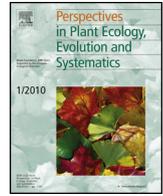




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Research article

Community attributes determine facilitation potential in a semi-arid steppe

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ABSTRACT

Studies on positive plant–plant relations have traditionally focused on pair-wise interactions. Conversely, the interaction with other co-occurring species has scarcely been addressed, despite the fact that the entire community may affect plant performance. We used woody vegetation patches as models to evaluate community facilitation in semi-arid steppes. We characterized biotic and physical attributes of 53 woody patches (patch size, litter accumulation, canopy density, vegetation cover, species number and identity, and phylogenetic distance), and soil fertility (organic C and total N), and evaluated their relative importance for the performance of seedlings of *Pistacia lentiscus*, a keystone woody species in western Mediterranean steppes. Seedlings were planted underneath the patches, and on their northern and southern edges. Woody patches positively affected seedling survival but not seedling growth. Soil fertility was higher underneath the patches than elsewhere. Physical and biotic attributes of woody patches affected seedling survival, but these effects depended on microsite conditions. The composition of the community of small shrubs and perennial grasses growing underneath the patches controlled seedling performance. An increase in *Stipa tenacissima* and a decrease in *Brachypodium retusum* increased the probability of survival. The cover of these species and other small shrubs, litter depth and community phylogenetic distance, were also related to seedling survival. Seedlings planted on the northern edge of the patches were mostly affected by attributes of the biotic community. These traits were of lesser importance in seedlings planted underneath and in the southern edge of patches, suggesting that constraints to seedling establishment differed within the patches. Our study highlights the importance of taking into consideration community attributes over pair-wise interactions when evaluating the outcome of ecological interactions in multi-specific communities, as they have profound implications in the composition, function and management of semi-arid steppes.

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Introduction

Biotic interactions determine community assembly and ecosystem functioning. Competition has been traditionally considered as the main driver in structuring plant communities (Grime, 1974). However, over the last decades, an increasing number of studies have emphasized the importance of facilitation as a major ecological interaction (Bertness and Callaway, 1994; Callaway, 1995, 2007; Brooker et al., 2008). Studies on plant–plant relations have traditionally focused on pair-wise interactions, paying scarce attention to other co-existing species (Brooker et al., 2008). This topic was

reviewed by Jones and Callaway (2007), where they discussed the context-dependency of plant interactions and emphasized the role of third species. When many benefactor and beneficiary species co-occur, a complex network of interactions arises, leading to indirect effects, such as indirect facilitation (Callaway, 2007; Brooker et al., 2008; Gross, 2008). Thus, the net outcome of multi-species interactions may not necessarily be the additive effect of pair-wise relationships (Weigelt et al., 2007; Zhang et al., 2011).

In recent years, there have been an increasing number of studies employing the community approach to study facilitation (Verdú and Valiente-Banuet, 2008; Cavieres and Badano, 2009; Gilbert et al., 2009; Soliveres et al., 2011a; Granda et al., 2012). However, most of those studies are either extrapolations of individual responses to a community scale, or studies focused on the effect of nurse species on biodiversity, but not on the opposite, i.e., on the

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capacity of species assemblages to act as nurses (but see [Castillo et al., 2010](#) for an analysis of the effect of phylogenetic distance of the nurse community on seedling establishment). Drylands are not the exception and pairwise approaches dominate the study of positive interactions ([Pugnaire et al., 2011](#)). However, species in drylands do not occur in isolation. Harsh conditions, especially water scarcity, promote spatially aggregated vegetation patterns ([Aguiar and Sala, 1999](#)).

In drylands, vegetation is frequently arranged in multi-species patches where direct and indirect facilitation promotes species coexistence ([Flores and Jurado, 2003](#); [Callaway, 2007](#)). Attributes defining the physical and biotic structure of these patches, such as patch size, litter accumulation, canopy structure, and species number and identity may affect seedling establishment. Communities of putative benefactor species in vegetation patches may promote species coexistence by favoring seedling performance. As not all species co-occurring in a patch act as nurses, patches with high species richness are more likely to contain benefactor species than those with fewer species (i.e., sampling effect), and thus species richness may enhance the recruitment of new individuals. Conversely, as species richness increases, the probability that species with contrasted functional traits co-occur may also increase. Due to niche saturation, patch biotic and physical dimensions may be limited, and the establishment of new individuals may be hindered with patch size and age ([MacArthur and Levins, 1967](#); [Case, 1991](#)). In this case, increased species richness would reduce patch potential to accept new individuals. The positive and negative relationship between species richness and community capacity to accept further species, together with the influence of spatial scale, has been discussed around the theory of the invasion paradox ([Levine, 2000](#); [Stohlgren et al., 2003](#); [Fridley et al., 2007](#)). According to this theory, community diversity and invasibility should be negatively related at small spatial scales. However, facilitation often promotes invasive species richness ([Von Holle, 2005](#); [Fridley et al., 2007](#); [Vellend, 2008](#); [Altieri et al., 2010](#)), and accordingly, we would expect increased establishment rates in species-rich patches, particularly under the stressful conditions of semi-arid areas ([Von Holle, 2005](#)). Species identity may also be crucial for the establishment of new individuals, because of similarity of ecological niches, species competitive ability and species capacity to enhance microclimate conditions for the newcomers. Phylogenetic distance between species may directly affect the net outcome of the interaction, as closely related species are likely to share important ecological traits and therefore to compete among each other ([Webb et al., 2002](#); [Valiente-Banuet and Verdú, 2007](#)). However, in multi-specific assemblages, phylogenetic composition of the entire community, rather than the phylogeny of a dominant species, may control seedling establishment. The mechanisms of competition in multi-species communities in dry grasslands showed that non-additive effects of pair-wise interactions drive the net outcome of the interaction ([Weigelt et al., 2007](#)). However, to our knowledge, no study has evaluated the facilitative effect of whole communities in seedling establishment in drylands. Neither the attributes of communities that are involved in seedling recruitment have been explored. Still, species identity, patch composition and the physical structure of woody vegetation patches may be crucial for seedling establishment.

