Community structure and positive interactions in constraining environments

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Spatial patterns in plant communities are thought to be controlled by the interplay of species interactions and environmental constraints. To evaluate the role of plant–plant interactions in shaping these communities we quantified species co-occurrence and interaction in seven environmentally distinct communities. These included four different semiarid habitats in southeast Spain, one alpine system in the Sierra Nevada range (Spain), and two sites in Venezuela, a secondary savanna near Caracas (Altos de Pipe), and a sclerophyllous shrubland in the Gran Sabana plateau. We expected that facilitation would be stronger at sites with more spatial associations. The four semiarid sites in Spain and the shrubland in Gran Sabana showed a high degree of positive species associations. Of the other two communities, one showed both positive and negative associations while negative ones predominated in Altos de Pipe. The direct experimental measure of neighbors' effect showed that positive interactions among species prevailed in communities where positive species associations dominated. The appearance of benefactor species in patches increased species richness compared with the surrounding inter-shrub spaces. Our results provide a link between spatial patterns and species interactions, where aggregation points to positive interactions and segregation to competitive or interference effects. Facilitation appears as a relevant process shaping communities under environmental constraints.

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Individuals of different species in a community may be arranged spatially at random or otherwise show a structured organization determined by several factors, including species interactions, microsite requirements, and dispersal (Diamond 1975, Case and Sidell 1983, Drake 1990, Keddy 1992). Although community ecology has primarily focused on the role of competitive interactions in shaping plant communities (Crawley 1997, Tofts and Silvertown 2002) the importance of positive interactions has recently been shown (Callaway 1997, Stachowicz 2001, Callaway et al. 2002, Bruno et al. 2003), particularly in communities under physically demanding conditions where plants are often distributed in clumps of vegetation in a matrix of bare ground. This

clumped distribution pattern was frequently presented as evidence for positive interactions (Haase et al. 1996, Kikvidze and Nakhutsrishvili 1998, Eccles et al. 1999) but the importance of positive plant–plant interactions in determining how species distribute within communities was rarely tested in the field. Theory predicts a continuum between positive and negative interactions along environmental gradients (Bertness and Callaway 1994, Callaway and Walker 1997, Pugnaire and Luque 2001, Lortie et al. 2004), with positive effects prevailing at the most infertile conditions. In this framework, it could be expected that facilitation by neighbors leads to clumped patterns, as association would improve survival and growth; opposite, strong competition between

neighbors will lead to a random or regular distribution through thinning and density-dependent mortality (Kikvidze et al. 2005).

Plant community structure results from ecological processes in a spatial context (Silvertown and Wilson 1994, Wiegand et al. 2003). We can therefore use plant community structure to infer the spatial nature of ecological processes. By combining indirect methods of estimation (i.e. species distributions tested against null models, Harvey et al. 1983) and direct data on the intensity of species interactions, we could link observed patterns and underlying processes (Wiegand et al. 2003).

Here we report on seven plant communities where we investigated the processes that led to their current structure. We asked how these patchy shrublands were structured, and whether interactions had a role in generating these patterns.

First, we quantified four aspects of plant community structure: degree of species association, variance of species richness across patches, nestedness and checkerboard patterns. We expected that in communities where positive plant–plant interactions determine species arrangement, the spatial pattern would show evidence in: 1) species association, as species would be more spatially associated than expected at random; 2) variance of species richness, since clumps with the higher number of species will potentially be indicative of facilitation by neighbors; 3) checkerboarding, being mutual competitive exclusion less important in less productive environments, communities will not show a range of checkerboard patterns; 4) nestedness, when the sequence of species aggregation in clumps occurs in an ordered manner, so that less frequent species will appear only when a certain set of species are already present in a patch.

This hypothesized link between structured spatial pattern and plant interactions does not exclude microsite effects and differential dispersal as additional factors shaping communities, but we focused here in the importance of plant–plant interactions.

