahn, T.R. Baker, D. Baldocchi, R. Bekker, C.C. Blanco, B. Blonder, W.J. Bond, R. Bradstock, D.E. Bunker, F. Casanoves, J. Bahn, J.Q. Chambers, F.S. Chapin Iii, J. Chave, D. Coomes, W.K. Cornwell, J.M. Craine, B.H. Dobrin, L. Duarte, W. Durka, J. Elser, G. Esser, M. Cornwell, W.F. Fagan, J. Fang, F. Fernández-Méndez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G.T. Freschet, N.M. Fyllas, R.V. Gallagher, W.A. Green, A.G. Gutierrez, T. Hickler, S.I. Higgins, J.G. Hodgson, A. Jalili, S. Jansen, C.A. Joly, A.J. Kerkhoff, D. Kirkup, K. Kitajima, M. Kleyer, S. Klotz, J.M.H. Knops, K. Kramer, I. Kühn, H. Kurokawa, D. Laughlin, T.D. Lee, F.S. Leishman, F. Lens, T. Lenz, S.L. Lewis, J. Lloyd, J. Llusià, F. Louault, S. Ma, M.D. Mahecha, P. Manning, T. Massad, B.E. Medlyn, J. Messier, A.T. Moles, S.C. Müller, K. Nadrowski, S. Naeem, Ü. Niinemets, S. Nöllert, A. Nüske, R. Ogaya, J. Oleksyn, V.G. Onipchenko, Y. Onoda, J. Ordoñez, G. Overbeck, W.A. Ozinga, S. Patiño, S. Paula, J.G. Pausas, J. Peñuelas, O. L. Phillips, V. Pillar, H. Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack, B. Salgado-Negret, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E. Sosinski, J.-F. Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, M. Waldram, E. Weiher, M. White, J.M. White, S.J. Wright, B. Yguel, S. Zaehle, A.E. Zanne, C. Wirth, TRY – a global database of plant traits, Glob. Change Biol. 17 (2011) 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x.

[9] E.S. Saumell, F.J. Gracia (Eds.), Las dunas en España, Sociedad Española de Geomorfología, Zaragoza, 2011.

[10] J.P. Doody, Sand dune – Country Report, Spain. Available from: 〈http://www.coastalwiki.org/wiki/Sand_dune_-_Country_Report,_Spain〉, (Accessed on 2-09-2016).

[11] S. Rivas-Martínez, A. Penas, T.E. Días, Bioclimatic map of Europe: bioclimates, 2004. 〈http://www.globalbioclimatics.org/form/bi_med.htm〉, (Accessed 9 February 2017).

[12] S. Rivas-Martínez, S. Rivas-Sáenz, S.P. Merino, Worldwide bioclimatic classification system, Glob. Geobot. 1 (2011) 1–634.

[13] N.G. Swenson, Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities, PLoS One 4 (2009) e4390. https://doi.org/10.1371/journal.pone.0004390.

[14] N. Wikström, V. Savolainen, M.W. Chase, Evolution of the angiosperms: calibrating the family tree, Proc. R. Soc. B Biol. Sci. 268 (2001) 2211–2220. https://doi.org/10.1098/rspb.2001.1782.

[15] C.O. Webb, D.D. Ackerly, S.W. Kembel, Phylocom: software for the analysis of phylogenetic community structure and trait evolution, Bioinformatics 24 (2008) 2098–2100. https://doi.org/10.1093/bioinformatics/btn358.

[16] C.O. Webb, Exploring the phylogenetic structure of ecological communities: an example for rain forest trees, Am. Nat. 156 (2000) 145–155.

[17] E. Garnier, J. Cortez, G. Billès, M.-L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, et al., Plant functional markers capture ecosystem properties during secondary succession, Ecology 85 (2004) 2630–2637. https://doi.org/10.1890/03-0799.

[18] C. Ricotta, M. Moretti, CWM and Rao's quadratic diversity: a unified framework for functional ecology, Oecologia 167 (2011) 181–188. https://doi.org/10.1007/s00442-011-1965-5.

[19] L. Pla, F. Casanoves, J. Di Rienzo, Quantifying Functional Biodiversity, Springer, Netherlands, Dordrecht, 2012 〈http://link.springer.com/10.1007/978-94-007-2648-2〉 (Accessed 2 September 2016).

[20] D.D. Ackerly, W.K. Cornwell, A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components, Ecol. Lett. 10 (2007) 135–145. https://doi.org/10.1111/j.1461-0248.2006.01006.x.

[21] C.R. Rao, Diversity and dissimilarity coefficients: a unified approach, Theor. Popul. Biol. 21 (1982) 24–43. https://doi.org/10.1016/0040-5809(82)90004-1.

[22] S. Pavoine, S. Dolédec, The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data, Environ. Ecol. Stat. 12 (2005) 125–138. https://doi.org/10.1007/s10651-005-1037-2.

[23] J. Leps, F. De Bello, S. Lavorel, S. Berman, Quantifying and interpreting functional diversity of natural communities: practical considerations matter, Preslia 78 (2006) 481–501.

[24] S. Villéger, N.W. Mason, D. Mouillot, New multidimensional functional diversity indices for a multifaceted framework in functional ecology, Ecology 89 (2008) 2290–2301. https://doi.org/10.1890/07-1206.1.

[25] M.J. Anderson, A new method for non-parametric multivariate analysis of variance, Austral Ecol. 26 (2001) 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

[26] K. Clarke, R. Gorley, PRIMER v6: User Manual/Tutorial, PRIMER-E, Plymouth (2006) 192.
[27] M.D. Cáceres, P. Legendre, Associations between species and groups of sites: indices and statistical inference, Ecology 90 (2009) 3566–3574. https://doi.org/10.1890/08-1823.1.
[28] R Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2015 ⟨https://www.R-project.org/⟩.