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ARTICLE

Regional metacommunities in two coastal systems: spatial structure and drivers of plant assemblages

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ABSTRACT

Aim Biogeographical patterns in metacommunities are still poorly understood, and different processes are expected to occur in different habitats. We analysed the regional plant metacommunities of coastal habitats to test whether (1) the influence of space and climate differs between two habitats differentiated along the seashore–inland gradient, and (2) regional variation in species composition of these habitats can be ascribed to different metacommunity paradigms.

Location The entire coast of the Iberian Peninsula, south-western Europe.

Methods We collected data on the plant species composition of coastal sites on sand dunes across 3000 km of coastline. The sites were classified into two habitats corresponding to shifting and stable sand dunes, and divided into three distinct geographical regions: Cantabrian, Atlantic and Mediterranean. We assessed the geographical structure of the species composition using ordination, estimates of species turnover and spatial autocorrelation. We then used multivariate models and variation partitioning to test the influence of climatic and spatial effects. Analyses were conducted for the whole data set and the geographical subsets.

Results Metacommunities from shifting and stable dunes showed similar spatial patterns, with the highest species turnover occurring in the Mediterranean region. Similarities between communities that were nearer each other (typically < 100 km) were weaker in shifting than in stable dunes, although the distance decay for sites that were further apart was similar in both habitats. Variation in species composition in shifting dunes was mainly explained by distance and climate, while in stable dunes the effect of climate was clearly dominant. The observed differences were relatively consistent across geographical regions.

Main conclusions Distinct processes structure the metacommunities in two dune habitats differentiated along the seashore–inland gradient. Communities of shifting dunes seem to be structured by an interplay of neutral or patch-dynamic processes and to a lesser degree by species sorting. In contrast, communities of stable dunes are mainly governed by species sorting in response to climatic gradients. These results highlight the importance of differentiating habitats according to local ecological factors when analysing regional patterns in metacommunities.

Keywords

Community assembly, dispersal limitation, distance decay, dune habitats, environmental filtering, Iberian Peninsula, metacommunity, species sorting, vegetation databases.

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INTRODUCTION

The relative influence of environmental versus spatial factors on community structure is an important but still poorly

understood topic in ecology and biogeography (Astorga *et al.*, 2011; Peres-Neto *et al.*, 2012). At the regional scale, these phenomena can be approached within the metacommunity framework, by considering the variation across

related communities influenced by environmental gradients and linked by dispersal (Wilson, 1992). From this viewpoint, local species composition is a function of the degree of regional heterogeneity, dispersal between communities and individual species' responses (Mouquet & Loreau, 2002). According to the relative importance of these processes, Leibold *et al.* (2004) recognized four metacommunity paradigms. On the one hand, the patch-dynamic, species-sorting and mass-effect paradigms assume habitat heterogeneity and differences between species, but with a different role for dispersal processes. On the other hand, the neutral paradigm assumes no differences between species niches or fitness, and a determinant effect of dispersal (Logue *et al.*, 2011). As experimental studies of these processes at large scales are difficult, useful insights can be obtained by testing the influence of environmental versus spatial components using empirical data at a regional level (Hájek *et al.*, 2011; Moritz *et al.*, 2013).

Using examples from different organisms, Cottenie (2005) showed that metacommunity structure (i.e. the spatial aggregation and combination of species across communities) can generally be interpreted by applying a species-sorting perspective (emphasizing species niche separation along environmental gradients) or a combination of species sorting and mass effect (the latter emphasizing the role of dispersal on immigration and emigration). In general, communities are expected to be more similar at shorter rather than longer distances, showing a pattern of spatial autocorrelation and a 'distance decay' effect (Nekola & White, 1999). This pattern can be explained by environmental filtering (nearby sites tend to have similar environmental conditions) or spatial effects (because dispersal limitation reduces the connectivity of distant sites). The importance of both of these factors can vary across scales, with a predominance of dispersal limitation at coarser resolutions (Meynard *et al.*, 2011). Although metacommunities driven only by purely spatial effects (i.e. without a clear role of the environment) can be explained by dispersal limitation and neutral processes (Cottenie, 2005), the real effect of spatial variation is difficult to interpret in empirical studies (Logue *et al.*, 2011). A crucial issue, therefore, is to understand the spatial structure of communities at a given geographical extent (Presley *et al.*, 2010; Peres-Neto *et al.*, 2012). Moreover, broad-scale studies have to deal with multidirectional connectivity between sites (Moritz *et al.*, 2013), which complicates the interpretation of patch connectivity and dispersal limitation (Leibold, 2011). In other habitats (e.g. rivers), communities are structured linearly and dispersal events are unidirectional or bidirectional (Landeiro *et al.*, 2011), providing a suitable context for assessing the spatial patterns within metacommunities.