In a second step, we measured the strength of interactions as the response of plants to the presence of neighbors, and related these data to the spatial pattern of each community, testing whether the spatial distribution of species mirrored the actual interaction intensity. In harsher environments we expected to find a higher proportion of species being associated to neighbors, as well as stronger positive interactions among the associated species.

Methods

Study sites

We conducted the study in seven scrub communities with low productivity differing in patchiness, species richness, and abiotic conditions (Table 1). We selected four sites in the semiarid region of southeast Spain, one alpine site in the Sierra Nevada range (Spain) and two sites in Venezuela (a secondary savanna near Caracas and a sclerophyllous scrub in the Gran Sabana). All communities showed a pattern in which vegetation patches were scattered in a matrix of scarce plant cover, except the Venezuelan savanna, where inter-shrub spaces were occupied by grass. All sites were characterized by harsh environmental conditions (Table 1). In semiarid southeast Spain rainfall is low and communities are subjected to strong water deficits and high temperatures and radiation for at least four months each year (Tirado 2003). Alpine scrubs in Sierra Nevada are subjected to extreme cold temperatures in winter along with summer water deficits, in addition to desiccating winds and high summer irradiance (Körner 1999). The Venezuelan

Table 1. Location of study sites and their main characteristics.

Location	Dominant focal shrub	Type of community	Elev. m	Rainfall* mm.	Mean T °C	Limiting conditions
Altos de Pipe Venezuela	*Eupatorium amigdalum*	tropical secondary savanna	1750	1000	18	poor soils
Cabo de Gata[†] Spain	*Chamaerops humilis*	semiarid coastal range	40	157	19.5	poor soils strong water deficit
El Ejido Spain	*Maytenus senegalensis*	semiarid coastal plain	85	317	18.3	poor soils strong water deficit
Gran Sabana Venezuela	*Humiria balsamifera*	tropical upland scrub	1080	2428	20.6	poor soils strong water deficit
Sierra Nevada Spain	*Cytisus purgans*	alpine shrubland	2400	730	8.5	extreme temperatures strong water deficit
Tabernas Spain	*Hamada articulata*	semiarid desert	490	221	17.9	poor soils strong water deficit
Torregarcia Spain	*Ziziphus lotus*	semiarid coastal plain	20	190	18.5	poor soils strong water deficit

*Climate values are from the closest available weather station to each site.
[†]Two additional sites were measured in Cabo de Gata (following the exact same procedure as for the other sites), but only included in the analyses to improve the goodness of fit in regressions with relevant variables.

secondary grassland occurs in poorly developed soils with low nutrient level, induced by recurrent fires that destroy vegetation and soil litter (F. I. Pugnaire, unpubl.). Sclerophyllous scrubs in the Gran Sabana occur on poorly developed soils on white sands with low nutrient levels (Dezzeo et al. 2004), and are subjected to water shortage during the dry season (Huber 1986, 1995).

Community structure

At each site we chose a random point from which we placed parallel transects systematically in an east–west direction and sampled until approximately 1000 patches were recorded, although we sampled only 400 in Sierra Nevada and the Venezuelan savanna. Transects were separated 20 meters in sites with large patches (diameter >0.5 m), and five meter in sites with small patches (diameter <0.5 m: cushion shrubs in Sierra Nevada and regenerating shrubs in Altos de Pipe). We recorded the shrub species composition of patches, i.e. one or more shrubs surrounded by bare ground or non-perennial vegetation, if any part of the patch was encountered along the transect. We only considered shrub species (i.e. woody plants ramifying from the base, usually achieving low height, Judd et al. 1999), and those occurring in fewer than five patches were omitted from analyses.