Woody patches may affect seedling establishment in various ways, including microclimate regulation, changes in water and nutrient availability, and the presence of symbiotic fungi, to mention a few ([Vetaas, 1992](#); [Nara and Hogetsu, 2004](#); [Smith and Read, 2008](#); [Cable et al., 2009](#); [Soliveres et al., 2011a](#); [Anthelme et al., 2012](#)). Their combined effect cannot be easily predicted, as interactions are common and complex. For example, nutrient and organic matter accumulation, and the formation of a thick

litter layer depend on plant size and species identity ([Vivanco and Austin, 2006](#)). However, whilst higher soil fertility may enhance seedling establishment, litter frequently hinders seed germination and rooting ([Rotundo and Aguiar, 2005](#); B. Amat, pers. obs.). The outcome of the interaction between established patches and seedlings may also depend on the particular location within the patch where the new individual thrives. For example, the relative importance of aboveground interactions (e.g., competition for light, excess radiation, herbivory) vs. belowground interactions (allelopathy, competition for nutrients and water, mycorrhizae) may substantially change if seedlings germinate underneath the patches or on their periphery.

We studied the facilitative potential of whole communities of woody vegetation patches on the establishment of a key-stone species in *Stipa tenacissima* L. steppes. These semi-arid steppes show a combination of bare soil, *S. tenacissima* tussocks and woody patches, formed by large resprouting shrubs (hereafter 'dominant species'), accompanied by small shrubs and perennial grasses (hereafter 'accompanying species'). These woody patches improve ecosystem functionality, and favor the presence of frugivorous birds and vascular plants ([López and Moro, 1997](#); [Maestre and Cortina, 2004a](#); [Maestre et al., 2009](#)). Positive interactions between *S. tenacissima* and large woody species have been widely described ([Maestre et al., 2001, 2003a](#); [Soliveres et al., 2011a](#)), and dominant species of woody patches act as benefactors in other areas ([Castro et al., 2004](#)), but little is known about the facilitative potential of patch forming species and patch communities in these semi-arid steppes. As woody patches in *S. tenacissima* steppes form spatially delimited plant communities, they are suitable environments to test the facilitative effects of communities and explore the role of different community attributes in that interaction. The aims of our study are (1) to evaluate how patches modify their immediate environment, (2) to assess the net effect of woody patches on the performance of new individuals, (3) to quantify the relative importance of physical and biotic community (patch) attributes as drivers of seedling recruitment, and (4) to explore the underlying mechanisms of such interactions. To achieve this, we characterized biotic and physical attributes of multi-specific woody vegetation patches in *S. tenacissima* steppes, and evaluated the performance of shrub seedlings planted underneath them compared to seedlings planted in open areas. We expected substantial differences in aboveground and belowground interactions in different parts of the patch. To take this into account, we evaluated seedling performance in three different locations within the patch.

Materials and methods

Study site

Our study was established in a semi-arid area in southeastern Spain. Mean annual temperature is 18 °C and mean annual precipitation ranges between 286 and 330 mm ([Ninyerola et al., 2005](#)). Soil is Lithic Calciorthid developed from marl and limestone ([Soil Survey Staff, 1994](#)). The area is covered by *S. tenacissima* steppes with sparse patches of woody vegetation (Fig. S1). We considered a woody patch any combination of adults of the species *Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., *Juniperus oxycedrus* L., *Ephedra fragilis* Desf. and *Osyris lanceolata* Hochst. & Steud. (the dominant species) whose physiognomy was different from the adjacent matrix (Fig. S1). We selected 8–13 patches in five independent sites (53 patches in total). Patches were selected to provide a balanced representation of number and identity of dominant species.

Seedling plantation and monitoring

In November 2008 we planted 1-year-old seedlings of *P. lentiscus* in four locations per patch (212 seedlings in total): (1) underneath the patch, where aboveground and belowground interactions take place, (2) south of the patch, outside the canopy projection, where only belowground interactions are expected, (3) north of the patch, outside the canopy projection area where belowground interactions occur and seedlings are partially shaded; and (4) in open areas, at least 2 m apart from any woody patch (Fig. S2). Seedlings in this location (open areas) were independent from each other and from any woody patch, but we sampled them as “belonging” to a patch only for logistic purposes. In this way, we took spatial heterogeneity in biotic and abiotic conditions occurring within the patches into account. Planting holes were dug manually with a 5 cm × 5 cm × 20 cm soil auger to minimize soil disturbance. We recorded seedling survival and stem height 2 months after planting, and before and after summer 2009 and 2010. During the first survey, we noticed that almost all seedlings from one of the study sites were dug up or eaten by rabbits, thus we replaced those plants, and protected all seedlings with plastic mesh cages. These cages have a negligible effect on seedling microclimate. We considered these records as baseline survival (191 alive seedlings: 51 seedlings underneath, 48 seedlings north, 48 seedlings south, 44 seedlings in open areas), once transplant shock was excluded and predated seedlings were replaced. We assessed water use efficiency (WUE), integrated transpiration rate and N source using ^{13}C , ^{18}O and ^{15}N enrichment, respectively, from leaf samples collected during first pre-summer survey (June 2009). The number of (alive) seedlings for this survey at each location of plantation was: 38 seedlings underneath, 41 seedlings north, 37 seedlings south, 35 seedlings in open areas. Leaf samples were ground in a MM200 Retsch ball mill and isotope concentration together with foliar C and N concentration were determined at the University of California–Davis Stable Isotope Facility (CA, USA) using a continuous flow isotope ratio mass spectrometer (Europa 20-20 Scientific, Sercon Ltd., Cheshire, UK) in the dual-isotope mode, interfaced with a CN elemental analyzer and Hekatech HT Oxygen Analyzer. Results for isotopes enrichment are expressed as $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, relative to the Pee Dee Belemnite (PDB), atmospheric N_2 and Vienna-Standard Mean Ocean Water (V-SMOW), respectively.