In this study, for the first time we tested the effect of environmental and spatial factors on coastal dune communities across biogeographical regions. Because of their geographical linearity, vegetation growth and average biomass production, these habitats are influenced by climatic factors such as temperature and precipitation (Maun, 2009), while the plant species distributions are also affected by broad-scale dispersal

processes (Clausing *et al.*, 2000; He & Lamont, 2010). In Europe, floristic diversification in these systems seems to be evolutionarily driven at a regional scale (Brunbjerg *et al.*, 2014). Sand dunes are dominated by a set of widely distributed taxa (e.g. *Ammophila arenaria*) that have been described as having long-distance dispersal by water and wind (Bakker *et al.*, 2008; Maun, 2009). However, these habitats also harbour species with narrow geographical ranges that are related to specific climatic conditions or regional biogeographical histories (Piñeiro *et al.*, 2007). This pattern is reflected in the classification of European coastal vegetation, supporting a plethora of community types confined to different geographical regions (Géhu, 1999; Feola *et al.*, 2011) and indicating geographical barriers driven by environmental or spatial factors.

It has been suggested recently that dispersal limitation is of little importance in coastal dunes, where community structure is mainly driven by environmental filtering under the species-sorting paradigm (Brunbjerg *et al.*, 2012). However, such a conclusion is based on complex dune systems studied mainly on a local scale, in which the observed variation in species composition is related to small-scale succession, with the earliest stages begin seen towards the shoreline and the more developed stages landwards (Doing, 1985; Acosta *et al.*, 2008). This variation is described by the shoreline–inland gradient, which is influenced by edaphic and hydrological factors such as wind, waves, sediment accumulation and salt concentration (Rozema *et al.*, 1985; Hesp, 1991). This results in a typical zonation of two habitats generally referred to as shifting sand dunes and stable sand dunes (Barbour, 1992; Feola *et al.*, 2011). Although studies that focus on the shoreline–inland gradient can be interpreted within a local context, they give little information about the factors driving the structure of metacommunities at larger scales.

We argue that differentiating these two habitats as different metacommunity systems might minimize the influence of local environmental gradients. Species characteristic of shifting dunes are more often pioneers or stress tolerators than species of stable dunes; they are well adapted to mobile habitats with little organic matter, high salinity and strong winds (Oosting & Billings, 1942). In contrast, species characteristic of stable dunes colonize the inner coastal dunes, where the limiting factors mentioned above are weaker while others (e.g. higher productivity and increased competition) become stronger (Barbour, 1992). In consequence, the relative influence of environment and space is expected to differ in the metacommunities of stable and shifting sand dunes, as detected in other habitats with unique ecological properties (Cottenie, 2005). At larger scales, we expect environmental factors to be related mainly to climatic patterns, which are largely recognized as influencing species richness (Doing, 1985), plant adaptations (Hesp, 1991), life forms (Barbour, 1992) and successional dynamics (Miller *et al.*, 2009) in coastal dunes. We also expect an effect of space on community variation, by reflecting changes in coastal connectivity as a function of distance. However, the relative influence of climate and space in the dune systems remains unclear.

We focused on the coastal dunes of the Iberian Peninsula, which are suitable systems for analysing the spatial structure of metacommunities because of the existence of three geographically well-defined coastlines (Fig. 1). Because the coast of the Iberian Peninsula was not glaciated in the Pleistocene (Pérez Alberti *et al.*, 2004), the diversity of sand dune communities there has developed over a long time period and has been influenced less by post-glaciation species migrations than other habitats. The Iberian Peninsula is also a meeting point for the Atlantic temperate and mediterranean floras of Europe (van der Maarel, 2003; Feola *et al.*, 2011), allowing us to compare metacommunity structure across different biogeographical contexts. Our main objectives were to test whether (1) the effects of climate and space on plant community structure differ between shifting and stable sand dunes over the whole Iberian coast and its contrasting biogeographical regions, and (2) regional variation in plant communities of these habitats can be ascribed to different metacommunity paradigms.

MATERIALS AND METHODS

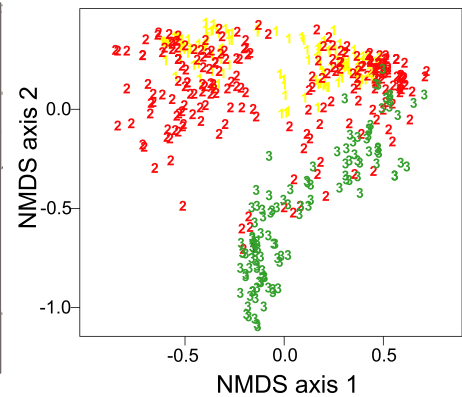
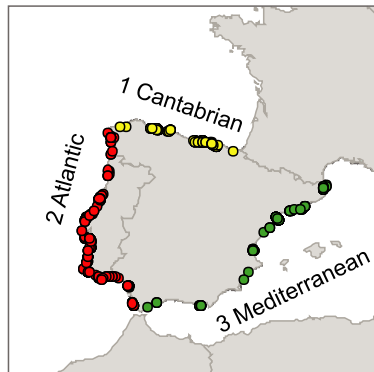
Study system

The Iberian coastline is *c.* 3000 km long and the coastal environments are highly variable because of the different

bedrocks and geomorphology of the three main geographical regions: Cantabrian, Atlantic and Mediterranean (Fig. 1). These regions also differ in the direction of sea currents and their climatic history (Moreno *et al.*, 2012). The Cantabrian (northern) coast is rocky and mainly dominated by high cliffs; the sand deposits are generally small and geographically dispersed, and wind trajectories produce dominant sea currents to the east. The Atlantic (western) coast is relatively rocky in the north, but with long and well-connected beaches in the central and south-eastern areas, where sea currents flow from north to south. The Mediterranean (south-eastern) coast is also predominantly rocky in the north, while the central and southern areas are characterized by rocky headlands alternating with sandy shores; water flows from north to south with a circulating system near the Strait of Gibraltar.