Four aspect of community structure were studied using different indices:

Species association-The index of species association determines whether the distribution of negative and positive associations between pairs of species differs from a random distribution of occurrence. For each pair of species (i, j) we calculated the association coefficient (AC) as $AC_{ij} = O_{ij} - E_{ij}$, where O_{ij} is the observed number of co-occurrences of species i and j, and E_{ij} is the number expected in a random distribution (calculated from each species occurrence). We compared the distribution of AC values to the randomized distribution of AC constructed from a null model. The null model reshuffles the occurrences of the species in patches within the matrix, keeping constant the observed species frequencies and richness per patch (Wilson 1987). The significance of the distribution of AC values was calculated using as confidence limits the standard deviations of the random AC values. We summarized the significance of the distribution of observed AC values at each site with an index (AI) that combines the frequency of significant positive and negative AC frequencies in the distribution:

$AI = [(significant\ AC > 1) - (significant\ AC < -1)]/$ (total significant AC) $\times 100$. The index ranges from 100 to -100, and represents a gradient of association of all species pairs within a community from fully positive to fully negative.

Variance of species richness-The variance in species richness indicates constraints to the number of coexisting species in a patch (Gotelli 2000). A value lower than expected indicates that patches share a similar number of species. Conversely, a variance higher than expected indicates aggregation of species in some patches. We used the variance ratio (VR) index (Wilson 1987) to gauge the deviation of observed from expected values.

Checkerboarding-In a checkerboard pattern the distribution of pairs of species is exactly complementary; i.e. either one of the species or the other is present on a patch, but never both, showing a mutual exclusion of species. Stone and Roberts (1990) provided an index for checkerboarding.

Nestedness-In nested communities the species composition in a species-poor site is a subset of the species composition in richer sites, so that a certain patch includes all the species found in poorer patches. Nestedness thus represents the tendency of scarce species to be found in communities with the highest diversity. The index takes the value of 1.0 for a perfectly nested matrix (Wilson 1988). The null model used follows recommendations by Silvertown and Wilson (1994) and Jonsson (2001).

The statistical significance of tests was performed by randomization, using a null-model algorithm (Gotelli 2000). Each index was first calculated with the observed data. Then, the original dataset was randomized to obtain 1000 simulated matrices and the index was calculated for each matrix. The p-value was obtained as the proportion of values (from the 1000 randomizations) that were more extreme than the observed value, multiplied by two to perform a two-tailed t-test.

Interaction between neighbors

In the Sierra Nevada site the effect of neighbors was assessed by removing neighbors 15 cm around target plants and comparing their performance to paired controls in patches without removal after two growing seasons (Callaway et al. 2002). In the four semiarid sites, neighbor removal was impracticable due to large patch size. In these sites we selected several species (1–7 per site, 6–15 replicates per species) that were present both associated with other species in patches and isolated in open interspaces. The effect of neighbors was assessed by comparing the performance of individuals in patches and in open interspaces in a paired manner. To select patches, a vegetation map was used when available (Torregarcía, El Ejido, and Tabernas; Tirado 2003, Tirado and Pugnaire 2003), and patches were chosen by generating random numbers; otherwise, patches were selected by encounters along parallel transects placed

from random positions (Cabo de Gata). For each species, we randomly selected an individual in a patch, and the closest conspecific individual found isolated in the open interspace. We measured aboveground biomass for small shrubs and herbs, and mass of new twigs and reproductive units for large shrubs (diameter >0.5 m). We estimated the neighbor effect by computing the relative interaction index (Armas et al. 2004), $RII = (Bp - Bi)/(Bp + Bi)$, where Bp and Bi are the biomass of plants living in patches and isolated in open interspaces, respectively. The index is symmetrical around zero (no significant interaction), and is constrained by $+1$ (facilitation) and -1 (competition). The index was computed for each pair of conspecific individuals at each site. We averaged the indices of all species coexisting in a site. This approach provided a conservative estimate of the interaction standardized across species, but kept the magnitude of variation within species. Although this approach has some limitations, we considered experimentally isolated and naturally isolated individuals as comparable. In the Venezuela sites it was not possible to sample plant material to estimate interaction intensity, therefore RII indexes were not available for the Altos de Pipe and Gran Sabana sites.