Patch characterization

Patch biotic structure was described by characterizing community composition and measuring species richness of dominant and accompanying species under the canopy of each patch, and determining the phylogenetic distance between *P. lentiscus* seedlings and the patch community. Dominant species composition was estimated in terms of species cover within the patch, by measuring two orthogonal diameters of the canopy of each species, and estimating canopy projected area as an ellipse. The cover of each accompanying species was estimated by using transects of consecutive 50 cm-quadrats underneath each patch along the canopy projected area, in upslope-downslope direction. An abundance weighted measure (M) of phylogenetic distance between dominant species present in a patch and *P. lentiscus* were estimated according to [Violle et al. \(2007\)](#). This measure estimates the mean trait value of the community weighted by the relative abundance of each species present in the community: $M = \sum_i^n p_i T_i$, where p_i is the abundance of species i and T_i is the phylogenetic distance between *P. lentiscus* and each patch-forming species i obtained from the TimeTree database ([Hedges et al., 2006](#)).

We estimated patch size (area and maximum height), patch canopy density, litter accumulation and total cover of accompanying species under the patches to describe patch physical structure. Patch area was estimated as described for the estimation of the cover of dominant species. As a measure of canopy density, we estimated the leaf area index (LAI) with a plant canopy analyzer LAI2000 (Li-Cor Inc., Nebraska, USA) in the same four locations where seedlings were planted. We measured litter depth in 6–10 points underneath patch canopy, depending on patch size.

We also evaluated soil fertility in the same four locations per patch where seedlings were planted by analyzing oxidable C and total N. We collected 5 cm × 5 cm × 5 cm soil samples in the four locations, ground them in a MM200 Retsch ball mill, and analyzed them for oxidable C (modified Moebius method, P. Rovira, Centre Tecnològic Forestal de Catalunya, pers. comm.) and total N content (semi-micro-Kjeldahl distillation in a Tecator Kjeltac Auto 1030 analyzer, Hogana, Sweden). We recorded soil moisture at 0–10 cm depth underneath 7 patches in a size gradient from 4 to 30 m² of canopy projection and in nearby areas beyond the influence of the patches. Soil moisture was recorded every hour by soil moisture sensors (10HS) and Decagon ECH2O data-logger (ECHO-10, Decagon Devices, Inc., Pullman, Washington, USA) from July 2009 to June 2011.

Statistical analyses

We performed Non-metric Multi-Dimensional Scaling (NMDS) to reduce the dimensionality of the species composition matrix. NMDS has been recommended over other ordination techniques for community analysis because it does not ignore community structure that is unrelated to environmental variables and it does not assume multivariate normality ([McCune and Grace, 2002](#)). We used Bray–Curtis distance measure with random starting configurations. We performed NMDS analyses for dominant and accompanying species separately and used the first two axes of each for the next analyses.

We evaluated the effect of location on soil organic C, total N and the C:N ratio in samples from the four locations by using General Linear Mixed Models (GLMM) with site as random effect and location as fixed effect. To avoid data dependence, we selected a random dataset that included only one patch-dependent location per patch (underneath, north or south), plus the 53 independent samples from open locations. We used the same procedure to analyze the effect of location on seedling performance (survival, relative growth rate, and stable isotope enrichment, C and N concentration in leaves of alive seedlings). For all dependent variables except for survival, samples in the four locations were selected to optimize the number of experimental units, while ensuring sample independence.

Short-term seedling survival and relative growth rate (RGR) were low, thus, we only kept seedling survival as a measure of seedling performance to evaluate its relationship with the physical and biotic structure of woody patches. We used GLMM with site and patch nested within site as random effects with a binomial error distribution. Patch size, LAI, patch composition (NMDS axes), cover and richness of dominant and accompanying species, soil organic C, soil total N, phylogenetic distance of the community of dominant species, and litter depth were included as covariates in the initial model. We made a simplification of the maximal model by removing the least significant covariates one by one. For each model, we estimated Akaike’s information criterion corrected for small samples (AIC_c) as the relation between sample size ($N = 159$) and the number of estimated parameters ($K = 13$) was less than 40 ([Burnham and Anderson, 2002](#)). Then, we selected the GLMM having the lowest AIC_c to determine the best model (model 9, Table