In general, the sand dunes of the Iberian Peninsula can form a narrow strip between the shore and the saltmarshes or extended complexes stretching a few hundred metres inland. Along the seashore–inland gradient, shifting and stable sand dunes are defined by plant communities that are the focus of coastal management and conservation planning across Europe (Feola *et al.*, 2011), identified as ‘shifting dunes’ (habitat 2120) and ‘fixed coastal dunes with herbaceous vegetation’ (habitat 2130). According to the Iberian vegetation classification (Rivas-Martínez *et al.*, 2001), three

(a) Shifting dunes



(b) Stable dunes

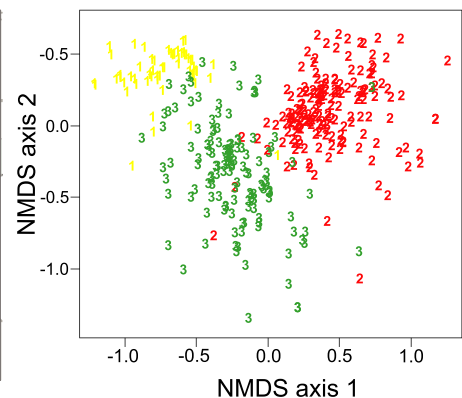
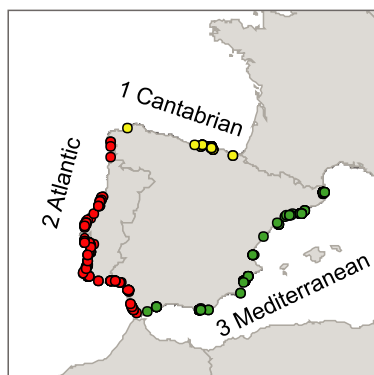


Figure 1 Geographical distribution and non-metric multidimensional scaling (NMDS) ordination diagram of the sites assigned to shifting dunes ($n = 467$) and stable dunes ($n = 367$) in a study of regional plant metacommunities in coastal habitats on the Iberian Peninsula. Colours and numbers refer to the three geographical subsets analysed in this study: Cantabrian (1, yellow), Atlantic (2, red) and Mediterranean (3, green).

major community types (alliances) can be distinguished on the shifting dunes. Two of them (*Ammophilion australis* and *Agropyro–Minuartion peploidis*) correspond to pioneer plant communities widespread over all three geographical regions, while the third (*Sporobolion arenarii*) is found exclusively in the Mediterranean region. In contrast, stable (= fixed) dunes are characterized by distinct community types along each of the three coastal regions: *Helichryson picardii* in the Cantabrian; *Euphorbio portlandicae–Helichryson maritimi* in the Atlantic; and *Crucianellion maritimae* in the Mediterranean.

Community data

We created a database of sites documenting the local species composition of sand dune vegetation on the Iberian Peninsula (including Spain and Portugal but excluding islands). We extracted data from 42 publications (see Appendix S1 in Supporting Information), including complete lists of vascular plants from 969 sites. The data collection focused on studies published after 1950 and originally assigned to perennial herbaceous vegetation, excluding communities dominated by woody species (e.g. *Juniperus* spp.) because they represent different habitats and are not equally distributed along the Iberian coast. The data were taken from studies using similar sampling methods, in which species importance was estimated from homogeneous vegetation sites using the Braun-Blanquet cover–abundance scale (Braun-Blanquet, 1964). The data were stored in the database format TURBOVEG (Hennekens & Schaminée, 2001). Taxonomical nomenclature was unified according to *Flora Iberica* (<http://www.floraiberica.org/>, accessed May 2014). The sites were assigned to geographical coordinates with the help of the online geolocator tool Iberpix version 1 (<http://www2.ign.es/iberpix/visoriberpix/visorign.html>, accessed in 2010). Sites from unknown localities or with uncertainties about their spatial location were excluded. Because the localities that referred to beach systems were spatially well identified, the estimated accuracy of the georeferencing was generally high.

To reduce possible oversampling of some areas, we randomly selected a maximum number of 10 sites per locality. A locality was defined as one dune system geographically located in the same square kilometre. The resulting 834 sites included a total of 332 species (mean number of species per site, 9.9; SD, 5.1; range 1–34) sampled from areas ranging from 10 to 100 m². We classified the sites into two groups using a two-way indicator species analysis (TWINSPAN) implemented in JUICE 7.0 (Tichý, 2002). The diagnostic species of each group (see Appendix S2) allowed us to characterize the groups as shifting dunes (467 sites) and stable dunes (367 sites). The two data sets showed some differences in the total species richness, number of species per site and the number of unique species, with higher values for the stable dunes (Table 1). We assessed possible differences in dispersal traits using the information available in *Flora d'Italia Digitale* (E. Pacini & C. Nepi, Department of Life Sciences, University of Siena, Siena, in prep.) and the *Dispersal and*

Table 1 Descriptive statistics of the two data sets analysed in a study of regional plant metacommunities in coastal habitats on the Iberian Peninsula, classified by two-way indicator species analysis (TWINSPAN). Exclusive species refer to those present only in the given data set. Frequencies of dispersal traits were based on those species for which seed dispersal data were available (111 in shifting dunes and 218 in stable dunes). Dispersal by anemochory was reported for 200 species, zoochory for 103, hydrochory for 25 and autochory for 91 (some species had more than one mode of dispersal), while no information was available for 66 species.