Results

Community structure

All seven communities included in our study showed a significant community organization, with structural differences among them shown by the analyzed traits (Fig. 1). The overall number of shrub species in each community ranged from 10 in Sierra Nevada to 31 in the Gran Sabana, and did not correlate with the mean number of species per patch, which varied from 5 in Altos de Pipe to 14 in Gran Sabana ($R^2 = 0.42$, $P = 0.12$, $n = 7$). The association index singled out five communities where positive associations prevailed (Torregarcia, El Ejido, Gran Sabana, Cabo de Gata and Tabernas). In these communities there were fewer associations around zero and more positive associations than expected at random (Fig. 1b, 2), although there was a number of significant negative associations always in lower frequency than positive ones. In Sierra Nevada and Altos de Pipe, on the contrary, associations around zero were more frequent than expected, with significant negative associations prevailing in Altos de Pipe (Fig. 2).

Five of the seven communities showed significantly higher variance in species richness than expected under the null model (Fig. 1c), suggesting the preference of
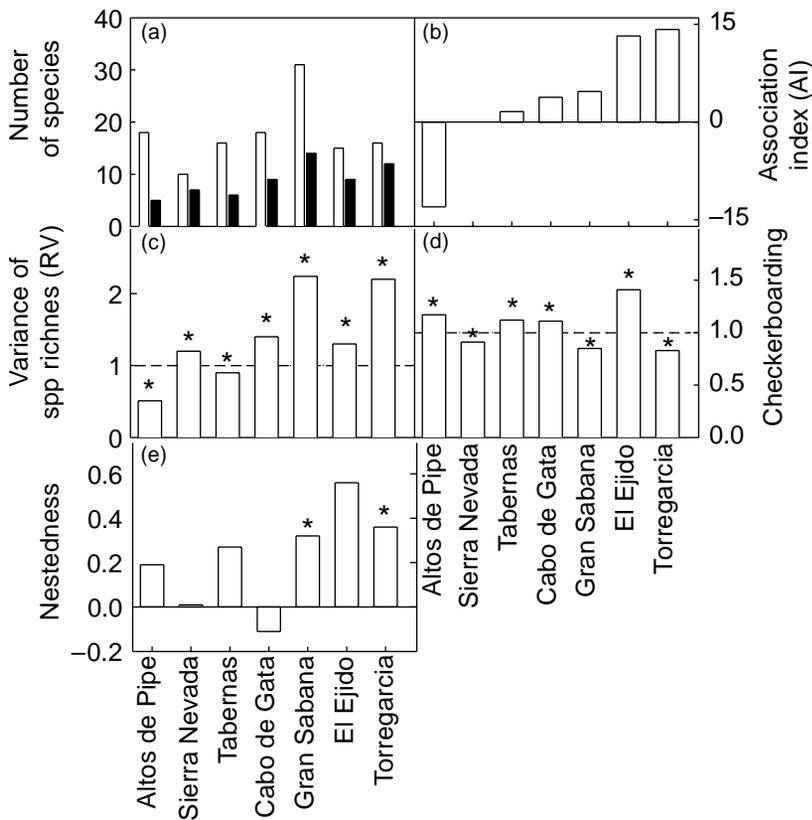

