Original article

Co-occurrence patterns and abiotic stress in sand-dune communities: Their relationship varies with spatial scale and the stress estimator

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A B S T R A C T

The analysis of co-occurrence patterns between plant species is being increasingly employed to study biotic interactions at the community level. We investigated changes in such patterns along two different abiotic stress gradients in eight sand-dune plant communities of the western coast of Portugal. We sampled a total of 72 transects consisting on 25 1 m^2 quadrats each, and we calculated the standardized effect size for each transect (SES), i.e. the differences between the observed co-occurrence patterns and simulated patterns for a random co-occurrence. The relationships between the average SES values for each site and the abiotic stress gradients, defined by the north–south geographic gradient (a surrogate of the climatic stress) and total plant cover (a surrogate of productivity), were analyzed. The factors driving co-occurrence patterns at smaller spatial scale were also investigated by a stepwise multiple regression analysis. Average SES values were significantly higher than zero in five of the studied sites, indicating lower species co-occurrence than expected by chance. These results suggest that the studied sand-dune communities studied are structured mainly by competitive interactions. At the site scale, SES values were not related to plant cover or the location along the north–south gradient. However, at the transect scale, SES values were inversely explained by different abiotic factors (the geographic position along the north–south gradient and the plant cover). Our results indicate that the magnitude and the shifts in co-occurrence patterns along environmental gradients varied with the spatial scale and the surrogate of abiotic stress considered.

1. Introduction

The structure of plant communities plays a key role in ecosystem functioning, dynamics and stability, and constitutes an "ecological fingerprint" that characterizes essential ecosystem processes (Goreaud and Pélissier, 2003; Maestre et al., 2005a; Pimm, 1984; Wilsey and Potvin, 2000). Additionally, the plant community structure is largely driven by biotic interactions such as competition and facilitation (Callaway, 2007; Keddy, 2001), and the complex balance between these opposite processes is influenced by factors like the degree of abiotic stress (Maestre and Cortina, 2004), the ontogeny of the interacting species (Miriti, 2006) and the traits of the interacting species (Michalet, 2007).

Since Diamond's assembly models, early in 1975, plant species in natural plant communities are predicted to co-occur less often than expected by chance due to competitive interactions among them (Diamond, 1975; Gotelli and McCabe, 2002). However, facilitative interactions among plant species are found virtually in all terrestrial ecosystems, and are prevalent in stressful environments (Callaway, 2007). In particular, there is substantial evidence for facilitation in sand-dune communities (e.g. Franks, 2003; Martínez, 2003; Shumway, 2000).

The interplay of facilitative and competitive interactions among plants, and the way it relates to abiotic stress, is a major research topic among community ecologists (Brooker et al., 2008; Callaway, 2007). The "stress gradient hypothesis" (SGH hereafter; Bertness and Callaway, 1994) states that positive interactions should be "particularly common" or increase in "frequency" under stressful conditions. The SGH predicts that the relative importance of facilitation and competition will vary inversely across gradients of abiotic stress, with facilitation being dominant under stressful conditions. Despite widely supported in the literature (Callaway, 2007) the generality of predictions from the SGH have been

recently debated (Maestre et al., 2005b, 2006; Lortie and Callaway, 2006), and refinements to its conceptual framework have been suggested to make it more capable to encompass or fit all situations that occur in nature (Maestre et al., 2009a).

The use of manipulative experiments to study biotic interactions at the community level has important logistic and analytic limitations, and thus most of the experimental tests of the SGH have evaluated only the magnitude and direction of change in pairwise interactions along stress gradients (see Callaway, 2007 and Maestre et al., 2005b for reviews). However, there is a clear need to explore facilitative/competitive interactions among all the members of a given community, if we aim to substantially advance our understanding of their role as drivers of ecosystem structure and functioning (Brooker et al., 2008). This is so because the study of one or a few particular pairs of species may not suffice to accurately predict how biotic interactions within a given community will change along abiotic stress gradients. The use of observational approaches is recommended to overcome logistic limitations imposed by experiments when working with whole communities (Brooker et al., 2008; Maestre et al., 2009a). Indeed, it has been recently shown that changes in net interactions at the community level along abiotic stress gradients can be tracked using the fine-scale spatial arrangement of species (Dullinger et al., 2007; Kikvidze et al., 2005; Maestre et al., 2009b). In this study we follow these recommendations and we contribute to the debated related with the SGH.