	Shifting dunes	Stable dunes
Total number of species	189	367
Number of exclusive species	51	143
Mean (\pm SD) number of species per site	8 \pm 4	13 \pm 5
Mean (\pm SD) cover (%) per site	51 \pm 21	63 \pm 19
Percentage of species with anemochory	76	74
Percentage of species with zoochory	34	35
Percentage of species with hydrochory	12	9
Percentage of species with autochory	27	33

Diaspore Database (Hintze *et al.*, 2013) and found no relevant differences between the two community types (Table 1).

Environmental and geographical data

The geographical coordinates of the vegetation sites were exported to a GIS (ArcGIS 9.2; ESRI, Redlands, CA, USA) and assigned to the three major geographical regions (Fig. 1). Coordinates were used to obtain climatic data according to a model extrapolated from meteorological stations at a resolution of 200 m \times 200 m (Ninyerola *et al.*, 2006). We extracted parameters for three climatic variables related to the growth and distribution of vascular plants in southern Europe: mean annual temperature, annual precipitation and summer precipitation. These parameters were selected from a set of eight climatic variables with high collinearity (Pearson's $r > 0.8$) because they were expected to reflect the climatic gradients of the study area better.

To estimate the distance between sites, we created a variable (coastline distance) reflecting the geographical position of the sites along the coastline. In linear systems this 'watercourse' approach offers a better estimation of spatial connectivity than 'overland' distances (Cottenie, 2005; Landeiro *et al.*, 2011). This was expected in our study system given that dispersal by sea water is highly important in coastal dunes (Clausing *et al.*, 2000). Thus, we assumed that the coastal distance would be a good proxy of the connectivity between dunes, even though some coastal areas were without dunes. To measure the relative position of the sites along the coastline, we calculated the linear distance (in metres) between the most north-eastern site of the data set (at the Spanish–French border at the Bay of Biscay) and each site, and the same principle was

applied to the three geographical regions (see maps in Fig. 2). Thus, the coastal distance reflected a linear geographical gradient to measure the proximity or remoteness between any pair of sites.

Metacommunity structure

We used multivariate analyses to assess the spatial structure of species assemblages in shifting and stable sand dunes separately. First, we focused on differences among geographical regions using a non-metric multidimensional scaling (NMDS) ordination to visualize the variation in species composition. We calculated the mean Sørensen dissimilarity for all pairs of sites within each geographical subset to quantify species turnover as $(1 - S)$, where S is the Sørensen similarity coefficient. Confidence intervals for turnover in the three geographical regions were determined using 100 bootstrap samples. These analyses were computed with the package *VEGAN* (Oksanen *et al.*, 2008) in R (R Foundation for Statistical Computing, Vienna, Austria). We also tested for differences in community structure among geographical groups using an analysis of similarities (ANOSIM), which is a non-parametric test based on the Mantel test and a standardized rank correlation between two distance matrices. The resulting statistic (R) ranges from -1 (indicating that the most similar samples are in different groups) to $+1$ (the most similar samples are in the same groups), while $R = 0$ indicates that the high and low similarities are mixed and do not have any relationship with the groups. One-way ANOSIM was computed in *PAST* software (Hammer *et al.*, 2001) using a Bonferroni-corrected pairwise comparison. Community distance matrices were calculated from cover values using the Bray–Curtis similarity.

Second, we focused on the spatial structure of metacommunities as a function of the geographical distance. We used Mantel correlograms (Borcard & Legendre, 2012) to analyse the multivariate spatial structure of the shifting and stable dunes within each geographical subset. In comparison with distance decay estimates based on the correlation between pairwise dissimilarity and distance, a Mantel correlogram computes a unique multivariate correlation for each of the predefined classes of geographical distance (i.e. distance classes). The Mantel statistic is then calculated to test whether the mean within-class similarity is higher or lower than the mean among-class similarity by providing positive or negative values, respectively (Borcard & Legendre, 2012). We created distance matrices for the taxonomic composition using presence/absence and the Jaccard index, and geographical distance matrices using the coastline distance. For each data set, distance classes were created from the geographical matrices by ensuring that each class had an equal number of observations. Mantel correlograms were then created to plot the results of Mantel tests (r) computed with 999 permutations along the distance classes. These analyses were carried out in *PASSAGE 2* (Rosenberg & Anderson, 2011).

Influence of climate and geography

To assess the relative importance of geography and climate on species composition, we used partial redundancy analysis (RDA) to deconstruct the total variation in the community matrix (Borcard *et al.*, 1992). RDA is a constrained ordination technique that is a multivariate extension of multiple regression with corresponding R^2 measures. We adopted a stepwise forward selection procedure for building a model within each data set, and measured the adjusted R^2 with a permutation P -value of 0.05 (Blanchet *et al.*, 2008). We used variation partitioning (Borcard *et al.*, 1992) to analyse the influence of climate and space (see below) using the total sum of RDA eigenvalues and calculating the residual variance as a percentage of the total inertia (Økland, 1999).