Fig. 1. Indices of community structure obtained from species occurrence in a species/patch matrix. (a) species richness: total number of shrub species (clear bars) and mean number of shrub species per patch (solid bars), (b) association between species, (c) variance in species richness, (d) checkerboarding, (e) nestedness. Dotted lines represent random expected values. Differences between expected and observed values indicated by * (P = 0.05), for b (AI) see significance of association coefficients in Fig. 2.
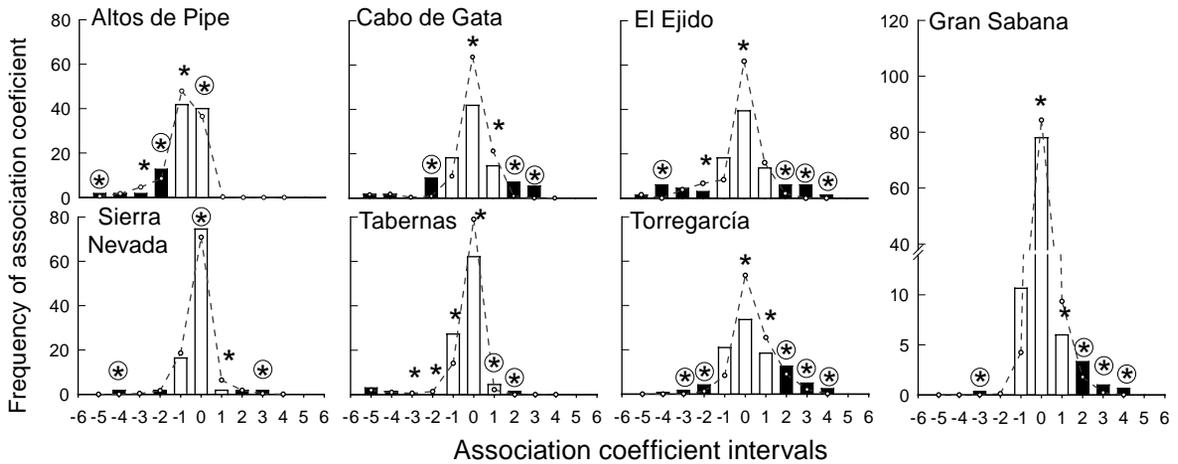
Fig. 2. Patterns of species association in seven plant communities under variable environmental constraints. Panels show the overall distribution of pair-wise species association coefficients (bars) and the expected distribution under the null model (line). Clear bars show intervals around zero [−1, 1] and solid bars the relative frequency of positive (>1) and negative (<−1) coefficients (AC). Circled asterisks show a frequency of observed AC coefficients significantly higher than expected, from a random distribution in each category; non-circled asterisks indicate significantly lower frequency than expected (P = 0.05).

species for some patches. Two sites, the *Ziziphus lotus* shrubland in Torregarcía and the sclerophyllous shrubland in Gran Sabana, showed a particularly high VR compared to the other sites. Overall, the variance ratio correlated with the mean number of species per patch ($R^2 = 0.92$, P < 0.01, n = 7), but not with total number of species in the community, meaning that the most patchy communities (those with high VR values) congregated the maximum number of species in a patch.

The checkerboarding index pointed out three communities where mutual exclusion was less frequent than expected (Torregarcía, Gran Sabana, and Sierra Nevada), while in four communities the tendency of species to be mutually exclusive was significant (El Ejido, Cabo de Gata, and Altos de Pipe, Fig. 1d).

Only in Torregarcía and Gran Sabana was nestedness significant (Fig. 1e), suggesting that colonization of patches in these two communities followed an ordered manner. In these communities, the less frequent species were found preferentially in richer patches, where dominant species like *Ziziphus* lotus in Torregarcía and *Humiria balsamifera* or *Hirtella racemosa* in Gran Sabana where always present.

Interaction between neighbors

The presence of neighbors was positive for plant performance in all the communities where we measured this effect. The interaction index (RII) was positive and significant (P < 0.05) in the four semiarid communities, El Ejido (RII = 0.68), Torregarcia (RII = 0.31), Tabernas (RII = 0.33), and Cabo de Gata (RII = 0.38). Only in Sierra Nevada the community showed a non-significant but still positive index (RII = 0.13). RII was positively

correlated with nestedness ($R^2 = 0.90$, P = 0.01, n = 5) suggesting that facilitation controlled patch colonization, as evidenced by the ordered sequence of species appearance in communities with higher degree of positive interactions. More importantly in relation to our hypothesis, the relative interaction index (RII) also correlated positively with the degree of species association at each site (Fig. 3), showing that the spatial association of species is linked to positive plant interactions.
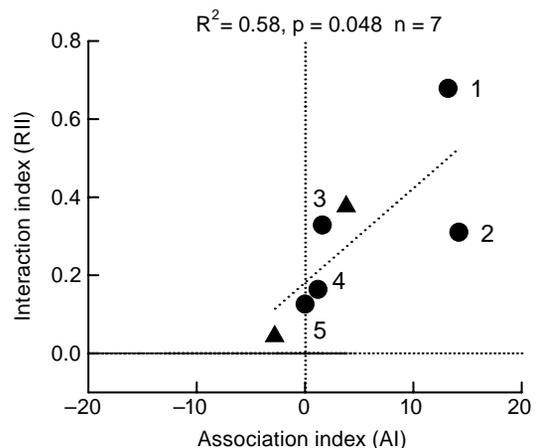