With the aim to explore variations in biotic interactions at the community level along stress gradients, and to contribute to the debate related with the SGH, we conducted a null model analysis of co-occurrence patterns (Gotelli, 2000) in sand-dune plant communities across a north–south gradient of the western coast of Portugal. These communities live in a hostile environment, characterized by permanent sand mobility, drought conditions (created by the particular hydrological characteristics of sand), strong salty winds, and constant sand movements; therefore a net dominance of facilitation on such stressful systems is expected (Houle, 1997). Our hypothesis were twofold: (i) the harsh environment of sand-dune systems will promote a net species aggregation (indicative of facilitation); and (ii) co-occurrence patterns will vary along abiotic stress gradients as predicted by the SGH, i.e. the fine-scale spatial arrangement of plants shift from prevailing interspecific segregation to aggregation as abiotic stress increases.

2. Methods

2.1. Study area

This study was carried out in eight sites located in well -preserved coastal sand dunes of western Portugal (Table 1). These communities are the habitat of many threatened species, hold a high number of endemisms, have high biogeographic interest, and are currently protected by the European (Habitats Directive, Annex II) and Portuguese laws. The study sites extend along a total distance of 247 km, with an average distance of 20 km between sites. Sampling was conducted in the yellow dunes of each site, i.e. in the dune area just after the fore dunes. These areas had more than 30% of bare soil, no more than 14% of litter cover on average, and sparse shrubs and forbs. The dominant species were *Carpobrotus edulis* (L.) N. E. Br., *Corema album* (L.) D. Don, *Juniperus phoenicea* L., *Helichrysum italicum* spp. *picardii* (Boiss. & Reuter) Franco, and *Artemisia campestris* ssp. *maritima* Arcangeli; the dominant forbs were *Lotus creticus* L., *Malcolmia littorea* (L.) R. Br., *Sedum forsteranum* Sm., and *Medicago marina* L.

The climate is Mediterranean, with mild wet winters and warm dry summers. In the northern area, the mean annual precipitation and temperature are 830 mm and 15 °C, respectively; in the southern sites, those values are 650 mm and 17 °C, respectively (Ninyerola et al., 2005). In all sites the uppermost soil is sandy and poor in organic matter, with no distinct organic horizon.

2.2. Vegetation sampling and assessment of abiotic stress

A total of 72 transects were surveyed along the 8 study sites (8–10 per site). Each transect consisted in a linear sequence of 25 plots of 1 m², and in each plot we estimated the cover of each perennial and bi-annual species. The plots were all surveyed by the same person, to minimize measurement errors.

We registered the geographic coordinates of each transect with a Ground Position System (GPS), and from them we calculated: a) the distance between each transect and the southernmost transect, i.e. the position of each transect along the north–south geographic gradient of the western coast of Portugal; and b) the distance of each transect to the shoreline. The former was expected to be a surrogate of the climatic gradient, with the temperature rising from north to south, and the precipitation rising in the opposite direction (Ninyerola et al., 2005). The distance to the shoreline is a surrogate of abiotic stress at small spatial scales, since blowing sand and salt sprays decrease, and soil nutrients increase, with that distance (Henriques and Hay, 1992; Rajaniemi and Allison, 2009). Additionally, we used the total cover of each transect as a surrogate of total biomass (Dullinger et al., 2007), which is commonly considered a surrogate of abiotic stress for the whole plant community (Grime, 1973; Lortie and Callaway, 2006). Although plant cover ignores the vertical arrangement of vegetation, it is likely to be closely related with biomass in the studied communities, which are commonly low-stature and open systems.