To account for the influence of space, we used two complementary approaches. First, we computed variation partitioning using the coastline distance alone, as performed by Cottenie (2005) for linear habitats. This is a more conservative approach because the use of only one variable tends to minimize the effect of space against the environment (with three environmental variables). Second, we computed a set of multi-scale spatial variables using eigenvectors from principal coordinates of neighbour matrices (PCNM; Borcard & Legendre, 2012). To prevent over-fitting the spatial component, we selected the first three (significant) PCNM vectors to equal the number of environmental factors (Cottenie, 2005). As the interpretation of PCNM vectors generally produces inflated statistics (Gilbert & Bennett, 2010), this approach provides a complementary view when the space effect is maximized. Moreover, interpretation of the forward-selected PCNM vectors allowed us to understand whether broad-scale or small-scale patterns (associated with first/large and last/short eigenvalues, respectively) were structuring the observed variation. RDAs and variation partitioning were performed for shifting and stable dunes and for each of the three geographical subsets separately, using Hellinger transformation of species cover in *CANOCO 5* (<http://www.canoco5.com/>).

RESULTS

Metacommunity structure

NMDS ordination identified the largest differences in species composition as being between the Cantabrian and Mediterranean sites in the shifting dunes (stress = 33.1; Fig. 1a) and a more distinct separation among the three geographical groups in the stable dunes (stress = 24.7; Fig. 1b). Sørensen dissimilarity among sites of shifting dunes increased from the Cantabrian (0.57 ± 0.01 , mean \pm SD) through the Atlantic (0.61 ± 0.01) to the Mediterranean (0.66 ± 0.01) regions. A similar pattern was found in the stable dunes, although in this case the dissimilarity values were higher (Cantabrian 0.63 ± 0.01 , Atlantic 0.66 ± 0.02 and Mediter-

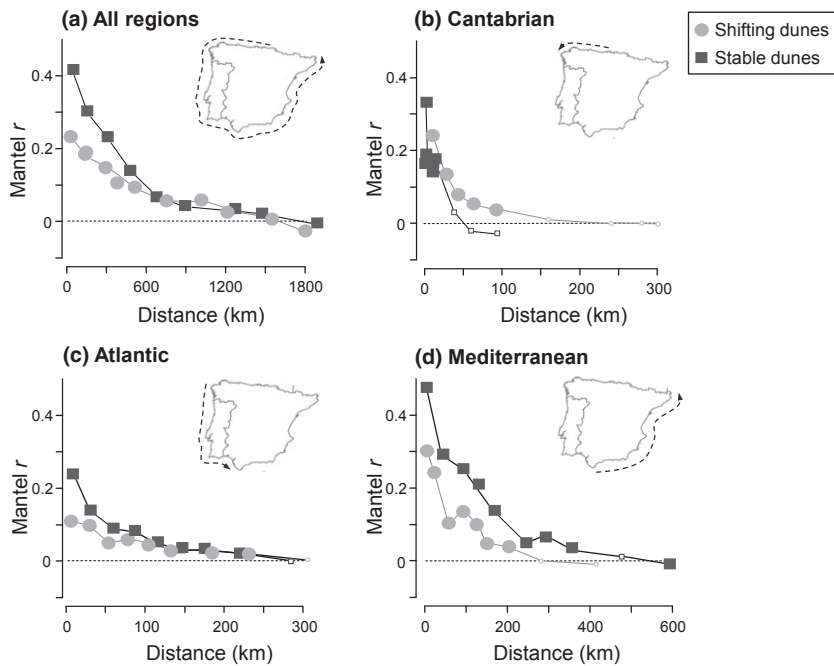


Figure 2 Mantel correlograms for communities of shifting and stable dunes in a study of regional plant metacommunities in coastal habitats on the Iberian Peninsula. The extent of the full data set (a) and the three geographical subsets (b, c, d) are depicted by dashed arrows in the inset maps (the arrows indicate the initial and final locations used to calculate relative distances between sites). Mantel r reflects the results of separate tests computed with equal numbers of sites for each lag distance. Small empty symbols indicate non-significant correlations ($P > 0.05$). The largest distances with no significant correlations are not shown.

reanean 0.73 ± 0.01). The results of ANOSIM confirmed the differences suggested by the NMDS, detecting lower differentiation in the data set for shifting dunes (global $R = 0.30$; $P < 0.001$) than stable dunes ($R = 0.55$; $P < 0.001$). Pairwise comparisons between groups were all significant (Table 2). They showed the highest differences to be between Cantabrian and Atlantic regions in the shifting dunes (global $R = 0.13$) but the lowest agreement was between the same regions in the stable dunes ($R = 0.75$).

According to the Mantel correlograms (Fig. 2), the geographical structure of the data reflected a general pattern of positive (and significant) similarity at nearer distances, with a gentle decrease, rarely reaching negative values, at further distances. Such a pattern was similar between shifting and stable dunes and among the three geographical regions. However, in stable dunes the correlation was generally higher than in shifting dunes along all distance classes, the only exception being the Cantabrian region, in which Mantel tests indicated high similarities at relatively short distances (< 20 km). In the other two cases, the Mediterranean region showed a higher correlation than the Atlantic region for the distance classes < 100 km, especially in the stable dunes.