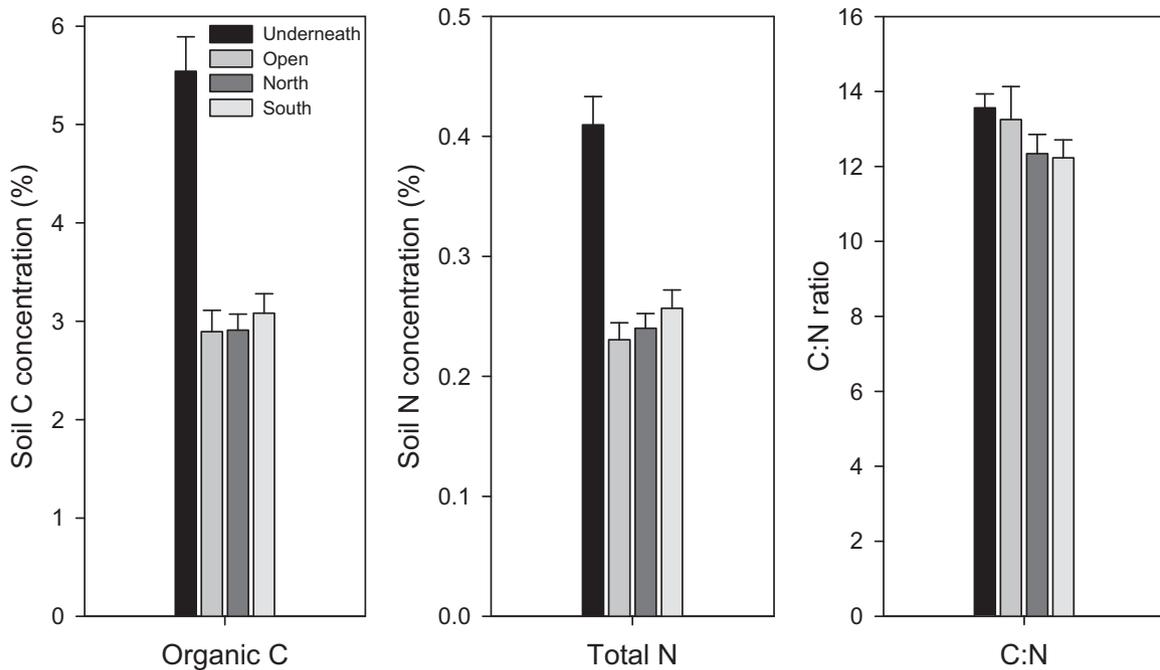


Fig. 1. Organic C, total N and C:N ratio in soil samples taken at different locations within woody patches (underneath, north and south) and in open areas in *Stipa tenacissima* steppes. The number of analyzed patches was 53. Mean and standard error bars are shown. Soil sampled underneath the patches differed from soil sampled on other locations for C and N, but not for the C:N ratio ($p < 0.05$).

S1). Only seedlings affected by patch properties (i.e., those planted under or close to the patch), were included in this analysis. Location could not be included in this analysis as a result of the lack of replication at this level. Thus, we fit one GLMM for each location ($N=53$) with site as random factor, to examine the drivers of seedling establishment in further detail. The model that minimized AIC_c was selected for each location. All analyses were performed in R 3.1.0 statistics software, package *vegan* for NMDS analyses and package *lme4* for GLMMs (R Development Core Team, 2014).

Results

Patch attributes

Patch area ranged from 3 to 44 m² and 72% of the patches were smaller than 20 m². Soil organic C and total N were significantly higher underneath the patches than in other locations (Fig. 1 and Table S2). In contrast, we found no effect of location on the C:N ratio. Soil water content was consistently higher in open areas than inside the patches (Fig. S3). Average litter depth ranged from 0 to 6.4 cm and LAI values from 0 to 3.8. Phylogenetic distance of the dominant species ranged from zero (where the only dominant species was *P. lentiscus*) to 331 million years (where *J. oxycedrus* and *E. fragilis* were the dominant species).

Patches hosted between 4 and 20 species. Each patch was formed by up to 5 dominant species, and 1–18 accompanying species. Of the six patch-forming species, the hemiparasite *O. lanceolata* was not dominant in any patch. Patch community composition was strongly influenced by the dominant species (Table 1). NMDS axis 1 was strongly and positively correlated with *P. lentiscus* cover, and negatively correlated with *J. oxycedrus* cover. NMDS axis 2 was strongly and positively correlated with *R. lycioides* cover and negatively correlated with *Q. coccifera* cover. Fifteen accompanying species showed a significant correlation with NMDS axes ($p < 0.05$; Table 1), but correlations were strong for only five of them (Pearson correlation coefficients $r > 0.5$). Thus, *Avenula muricata* Holub,

Helichrysum stoechas (L.) Moench and *Globularia alypum* L. correlated with NMDS axis 1, and *Brachypodium retusum* (Pers.) P. Beauv. and *S. tenacissima* correlated with NMDS axis 2.

Seedling performance

Patches had a positive effect on seedling survival as only open areas significantly decreased its probability (Fig. 2 and Table S3). This effect was stronger after the first summer (10 months after planting). Two years after planting, seedling survival underneath the patches was 55% compared to 18% in open areas. Relative growth rate (RGR) was estimated in 151, 72 and 65 seedlings corresponding to surveys at 5, 8 and 22 months after plantation. RGR was highly variable and showed no significant location effect in any of the surveys (Fig. 2 and Table S3).

Seedlings planted underneath the patches showed lower integrated WUE and higher foliar ¹⁵N enrichment than seedlings planted in open locations (Fig. 3 and Table S4). Integrated transpiration rates, as estimated by ¹⁸O analysis, were similar in all locations. There were no differences between seedlings planted in the northern and southern parts of the patches compared to seedlings planted underneath patches for the three stable isotopes analyzed. Seedlings planted underneath the patches showed higher foliar N concentration than seedlings planted on their northern edge, whereas there were no significant differences in N concentration between the former and seedlings planted in other locations (Fig. 3 and Table S4). Foliar C concentration was similar in all locations.

Drivers of seedling performance

Seedling survival was predicted by both physical and biotic patch attributes. Composition of the community of accompanying species affected seedling survival (Table 2 and Fig. 4). The increase in NMDS axis 2 (and thus, the increase in *B. retusum* cover and decrease in *S. tenacissima* cover) decreased the probability of

Table 1
Pearson correlation coefficients between species cover and NMDS axes 1 and 2. NMDS analyses for dominant and accompanying species were performed separately. Significant *p*-values (*p* < 0.05) are in bold.