2.3. Assessment of co-occurrence patterns

To assess the co-occurrence patterns of the studied plant communities, we conducted null model analyses with Ecosim 7.22 (Gotelli and Entsminger, 2003). For each transect, the data were

Table 1
Summary table on characteristics of the studied sites. Abbreviations: Lat, latitude; Long, longitude; Precip, annual precipitation; Min temp, minimum annual temperature; Max temp, maximum annual temperature; Mean temp, mean annual temperature; Rad, mean annual radiation; Elev, elevation; Plan cover, mean total plant cover; Lichens, mean percentage cover of lichens; Moss, mean percentage cover of mosses; Soil, mean percentage cover of bare soil; Litter, mean percentage cover or litter.

Site	Lat (N)	Long (W)	Precip	Min temp	Max temp	Mean temp	Rad	Elev	Plant cover	Lichens	Moss	Soil	Litter
Sines	37°59′18.0″	Z8°51′22.0″	664	12	24	18	2033	14.6	59.3	0.0	0.6	32.0	11.8
P. MonteVelho	38°4′56.2″	8°48′34.2″	650	12	24	17	2033	17.1	54.8	0.0	0.1	37.6	13.8
Melides	38°7′29.6″	Z8°47′37.5″	638	12	24	17	2056	12.9	58.4	0.3	1.0	33.5	1.0
Troia	38°25′38.9″	Z8°49′51.0″	646	12	24	17	2035	11.4	51.6	6.9	0.3	34.3	0.4
Nazaré	39°33′41.2″	Z9°05′51.9″	777	11	23	15	2035	15.1	62.4	0.0	0.7	28.0	0.0
P. Vieira	39°53′6.6″	8°58′2.4″	854	11	23	16	2039	12.8	52.5	0.0	2.0	42.6	0.0
Leirosa	Z40°03′50.9″	Z8°53′10.2″	831	11	23	16	2035	10.1	48.6	1.5	0.5	44.8	0.9
Quiaios	40°14′9.2″	Z8°53′1.2″	848	11	23	16	2033	13.3	50.1	0.2	0.6	42.0	1.4

organized as a presence-absence matrix, where each row and column represents a different species and plot, respectively. We used the C-score index to quantify the co-occurrence patterns of the sand-dune communities studied. The C-score was calculated for each pair of species as (Ri–S)(Rj–S), where Ri and Rj are the matrix row totals for species i and j, and S is the number of squares in which both species occur; this score was then averaged over all possible pairs of species in the matrix. If a community is structured by competitive or facilitative interactions, the C-score should be significantly larger or smaller than expected by chance, respectively (Gotelli, 2000).

The indices obtained from each matrix were compared with those derived from 10 000 randomly assembled matrices (null matrices). The null matrices were generated using a "fixed rows-fixed columns" null model, which keeps constant both the species frequencies and the number of species in each sample, and thus retains the rareness of each species in each site (Gotelli, 2000). This null model has good statistical properties, with low Type I error and good power to detect nonrandomness (Gotelli and Entsminger, 2003). Null matrices were created with a sequential swap algorithm by repeatedly swapping randomly selected submatrices of the form 01/10 (Gotelli and Entsminger, 2006). Extensive simulation analyses have shown that this algorithm is statistically well behaved (Gotelli and Entsminger, 2003).

To facilitate comparison with other studies, a standardized effect size (SES) was calculated for each matrix as $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} is the observed value of a given index of community structure, and I_{sim} and S_{sim} are the mean and standard deviation, respectively, of the index obtained from the 10 000 null communities (Gotelli and McCabe, 2002). Values of SES larger or smaller than 0 indicated prevailing spatial segregation or aggregation among the species within a community, respectively.