Influence of climate and geography

RDA showed that all the variables had a significant effect on species variation, but affected the two data sets in different ways (Table 3). In the shifting dunes the coastline distance was the most important explanatory variable; in contrast, summer precipitation was the most important in the stable dunes. The effect of each of the variables differed between the regions, especially in the shifting dunes. This was also true for the separate analyses of the Cantabrian and

Table 2 Results of an analysis of similarities (ANOSIM) for species assemblages in a study of regional plant metacommunities in coastal habitats on the Iberian Peninsula, using pairwise comparisons of three geographical regions (Cantabrian, Atlantic and Mediterranean), calculated for shifting (global $R = 0.30$; $P < 0.001$) and stable (global $R = 0.55$; $P < 0.001$) sand dunes. R values near 0 indicate that the similarities among samples do not fit the groups (i.e. there is less support for the geographical groups), while $R = 1$ indicates that the most similar samples are in the same groups (geographical groups have a distinct species composition). P -values after Bonferroni correction.

	Shifting dunes		Stable dunes	
	R	P -value	R	P -value
Cantabrian versus Atlantic	0.13	< 0.001	0.75	< 0.001
Cantabrian versus Mediterranean	0.50	< 0.001	0.43	< 0.001
Atlantic versus Mediterranean	0.37	< 0.001	0.49	< 0.001

Mediterranean shifting dunes, but not for the Atlantic coast, where precipitation and temperature were the most important variables. The same result was obtained for the Atlantic subset, while in the Cantabrian and Mediterranean subsets precipitation was more important.

Variation partitioning deconstructed the total variance into pure geographical effects, pure climatic effects and the shared effects of geography and climate (Fig. 3). Using the coastline distance as the unique spatial variable, geographical distances were slightly more influential than climatic variables in the whole data set for shifting dunes, and similar amounts of variation were shared. Similar patterns were found in the Cantabrian and Mediterranean subsets, although in these cases the shared variation was low. In the

Table 3 Effects of geographical distance and climatic variables on the species composition of shifting and stable sand dunes in a study of regional plant metacommunities in coastal habitats on the Iberian Peninsula, analysed by partial redundancy analysis (RDA) for the whole data set (all regions) and three geographical subsets. EV indicates the partial explained variance of each predictor in the whole model. F is the F -statistic obtained from RDA. The significance of P -values was calculated from a Monte Carlo test with 999 permutations (** $P < 0.01$; * $P < 0.05$; n.s., non-significant).

	All regions		Cantabrian		Atlantic		Mediterranean	
	EV	F	EV	F	EV	F	EV	F
Shifting dunes								
Coastline distance	9.5	48.8**	4.0	5.2**	n.s.	n.s.	4.7	5.8**
Annual precipitation	0.4	2.2*	n.s.	n.s.	1.5	3.4**	n.s.	n.s.
Summer precipitation	3.9	20.9**	1.9	2.5*	n.s.	n.s.	n.s.	n.s.
Mean temperature	1.0	5.3**	1.8	2.4*	1.8	3.9**	4.7	6.1**
Stable dunes								
Coastline distance	6.3	26.6**	4.3	2.8**	2.5	4.6**	3.1	4.7**
Annual precipitation	1.3	5.7**	7.5	4.5**	1.5	2.5**	6.7	9.6**
Summer precipitation	7.8	30.8**	4.9	3.0**	1.	3.6**	2.2	3.4**
Mean temperature	2.8	12.4**	n.s.	n.s.	4.5	8.0**	3.6	5.3**