Fig. 3. Relationships between the relative interaction index (RII) and the association index (AI) in communities where patch effect was measured. Points above zero on the RII axis indicate facilitation. Sites indicated by 1: El Ejido, 2: Torregarcía, 3: Tabernas, 4: Cabo de Gata, 5: Sierra Nevada. Triangles indicate additional data obtained from replicate communities in the Cabo de Gata region (similar dwarf palm communities differing in orientation and slope, Table 1). Collection of data and analysis of these additional points followed the same protocol described in the methods section. Regression result without these additional points is $R^2 = 0.51$, P = 0.17, n = 5.

Discussion

All seven communities under harsh environmental conditions had a species distribution that differed from the random model, showing significantly structured patterns. Five of the seven communities seem to be organized by species aggregations, with variable degrees of specificity and association strength. Overall our data provide a link between spatial patterns and species interaction, pointing to the importance of facilitation in structuring communities in extreme environments, as predicted by current theory (Bertness and Callaway 1994, Brooker and Callaghan 1998, Pugnaire and Luque 2001, Bruno et al. 2003).

A prevalence of positive associations was found in five out of the seven communities. The four sites under semiarid regime in southeast Spain (Torregarcía, El Ejido, Cabo de Gata, and Tabernas), and the sclerophyll scrub in Gran Sabana (Venezuela) showed a high degree of pair-wise species association, and most shrubs did occur in species-rich patches (Fig. 1). In addition, the variance of species richness was significantly positive in four of these five communities, suggesting the presence of "favorable" sites. Only in the desert community of Tabernas was the variance in species richness lower than expected from the random model, indicating that the canopy of the dominant shrubs provided similar growth conditions for all the species found underneath. Three aspects of community structure (association index, variance of species richness and number of species per patch), and the positive RII interaction index suggest that in these communities the dominant species: 1) interact positively with other species and produce a higher number of spatial associations, and 2) provide favorable conditions for other species in their patches. It is clear in these communities the importance of "facilitators" for the maintenance of species richness, as it has been shown in experimental microcosms with detritivorous species (Jonsson and Malmqvist 2003) and other plant communities (Callaway 1997).

Spatial heterogeneity of resources alone may influence our non-experimental estimates of plants response to neighbors if, for example, patches occur in microsites with better abiotic conditions. In arid and semi-arid ecosystems spatial heterogeneity of resources (e.g. fertile islands) have long been associated with the presence of shrubs (Went 1942, Wilson and Agnew 1992, Pugnaire et al. 1996a, 1996b, Reynolds et al. 1999). However, this spatial heterogeneity may also be stochastic, emerging even on rather homogeneous substrates with no observable geological differences. On the other hand, in the four semiarid communities where the interaction between neighbors was estimated with a non-removal natural experiment, the spatial distribution of patches was random (based on Ripley's K function analysis on mapped plants), suggesting that the observed effects are biological rather than caused by abiotic microsite conditions (Tirado 2003). We believe that the interaction intensity measurements were not affected by the non-removal nature of our experiment in several sites, as selected individuals in pairs were close to each other and presumably affected by the same abiotic conditions, so that RII results should not be influenced by microsite effects.