2.4. Statistical analyses

A Principal Components Analysis (PCA) of the climatic variables was performed to identify the climatic gradient at the larger scale and relate it with the geographic position of each site. One-sample t-tests were used to test the null hypothesis that the mean SES for each site did not differ from zero (Gotelli and Rohde, 2002). A one-way ANOVA was conducted to evaluate differences among sites in total plant cover. Simple regression analyses were used to interpret the co-occurrence patterns at the larger scale, with SES values as dependent variable, and the total plant cover and the geographic position along the north–south gradient as independent variables. Additionally, a stepwise multiple regression was used to relate the changes in SES values (dependent variable) with total plant cover, the geographic position along the north–south gradient, and the shoreline distance (independent variables). All these statistical analyses were performed in STATISTICA v6.0 (StatSoft, 2001).

3. Results

The first axis of the PCA conducted with the climatic variables explained almost 87% of the variance and was defined by an increasing gradient of temperature and a decreasing gradient of precipitation. The north–south geographic gradient was a proxy of that climatic gradient, with a spearman rank correlation of 0.7 between the first axis of the PCA and the geographic gradient.

Average SES values were greater than 0 in all the sites studied (Fig. 1), indicating prevailing spatial segregation, i.e. competition, among the species within the community. The null hypothesis that these values do not differ from zero was rejected in 5 of the 8 sites surveyed (Fig. 1). Although there were some differences among sites with respect to their plant cover (results from the one-way
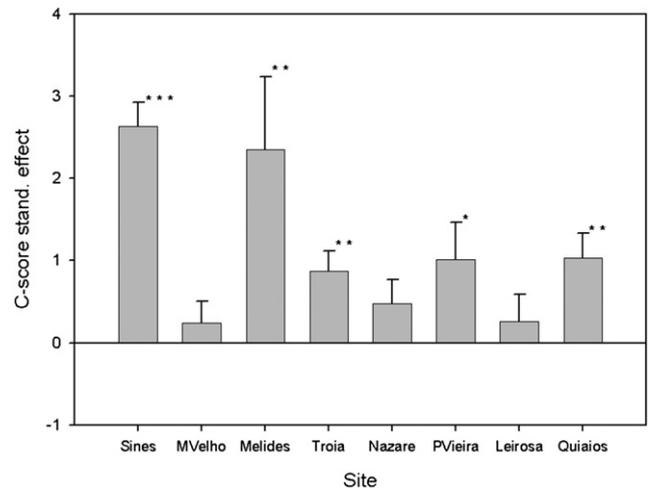

Fig. 1. Standardized effect sizes obtained in the sand-dune communities studied. Data represent means ± SE ($n = 8$–10). Asterisks indicate significant departures from 0 (t-test; ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

ANOVA, Fig. 2), average SES values were neither related to total plant cover ($r^2 = 0.18$, $p = 0.29$), nor to the position of the sites along the north–south geographical gradient ($r^2 = 0.25$, $p = 0.20$), at the site scale. At the transect scale, the stepwise multiple regression analysis showed that the geographic position along the north–south gradient and the plant cover, but not the shoreline distance, were significantly related with the SES values of each transect (F $(2,69) = 9.746$, $p < 0.0002$): higher SES values were found from north to south ($p = 0.004$), and in more dense vegetation ($p = 0.013$).

4. Discussion

The results obtained contradict our first hypothesis stating that positive interactions between species are particularly common in communities at stressful environmental conditions (Bertness and Callaway, 1994; Shumway, 2000). In contrast, there was a prevalence of lower species co-occurrence than expected by chance, which suggests the dominance of competitive interactions among
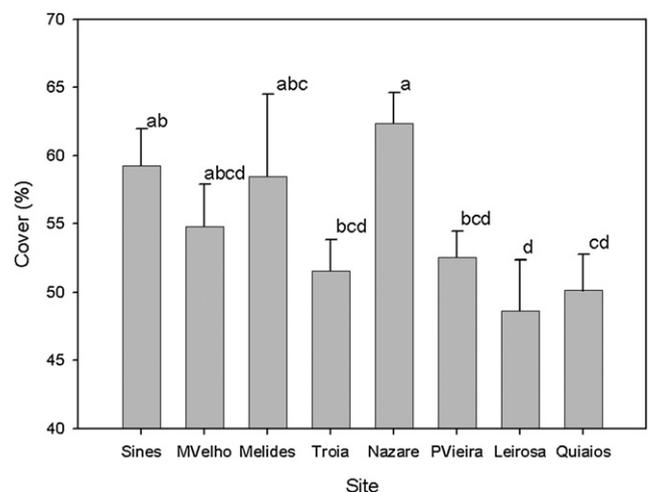