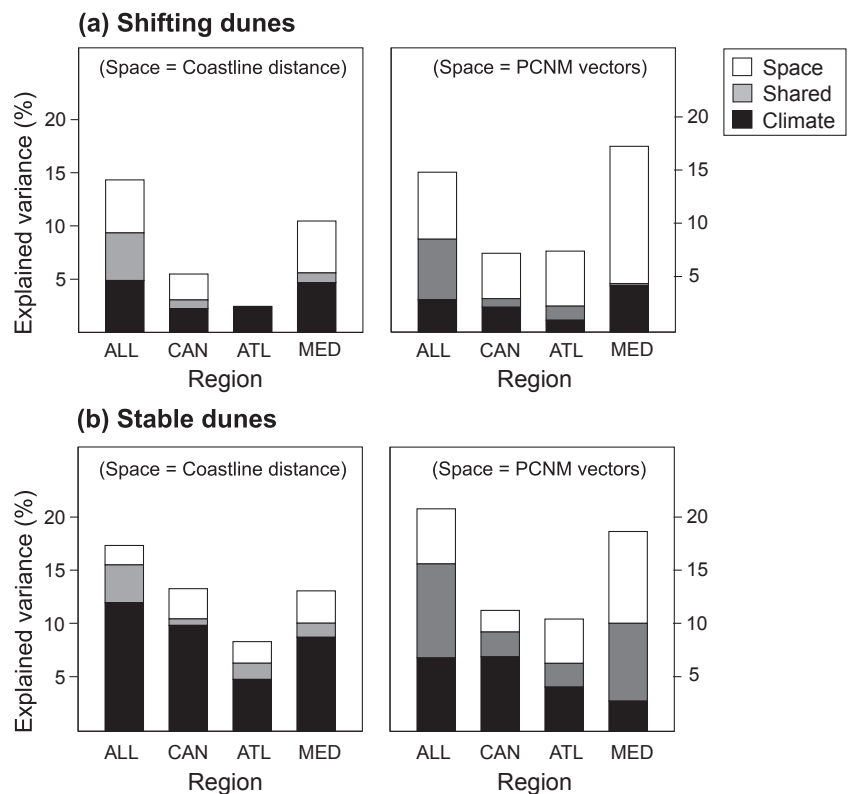


Figure 3 Results of variation partitioning for the effects of climate (variables as shown in Table 2), space [as a function of the coastline distance and derived principal coordinates of neighbour matrices (PCNM) vectors] and the fraction corresponding to the intersection of both factors (shared) in a study of regional plant metacommunities in coastal habitats on the Iberian Peninsula. The explained variation was calculated from adjusted R^2 -values after performing separate redundancy analyses (RDA) for shifting (a) and stable (b) sand dunes, for the whole data set (ALL) and geographical subsets representing the Cantabrian (CAN), Atlantic (ATL) and Mediterranean (MED) regions.

Atlantic subset, climate was the only factor that contributed to the explained variance. Different results were found in stable dunes, where the climatic variables explained much more variation than geographical distance in all cases. The shared variation was higher than the variation explained by distance only in the whole data set, but much lower than the individual effect of both factors in the geographical regions.

As expected, the use of the PCNM vectors led to an increase in influence of the spatial component in the two data sets. However, we found similar patterns with stronger

climatic influences on stable dunes than on shifting dunes, in most cases incrementing the shared explained variance. The components with significant eigenvalues (PCo) considered after forward selection mainly reflected broad-scale spatial variation. For shifting dunes, they were PCo1, PCo2 and PCo3 for the whole data set and the Cantabrian and Mediterranean subsets, and PCo3, PCo6 and PCo9 for the Atlantic subset. For stable dunes, the selected vectors were PCo1, PCo2 and PCo5 for the whole data set, PCo2 and PCo4 for the Atlantic, PCo2 for the Cantabrian, and PCo1, PCo2 and PCo3 for the Mediterranean subsets.

DISCUSSION

This study suggests that large-scale patterns in the structure of two coastal dune metacommunities are consistent across biogeographical regions. Our results also provide new insights about the spatial scales that are influencing between-site variation in dune plant communities. In both shifting and stable sand dunes, we detected a pattern of distance decay suggesting that spatial autocorrelation of communities is mainly acting at relatively short distances (typically below 100 km). Although the decrease of community similarity at larger distances is known (Soininen *et al.*, 2007), the pattern detected here differs from similar analyses of other organisms in which large distances provide negative similarities (Sokol *et al.*, 2011). Moreover, the spatial autocorrelation found in stable dunes was in general stronger than in shifting dunes, supporting the idea that different processes are structuring the metacommunities of the two habitats.

We found that space was the strongest factor influencing metacommunity structure in shifting dunes, but climate was more important in stable dunes. These results were relatively consistent across geographical regions with different coastal configurations, supporting at least partially the use of coastline distance as a proxy of connectivity between dunes. However, we note that the interpretation of dispersal patterns using coastal distance has to consider the assumption of linearity across dune habitats, potentially neglecting the irregular shape and complexity of coastal systems. Despite this, the results of variation partitioning using both the coastline distance and PCNM vectors agreed, giving more relevance to climate or [climate + space] in stable dunes than in shifting dunes. Assessing the relative importance of spatial and environmental components in the two habitats provides a useful background for developing hypotheses about the determinants of species distributions (Gilbert & Bennett, 2010). Thus, the more separated in linear space that two dune sites are, the more different the community pairs of shifting dunes are if compared with those of stable dunes. The effect of space in the data set of shifting dunes is especially relevant when using only the coastline distance, considering that the number of climatic variables included in the RDAs is higher, and thus they are expected to account for more variation (Blanchet *et al.*, 2008).

Although we cannot completely dismiss the effect of space on the data set of stable dunes, the strong influence of climatic variables in different geographical regions supports the hypothesis that the communities of this habitat are mainly regulated by climate. This effect reflects a metacommunity model mainly based on the species-sorting paradigm, which might be combined with mass effects by considering the complementary effect of space (Cottenie, 2005), especially in the Mediterranean data set. Large-scale dispersal predicted by mass effects in the Mediterranean could explain the higher turnover detected in this region, as a possible result of historical or recent connectivity between sites. This explanation

is supported by the existence of a thermohaline circulation system in the semi-closed Mediterranean sea (Pinaridi & Masetti, 2000), which could be a possible factor in the improved connectivity among coastal areas. However, some species from stable dunes (e.g. *Armeria pungens*) have populations that are clearly characterized by their genetic distances as a result of climatic drivers (Piñeiro *et al.*, 2007). Although a model emphasizing species sorting has already been proposed for dune metacommunities (Brunbjerg *et al.*, 2012), our study shows for the first time the influence of climatic drivers at broader scales. Summer precipitation was the best predictor of species composition in the whole data set of stable dunes, providing further proof of climatic gradients influencing communities in the temperate and Mediterranean climatic regions. This agrees with the dissimilarities detected between the Cantabrian and Atlantic coasts in stable dunes (Table 2), regions that are geographically contiguous but climatically different. Furthermore, the species composition of stable dunes may be more greatly influenced by the species pool of inland habitats, partially explaining the higher diversity in terms of species richness and turnover that we detected in this habitat.