Two sites, Torregarcía and Gran Sabana, stood out for their highly structured pattern. Both showed the highest values of variance in species richness, a high degree of positive species association, and had significant nestedness and negative checkerboarding indices. The negative checkerboarding indicates a low level of mutual exclusion among species, suggesting a lower relative importance of competitive interactions. These two communities may be under the more severe environmental conditions. Both are dominated by large shrubs that harbor rich communities in their understorey. As the shrub grows, soil properties and other environmental conditions under the canopy are improved, allowing the establishment of more demanding species (Pugnaire et al. 1996a, 1996b, Tirado 2003). Both communities have in common a sandy substrate, poor in nutrients and with low water-holding capacity (Tirado 2003, Dezzeo et al. 2004). The shrub activity is thus crucial to ameliorate adverse environmental conditions that otherwise would prevent the presence of many subordinate species.

The structure of communities in Sierra Nevada and Altos de Pipe differed from the other five communities. In Sierra Nevada, the alpine shrubland showed predominance of neutral associations, while at the same time showed a significant variance in species richness, suggesting a random clumping of species in patches, i.e. a tendency of species to aggregate spatially but in non-specific pair-wise associations. The RII interaction index was positive but not significant, pointing to weak positive interactions. Thus, the Sierra Nevada community seems to be structured by both positive and negative interactions. Plants seek protection from strong winds and low temperatures in patches (Callaway et al. 2002) although it may mean a stronger competition. The community in Altos de Pipe was different because of its higher productivity and because the regenerating shrubland appeared in a matrix of grasses. In this community negative associations prevailed and there were significant exclusions among species suggesting the dominance of negative interactions. Overall, it seems that many factors can influence the balance between facilitation and competition, even within constraining environments (Maestre and Cortina 2004), and we need further studies elucidating these factors.

Facilitation has been shown to dominate in physically demanding environments (Stachowicz 2001, Callaway et al. 2002), and it is often presumed in patchy communities (Kikvidze and Nakhutsrishvili 1998, Eccles et al. 1999, 2001). In our communities, facilitation appears to be related to the amelioration of environmental conditions by the dominant shrubs, as their presence means an increase in patch species richness. For example, patches in Torregarcía regularly involve the presence of *Ziziphus lotus*, which promotes the accretion of sand, litter, and sand-blown particles while lowering temperatures, shading neighbors, and protecting from herbivores with thorny branches (Tirado 2003, R. Tirado and F. I. Pugnaire, unpubl.). Likewise, in Gran Sabana the presence of species such as *Humiria balsamifera* or *Hirtella racemosa* induce the establishment of many other species under the canopy. These specific traits suggest that "facilitator" species act as ecosystem engineers changing their surrounding environment and affecting the overall community dynamics (Jones et al. 1994, 1997). The positive effects of "facilitator" species on neighbors could lead to a clumped spatial distribution if the benefits provided by neighbors on survival and growth exceed the associated costs of competition. Through soil enrichment, microclimate amelioration, protection from herbivores, and other mechanisms (Callaway 1995, Callaway and Pugnaire 1999), subordinate species may grow larger and be more likely to survive near "facilitator" species, thus leading to a clumped spatial distribution.

In the semiarid communities of southeast Spain, shrubs like *Lycium intricatum*, *Asparagus albus* or *Asparagus horridus* show the highest rate of pair-wise association and occur with high frequency in the richest patches. These species are spiny deciduous shrubs that survive better in the understorey of larger shrubs (Tirado and Pugnaire 2003), and that have fleshy fruits dispersed by birds (Nogales et al. 1998, Traveset et al. 2001) which perch on main shrubs. By contrast, two Labiataea species, *Thymus hyemalis* and *Teucrium lanigerum*, showed the lowest coefficient of association and were found mainly by themselves. *Thymus* and *Teucrium* species are small evergreen shrubs that produce small flowers and fruits abiotically dispersed. Thus, dispersion and positive interactions combine here to structure the community.

Overall, our results show that facilitation is particularly important in shaping plant communities strongly limited by environmental conditions, such as low water or nutrient availability. The degree of species aggregation correlated with the intensity of positive interactions in these communities. The mechanisms of facilitation point to the amelioration of microclimate and of soil fertility by dominant shrubs. The analysis of spatial patterns in combination with direct measurements of species interactions provided a valuable information on the process causing those patterns.

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