	NMDS axis 1	NMDS axis 2	<i>p</i> -Value NMDS1	<i>p</i> -Value NMDS2
Dominant species				
<i>Quercus coccifera</i>	−0.441	−0.773	0.001	0.000
<i>Rhamnus lycioides</i>	0.094	0.629	0.532	0.000
<i>Pistacia lentiscus</i>	0.757	−0.198	0.000	0.158
<i>Juniperus oxycedrus</i>	−0.615	0.384	0.001	0.005
<i>Ephedra fragilis</i>	0.376	0.389	0.008	0.004
<i>Osyris lanceolata</i>	0.261	0.212	0.061	0.145
Accompanying species				
<i>Rosmarinus officinalis</i>	−0.100	−0.101	0.478	0.472
<i>Avenula murcica</i>	−0.582	0.271	0.000	0.050
<i>Thymus vulgaris</i>	0.426	0.325	0.001	0.017
<i>Brachypodium retusum</i>	0.194	0.534	0.163	0.000
<i>Teucrium capitatum</i>	−0.061	−0.128	0.666	0.362
<i>Fumana ericoides</i>	−0.250	0.214	0.071	0.123
<i>Asparragus horridus</i>	0.171	0.078	0.221	0.580
<i>Dorycnium pentaphyllum</i>	0.034	0.090	0.808	0.523
<i>Helichrysum stoechas</i>	0.543	0.013	0.000	0.928
<i>Sedum sediforme</i>	0.408	0.171	0.002	0.222
<i>Helianthemum violaceum</i>	−0.227	0.073	0.102	0.606
<i>Sideritis leucantha</i>	−0.097	−0.268	0.490	0.052
<i>Phagnalon saxatile</i>	0.133	−0.437	0.342	0.001
<i>Globularia alypum</i>	−0.538	−0.164	0.000	0.239
<i>Anthyllis cytisoides</i>	0.341	−0.144	0.013	0.303
<i>Stipa tenacissima</i>	−0.081	−0.604	0.564	0.000
<i>Teucrium carolipau</i>	−0.268	0.204	0.052	0.143
<i>Teucrium pseudochamaepitys</i>	0.166	0.156	0.236	0.265
<i>Coronilla minima</i>	−0.036	0.285	0.800	0.038
<i>Rubia peregrina</i>	0.203	−0.017	0.144	0.905
<i>Bupleurum fruticosum</i>	0.296	−0.119	0.031	0.397
<i>Carex humilis</i>	−0.109	0.103	0.435	0.462
<i>Erica multiflora</i>	−0.113	0.245	0.419	0.077
<i>Polygala rupestris</i>	0.337	0.229	0.014	0.099
<i>Cistus clusii</i>	−0.065	−0.066	0.646	0.641
<i>Asparagus acutifolius</i>	0.248	−0.073	0.073	0.605
<i>Lapiedra martinezii</i>	−0.002	−0.281	0.988	0.042
<i>Satureja obovata</i>	0.422	0.230	0.002	0.097
<i>Fumana laevipes</i>	−0.305	0.279	0.027	0.043

survival. In addition, phylogenetic distance to the dominant species, cover of accompanying species and litter depth increased the probability of seedling survival (Table 2 and Fig. 4). Dominant species composition was included in the final model, but its effect was not statistically significant (Table 2). For each patch nested within site, the estimates of the model increased and decreased by a random value with expected mean of zero and variance of 0.2928.

Considering only seedlings planted underneath the patches, the composition of accompanying species and soil organic C successfully predicted seedling survival (Table 3). As for the whole dataset, as NMDS axis 2 of accompanying species increased, the probability of seedling survival under the patches decreased. An increase in soil organic C increased the probability of survival. Comparatively, survival probability in seedlings planted in the northern edge of the patches depended on a larger number of explanatory variables:

number of accompanying species, both NMDS axes of dominant species, NMDS axis 2 of accompanying species and phylogenetic distance of the dominant species (Table 3). This second NMDS axis of accompanying species decreased the probability of survival. In addition, an increase in the number of accompanying species decreased seedling survival. The identity of the dominant species also affected seedling performance in this location: NMDS axis 1 increased and NMDS axis 2 decreased the probability of survival. We found a direct relationship between phylogenetic distance of the dominant species and the probability of survival in seedlings planted in the northern edge of patches. Finally, the probability of survival of seedlings planted in the south of the patches was not significantly predicted by any patch attribute, but the number of accompanying species and the NMDS axis 2 of dominant species were included in the best model (Table 3).

Table 2
Parameter estimates for GLMM to evaluate the effect of community attributes on seedling survival (*N* = 159). Sites (5) and patches (53) were included as random effects. The additional variance in estimates ascribed to sites was 0.1292. Considering patches nested within sites the variance was 0.2928.

Fixed effects	Estimate	Std. error	<i>z</i> value	<i>p</i> -Value
(Intercept)	−2.629	0.465	−5.654	<0.001
Cover accompanying species	0.016	0.004	4.480	<0.001
Litter depth	0.980	0.374	2.619	0.009
NMDS axis 1 dominant species	0.633	0.405	1.564	0.118
NMDS axis 2 accompanying species	−6.602	2.164	−3.051	0.002
Phylogenetic distance of dominant species	0.006	0.002	3.010	0.003

Table 3

Parameter estimates of GLMM on the effect of community attributes on seedling survival planted in three different locations within woody patches (N=53). Only models with the lowest AIC_c are shown.

Fixed effects	Estimate	Std. error	z value	p-Value
Underneath				
(Intercept)	-1.493	0.869	-1.718	0.086
NMDS axis 2 accompanying species	-7.741	3.137	-2.468	0.014
Soil organic C	0.302	0.147	2.060	0.039
North				
(Intercept)	-1.270	1.694	-0.749	0.454
Number accompanying species	-0.628	0.309	-2.036	0.042
NMDS axis 1 dominant species	2.130	0.985	2.163	0.031
NMDS axis 2 dominant species	-2.092	1.208	-1.731	0.083
NMDS axis 2 accompanying species	-16.150	6.268	-2.577	0.010
Phylogenetic distance of dominant species	0.025	0.009	2.796	0.005
South				
(Intercept)	-2.447	1.095	-2.234	0.026
Number accompanying species	0.231	0.149	1.551	0.121
NMDS axis 2 dominant species	0.829	0.506	1.639	0.101
Random effects: site		Std. deviation		
Underneath (Intercept)		0.274		
North (Intercept)		0.328		
South (Intercept)		0.000		