The influence of climate also supports the idea that, at short geographical distances (< 100 km), regional communities are relatively more similar in stable dunes than in shifting dunes, as a possible effect of spatial autocorrelation of climatic variables. However, it is assumed that community similarity decays when species have limited dispersal capacity or when there are dispersal barriers (Hubbell, 2001), and this effect could explain part of the variance accounted for by space. Thus we cannot exclude the existence of dispersal limitation in both shifting and stable dunes at large distances. This is a general expectation in broad-scale systems, where large geographical distances provide less chance for dispersal and reduce spatial connectivity, supporting the patch-dynamic and the neutral metacommunity paradigms (Logue *et al.*, 2011). Dispersal limitation in evolutionary terms can also be recognized in dune communities at a global scale as a possible driver of regional diversification (Brunbjerg *et al.*, 2014). As the pure effect of space is a more important factor for structuring species assemblages in shifting dunes, we could argue that dispersal limitation has a strong effect on this habitat. Moreover, the similarities detected by ANOSIM suggest geographical barriers between the three regions, with the largest differences being between the Cantabrian and Mediterranean coasts (which are geographically strongly separated), followed by the differences between the Atlantic and Mediterranean coasts (separated by the Strait of Gibraltar). Interestingly, these geographical barriers agree with the patterns of sea currents in the coasts of the Iberian Peninsula (Moreno *et al.*, 2012). Thus metacommunities of shifting dunes are probably not fully explained by a combination of species sorting and mass effects: dispersal limitation may also contribute significantly.

The interpretation of dispersal limitation in the observed patterns contrasts with evidence that suggests high

connectivity among coastal dune habitats. Marine seed dispersal has been demonstrated for species of shifting dunes (Gandour *et al.*, 2008), in which long-distance dispersal through the sea is a relatively frequent event reflected in low interpopulation genetic variability (Clausing *et al.*, 2000; Kadereit & Westberg, 2007). The apparent contradiction of this evidence to our initial interpretation (dispersal limitation in shifting dunes) can be explained, on the one hand, by the heterogeneity of the analysed data. As the variation in communities is based on the whole species composition, dispersal of some specialists can be overridden by those of generalist species. Thus it is likely that shifting dunes support long-distance dispersal events of individual species in the context of heterogeneous communities. On the other hand, a pattern of dispersal limitation can be explained by a disturbance hypothesis. In general, the species of early successional habitats display more effective long-distance dispersal strategies than those of mid-successional habitats (Peroni, 1994; O'Connell & Eckert, 2001), explaining a higher connectivity within species of shifting dunes, which represent early successional stages. Only propagules (e.g. seeds) adapted to floating and viable after long periods of submersion can be dispersed (Walmsley & Davy, 1997), from which only a subset will be successful, depending on factors that are difficult to predict, like predation, water currents, winds and the successional stage of the sand dunes (Gandour *et al.*, 2008). Neutral processes are thus expected to be stronger in shifting dunes, and subjected to historical disturbances related to changes in sea level and connectivity among regions (Clausing *et al.*, 2000).

CONCLUSIONS

The metacommunity concept is relatively new and has been scarcely explored at larger scales (Leibold, 2011). In this study we provide a general view of the patterns structuring regional plant metacommunities in coastal dunes, suggesting different assembly processes in two habitats with different ecological features. Overall, we demonstrate that regional metacommunities of dune habitats are not fully dominated by species sorting, as has been described at local scales (Brunbjerg *et al.*, 2012). Thus, spatial patterns related to patch-dynamic or neutral processes must also be considered as driving factors, supporting the expectation that increasing spatial scale of analysis tends to increase the signal of spatial dynamics (Cottenie, 2005). We suggest a certain influence of neutral processes as a result of the historical contingencies and spatial factors widely recognized in coastal dunes (Clausing *et al.*, 2000; Gandour *et al.*, 2008) but also hypothesize the presence of other causes related to the disturbance of pioneer habitats, minimizing the influence of climatic factors in shifting dunes. Although it is still necessary to test such a disturbance hypothesis, the stochasticity of dispersal routes and seed establishment in disturbed soils might be a good explanation for the unpredicted patterns in these communities. Our results from different geographical subsets are

consistent enough to support the existence of large-scale variation governed by different paradigms in the two habitats. We therefore highlight the importance of differentiating related habitats along local gradients when analysing broad-scale patterns in metacommunities, in order to integrate diversity patterns properly at local and regional scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Bibliographic details of the data sources.

Appendix S2 Species diagnostic of shifting and stable sand dunes.

BIOSKETCH

Borja Jiménez-Alfaro is a postdoctoral fellow at the Vegetation Science Group of Masaryk University. His research focuses on the diversity and distribution of plant communities, with a special focus on understanding large-scale vegetation patterns in Europe.

Author contributions: B.J.-A. and C.M. contributed equally; B.J.-A. and C.M. conceived the idea; C.M. developed the database; B.J.-A. conducted the analyses and led the writing; all authors contributed to the experimental design, interpretation of the results and commented on the manuscript.

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