Fig. 2. Plant cover values obtained at each study site. Data represent means ± SE ($n = 8$–10). Different letters indicate differences among sites (one-way ANOVA; $p < 0.05$).

the plants forming the sand-dune communities studied (Dullinger et al., 2007; Gotelli, 2000). In the coastal dunes of the southeastern United States, Franks (2003) studied facilitation processes by adult plants at early life stages, and found that the most probable mechanism of facilitation was the influence of adult plants on the stability of the substrate and the patterns of movement of sand and seeds. Martínez (2003) also found that in dune environments the facilitative plant–plant interactions are favored mostly during the early stages of primary succession. Finally, Armas and Pugnaire (2009) showed that there are ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand-dune system. These authors found that mature individuals facilitated the establishment of seedlings, which competed with them at later life stages. Therefore, our results, showing no dominance of facilitative interactions, can be attributed to the fact that the sand-dune communities studied are not in the early stages of succession, and to the predominance of adult individuals.

Although sand instability has been identified as a major driver of the composition of sand-dune communities (Forey et al., 2008), the distance to the shoreline was not an important variable in explaining the co-occurrence patterns of the surveyed communities. Probably this was because all sites and transects were positioned in the yellow-dune zone, within homogeneous areas, and therefore they were probably subject to similar levels of salt sprays, soil nutrients and salinity.

Our second hypothesis, i.e. that co-occurrence patterns vary along abiotic stress gradients as predicted by the SGH, was partially supported by the results. As predicted by the SGH, co-occurrence decreased with the increase in plant cover, suggesting that competition increased under the less stressful conditions. However, our results showed that variations in co-occurrence patterns were dependent on the spatial scale and the surrogate of abiotic stress considered. At the site scale, there was not a clear trend in the SES values; at the transect scale, both the north–south geographic gradient and the total plant cover were important drivers of the observed variation in species co-occurrence. These contrasting results highlight the difficulties associated with measuring stress (Lortie et al., 2004; Lortie and Callaway, 2006). Besides, our results mirrored those obtained by Dullinger et al. (2007), who evaluated co-occurrence patterns in alpine plant communities using different grain sizes. These authors also found weak and variable relationships between co-occurrence patterns and abiotic stress, dependent on the surrogate of abiotic stress considered. In addition, most of these relationships were found at the smallest grain size, and disappeared when the observation scale increased. Similar responses were also reported by Maestre et al. 2009b, who studied co-occurrence patterns between soil lichens across complex abiotic stress gradients driven by nutrient and water availability.

The bulk of facilitation research is constituted by studies evaluating interactions among a few pairs of species (see Callaway, 2007, for a recent review). However, pairwise interactions do not necessarily reflect what is happening at the community level (Valiente-Banuet and Verdú, 2008), and indeed may not suffice to explain processes such as the abundance of species within complex communities (Engel and Weltzin, 2008). To our knowledge, our study is the first aiming to explicitly evaluate changes in biotic interactions at the community level in sand-dune communities, and provides novel insights on their response to abiotic stress. Our results show that variations in co-occurrence patterns depend on the spatial scale and the surrogate of abiotic stress considered. Incorporating these aspects in the conceptual framework of biotic interactions, which currently focuses on pairwise interactions (e.g. Maestre et al., 2009a), may substantially help to explain and reconcile results obtained at different spatial scales and in diverse communities (see Lortie and Callaway, 2006; Maestre et al., 2005b, 2006; Michalet, 2007), and to advance in our understanding of biotic interactions as a driver of community structure and dynamics.

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