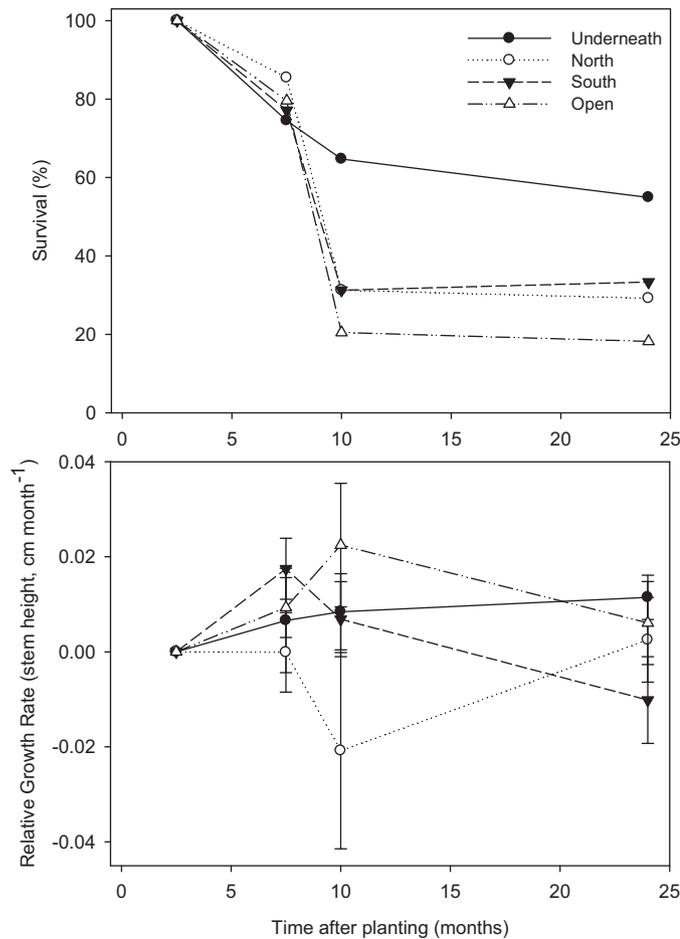


Fig. 2. Survival and growth of *Pistacia lentiscus* seedlings planted on different locations within woody patches (underneath, north and south) and in open areas in *Stipa tenacissima* steppes. Survival baseline was considered 2.5 months after planting, once transplant shock was excluded and seedlings predated immediately after planting were replaced. RGR was only measured in those seedlings that were alive 22 months after planting. Mean \pm 1 SE are shown for seedling growth of living individuals.

Discussion

Patch effect on seedling performance

We found evidence that patches positively affected seedling survival. This effect was more intense during the first summer, when mortality was higher, and it was larger in seedlings planted underneath the patches than in seedlings planted on their periphery. The restricted spatial extent of facilitation illustrates the spatial-temporal dynamics of the interaction, as slight modifications in environmental conditions may shift the relationship from positive to neutral or negative. This is in agreement with the temporal variability of positive interactions observed in *S. tenacissima* steppes (Maestre and Cortina, 2004b). On the other hand, the limited span of the interaction has strong implications for the distribution of plant cover and the functioning of *S. tenacissima* steppes, and the restoration of degraded steppes (Puigdefábregas, 2005; Cortina et al., 2011).

Seedlings planted under the patches were less efficient in using water than those planted outside them, suggesting that water stress was lower in the former. However, we found that the decrease in water use efficiency (WUE) resulted from a decrease in photosynthetic rate rather than an increase in transpiration rate, as ¹⁸O enrichment was not affected by location. Thus, the reduction in evaporative demand under the patches was probably offset by the decrease in soil water availability and, as a result, competition for light was indeed the main responsible for the decrease in WUE. The combination of shade and water stress may have deleterious effects on seedling survival (Valladares and Pearcy, 2002). However, this was not the case in *P. lentiscus* seedlings, probably because other factors, including the reduction in irradiance stress, compensated for low water availability.

Higher ¹⁵N enrichment in seedlings planted near patches may indicate rapid N cycling and relatively high N losses, as major pathways of N loss such as nitrification, denitrification and ammonia volatilization promote soil ¹⁵N enrichment (Shearer et al., 1974; Peñuelas et al., 1999). In agreement with this, we found higher foliar N concentration in seedlings planted underneath the patches than in seedlings planted north of them, suggesting that N availability was higher in the former. In addition, soil total N and organic C were higher underneath the patches than in any other location. Thus, the positive effect of patches on seedling performance was

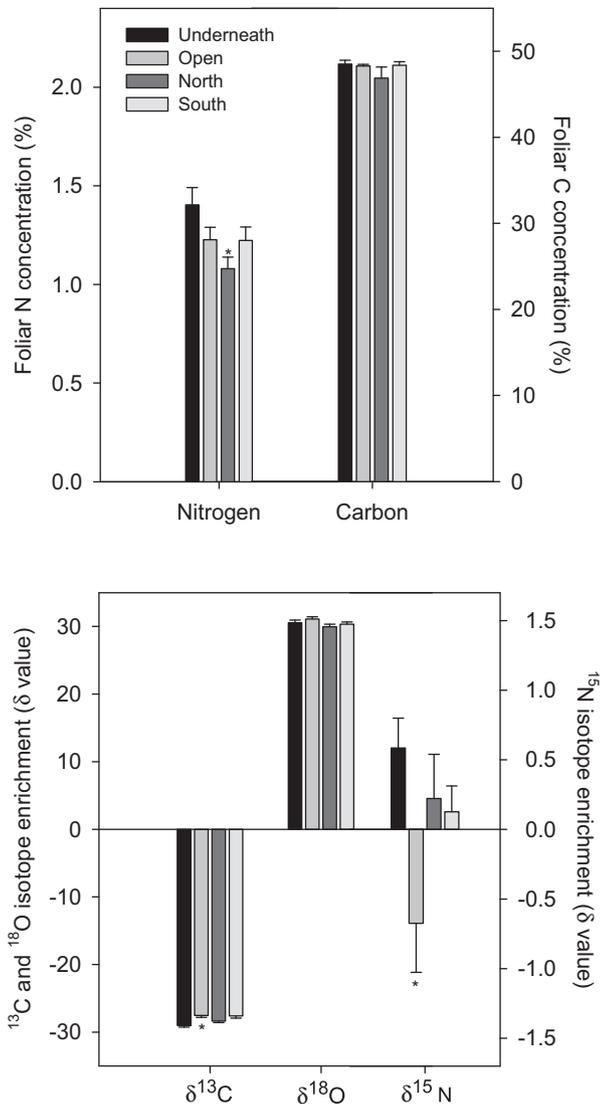


Fig. 3. Foliar C and N concentration and isotope enrichment of *Pistacia lentiscus* seedlings planted on different locations within woody patches (underneath, north and south) and in open areas in *Stipa tenacissima* steppes. Only seedlings that were alive 7 months after planting were analyzed. Asterisks indicate significant differences with seedlings planted underneath the patches for a given element or isotope. Note the different scale for different axes.

probably the result of amelioration in microsite conditions resulting from both the reduction in irradiance and the improvement in soil fertility. This is in agreement with studies in semi-arid areas where microsite has been identified as one of the major drivers of facilitation (Barberá et al., 2006; Soliveres et al., 2011a). On the other hand, the reduction in photosynthetic rate may partly explain the lack of a significant effect of patches on seedling growth.

Seedling protection against predation was not evident, as two months after planting rabbits affected some seedlings regardless of their location. This observation contrasts with Soliveres et al. (2011a), as these authors found that tussocks provided protection against rabbit predation in a *S. tenacissima* steppe in central Spain. Soliveres et al. (2012) also showed that protection against predation was more likely below 450 mm annual average precipitation.

Community attributes driving seedling survival

Our study showed that the physical and biotic structure of woody patch communities and, particularly, their composition, explained their potential for facilitation. It also showed that the importance of community attributes as drivers of seedling performance depended on location within the patch. The general model, that included seedlings from all locations, identified the composition and cover of accompanying species, litter depth and phylogenetic distance of the dominant species as major drivers of facilitation. The composition of dominant patch species completed the model, but its effect was not statistically significant. The relatively high variance ascribed to the random effects of patches nested in sites emphasizes the importance of site conditions, above microsite properties, as determinant of seedling performance (Maestre et al., 2003b; Cortina et al., 2011).

The second axis of the NMDS for accompanying species had a negative effect on seedling survival, and thus on patch potential for facilitation. This axis was correlated with the cover of several species. For example, NMDS axis 2 was correlated with the cover of *B. retusum*, a species that may interfere with *P. lentiscus* seedlings by reducing irradiance and competing for soil resources (Maestre et al., 2004). The second axis of the NMDS analysis of accompanying species was also related to *S. tenacissima*. The cover of this species was related with an increase in seedling survival, which may be associated to the facilitative effect of *S. tenacissima* on *P. lentiscus* that has been previously described in the literature (Maestre et al., 2003a). The cover of accompanying species also increased survival probability. The positive effect of plant cover on seedling performance has been associated to protection from excessive radiation (Rey-Benayas et al., 2002; Sánchez-Gómez et al., 2006; Soliveres et al., 2011b), which may disappear under mesic conditions (George and Bazzaz, 1999; Beckage and Clark, 2003).

The positive effect of litter on the probability of seedling survival may result from its capacity to act as mulch. Litter increases soil moisture by reducing runoff, increasing water infiltration and reducing evaporative losses through shading and lowering soil temperatures (Facelli and Pickett, 1991; Guevara-Escobar et al., 2007; Goldin and Brookhouse, 2014). Phylogenetic distance of the dominant species also increased the probability of survival, which is in agreement with studies suggesting that closely related species are likely to share important ecological traits, and thus compete more severely than distant species (Webb et al., 2002). In addition, phylogenetically distant species frequently differ in their ecological traits and the environmental conditions they can cope with, and thus facilitative interactions among them are more likely to occur (Valiente-Banuet et al., 2006; Valiente-Banuet and Verdú, 2007; Castillo et al., 2010).

The analysis of community attributes affecting patch potential for facilitation at each of the three patch locations was consistent with the general analysis, and revealed different sensitivity to community attributes. While survival of seedlings planted underneath or in the northern edge of the patches was driven by one or several biotic community attributes, respectively, no community attribute was related to the survival of seedlings planted in the southern edge of the patches. As overall seedling performance underneath the patches was better than in their periphery, our results suggest that seedlings planted in the latter experienced higher level of stress than those planted under the patches, but they also indicate that the source of stress differed at the different locations. Thus, biotic factors related to the composition of the communities of dominant and accompanying species were major drivers of the performance of seedlings planted in the northern edge. In contrast, biotic factors did not affect the survival of seedlings planted in the southern edge, suggesting that the source of stress may have

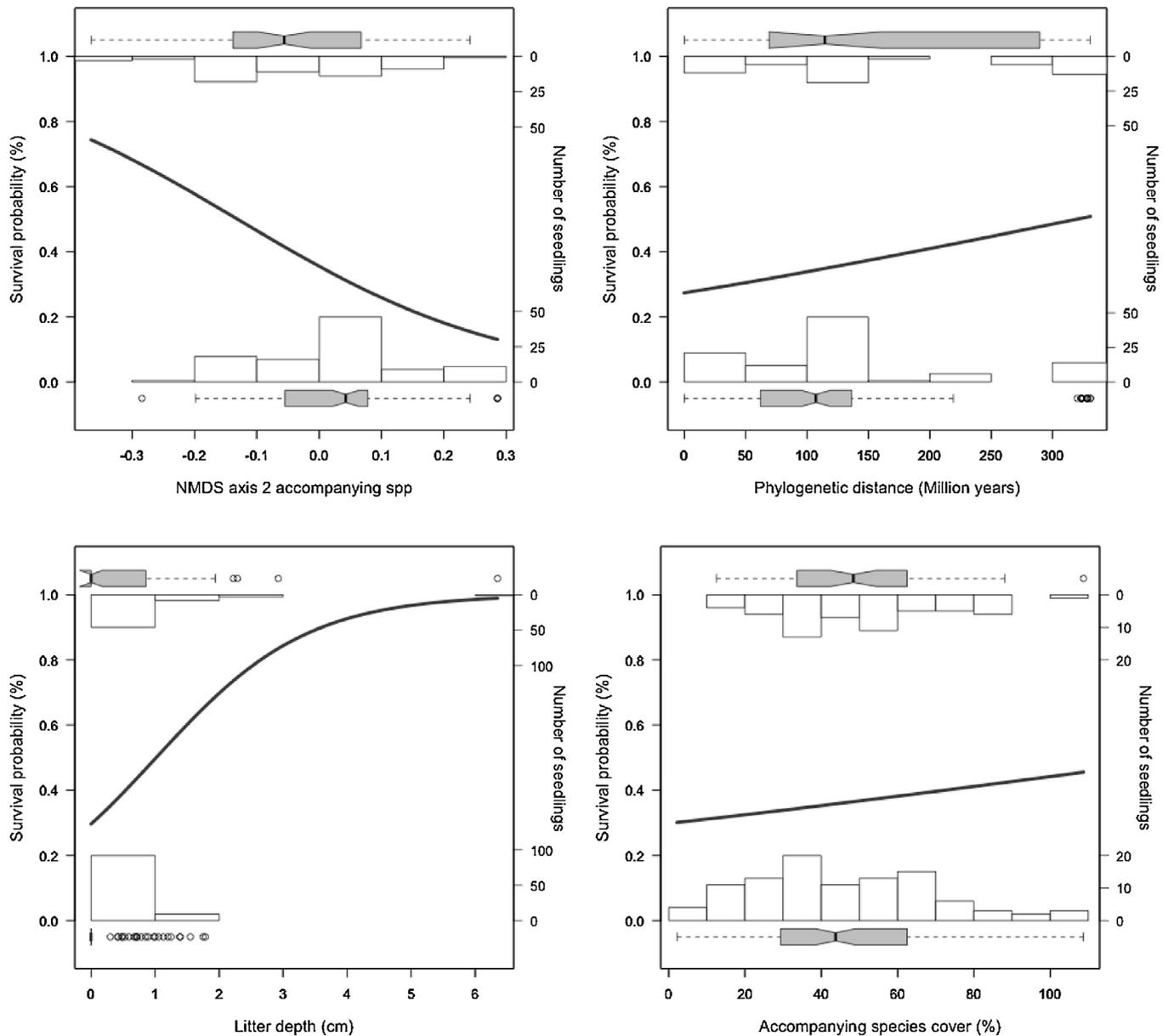


Fig. 4. Survival probability of *Pistacia lentiscus* seedlings ($N=159$) against accompanying species composition, phylogenetic distance to dominant species, litter depth and cover of accompanying species in woody patches in *Stipa tenacissima* steppes. Histograms show number of seedlings (right axis) of alive (superior histograms) or dead (inferior histograms) individuals. Data range for both alive and dead seedlings is represented by the dotted lines, and the box plots represent data between the first and third quartiles, and the median (black line within the box). Solid line is the logistic regression fit of survival probability against each variables of X-axis.

been predominantly abiotic in this location. The composition of the accompanying species community and soil organic C affected the potential for facilitation underneath the patches. In models where the former variable emerged (the general model, and the models for seedlings planted underneath and in the northern edge of the patches), it had a negative effect on seedling survival. The mechanisms underlying this effect may be similar to those described for the general model. There is no clear ascription of NMDS axes for accompanying species to single species, thus we consider the effect of species composition on facilitative potential as a global effect of the community.

The composition of the community of dominant species was only included in the model for seedlings planted on the northern edge of the patches. There, high cover of *P. lentiscus* and low cover of *J. oxycedrus* positively affected seedling survival. This result contrasts with the positive effect of phylogenetic distance

of the dominant species on seedling survival described above, as *P. lentiscus* and *J. oxycedrus* are the phylogenetically closest and most distant species to planted seedlings, respectively. There are some potential explanations for this apparent mismatch. On the one hand, the effect of community composition was not significant in other locations, and it may disappear when all locations are pooled. On the other hand, patches were not monospecific, and differences in the cover of dominant species, other than *P. lentiscus*, may have been indeed responsible for this effect.

A high number of accompanying species decreased the potential for facilitation in the northern edge of the patches. These results support the hypothesis that in this location, patches act as finite communities, in which niche saturation occurs (MacArthur and Levins, 1967; Case, 1991), and are in agreement with the low invasibility of species-rich native communities observed at small spatial scales (Levine, 2000; Stohlgren et al., 2003; Fridley et al., 2007), but

not with studies emphasizing the prevalence of positive interactions in species-rich communities (Von Holle, 2005). Thus, a high number of accompanying species may increase the probability that existing species occupy a similar niche as *P. lentiscus* seedlings and outcompete them, compared to the probability that a number of species in the extant pool facilitate *P. lentiscus*.

Finally, we should bear in mind that we have evaluated the short-term effects of communities on facilitation. Ecological niches may change with ontogenetic development (Mediavilla and Escudero, 2004), and so may do the net outcome of the interactions. We have demonstrated important ecological interactions, but we should be careful extrapolating our results to predict long-term dynamics.

Conclusions

Woody patches had positive effects on the incorporation of new individuals of a key-stone species in *S. tenacissima* steppes. The potential of woody patches to behave as benefactor communities was mainly determined by the cover and composition of the community of accompanying species, litter depth and phylogenetic distance of the dominant species. Furthermore, within-patch differences in the drivers of seedling survival revealed the existence of spatial heterogeneity in stress type and intensity, and facilitation potential, at this scale. Our study highlights the importance of taking into consideration community attributes over pairwise interactions to predict facilitation potential in multi-specific communities. Community-wide interactions and within-patch heterogeneity should be taken into account when evaluating the outcome of ecological interactions, as they may have profound implications for the composition, function and management of these semi-arid steppes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2014.10.001>.

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