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The role of nurse shrubs on the spatial patterning of plant establishment in semi-arid gypsum plant communities

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ABSTRACT

Plants may depend on nurse plants to establish and survive on gypsum environments, which are stressful for plant life. Shrubs may act as nurse plants by ameliorating micro-environmental conditions in their local vicinity. Despite its importance, the role of nurse shrubs on the spatial patterning of plant establishment remains largely unknown in gypsum communities. Our aim was to understand the patterns of plant establishment and to identify key nurse species in facilitating plant establishment and structuring plant diversity at community level in these environments. We set an observational study in two gypsum plant communities of NE Spain to assess the microsites where seedlings germinate. Also, we assessed the role of six dominant shrubs (gypsophytes and gypsovags), in spatially structuring plant diversity by assessing species-area relationships in their local vicinity to identify key nurse species. To assess the potential amelioration of micro-environmental conditions associated to shrubs, we analyzed physical-chemical soil properties under shrub canopies compared to open areas. Most plants were spatially associated with adult shrubs. Gypsophytes accumulated more diversity than gypsovags, despite both showing ameliorated conditions under canopy compared to open areas. In conclusion, gypsophyte shrubs play key roles in the structure of gypsum plant communities by facilitating plant establishment.

1. Introduction

Facilitation is a well-known biotic interaction occurring in arid and semi-arid ecosystems, where harsh environmental conditions prevail (Bertness and Callaway, 1994). Since plants in early life stages are highly vulnerable to environmental stress (Escudero et al., 2005), the likelihood of plant establishment and survival to the adult stage in these environments may increase with the presence of nurse plants (Escudero et al., 2005; Flores and Jurado, 2003). Specifically in semi-arid gypsum plant communities, along with water scarcity and extreme temperatures, soils present physical and chemical constraints for plant development (Escudero et al., 2015). Nevertheless, there are gypsum specialist plants, known as gypsophytes, which can overcome these limitations at establishment stage (Escudero et al., 2015). Gypsophytes coexist with the so-called gypsovags, which might be less tolerant to gypsum soil conditions than gypsophytes and may require assistance by nurse plants to become established in the community (Romão and Escudero, 2005). Stress-tolerant shrubs provide shade under their canopy at the adult stage, then reducing stress conditions (Gómez-Aparicio et al., 2005) and usually acting as nurse plants (Navarro-Cano et al., 2016, 2014). As a consequence, less tolerant species may establish in these favorable microsites, allowing species-rich areas in the vicinity of nurse plants (Soliveres et al., 2011).

Despite the relevance of gypsum outcrops for biodiversity conservation, the research interest in gypsophily (Escudero et al., 2015), and the studies about biotic interactions occurring in gypsum outcrops at species level (*e.g.*, Escudero et al., 2000), the role of biotic interactions on the patterns of plant establishment in these ecosystems remain largely unknown at community level. Moreover, for ecosystem conservation and restoration purposes, it is important to identify key nurse species which may influence gypsum plant community dynamics and structure, and therefore increase diversity, productivity and resilience of these communities (Michalet, 2006). The aim of this study was to understand the patterns of plant establishment in gypsum plant communities and to identify key nurse species, assessing their role in facilitating plant establishment and structuring plant diversity at community level. Specifically, addressing the following questions: Q1) do plants need to be facilitated in gypsum plant communities?; Q2) are there key nurse species facilitating plant establishment?; and consequently Q3) which is the role of key nurse species in structuring plant

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diversity in gypsum plant communities?

To address these questions, we carried out an observational study in two gypsum plant communities of the Middle Ebro Valley (NE Spain). We first determined the microsites where seedlings and adults of perennial plants preferentially establish (i.e., spatially associated to adult shrubs or in open areas) to assess whether these plants need to be facilitated (Q1). We hypothesized that H1) while gypsophytes might be able to establish in open areas, becoming pioneer species in the community (Martínez-Duro et al., 2010; Mota et al., 2003), gypsovags may need to establish close to the canopy of adult shrubs. Further, to identify key nurse species in the community (Q2), we surveyed richness and abundance of plants under the canopy of six dominant shrubs (both gypsophytes and gypsovags). Additionally, we evaluated physical-chemical soil properties under the shrub canopies compared to open areas to examine for potential micro-environmental conditions amelioration that would drive facilitation mechanisms (Callaway, 2007). We expected that H2) gypsophyte shrubs would act as key nurse species in the community, finding a high richness and abundance of plants under shrub canopy. Accordingly, we expected to find ameliorated conditions under nurse species compared to open areas (soil humidity and nutrients increasing, surface mechanical resistance decreasing and temperatures softening; Callaway, 2007). Given that pairwise biotic interactions are ultimately reflected in the spatial structure of the community (Arroyo et al., 2015; Saiz et al., 2014), we also surveyed the spatial distribution of plant diversity in the vicinity of nurse species (beyond their canopies) compared to other shrubs (Q3). We predicted that H3) nurse-facilitated positive interactions would lead to species-rich areas in the vicinity of nurse gypsophytes (Fig. A1). In this observational study, we considered plant spatial associations as a commonly used proxy for assessing interactions among plants at community level (Arroyo et al., 2015; Cavieres et al., 2006; Saiz and Alados, 2012; Soliveres and Maestre, 2014).

2. Methods

2.1. Study area

The study was conducted in the Middle Ebro Valley (NE Spain), which is one of the largest gypsum outcrops in Europe (Machín and Navas, 1998). The lithology is mainly gypsum alternating with marls, limestones and clays (Quirantes, 1978). This area has a semi-arid Mediterranean climate with high continental influence and encompasses a north-south aridity gradient (Cuadrat et al., 2007). Average annual temperature in the study area is 14.9 °C and average annual precipitation is 353.9 mm yr^{-1} ("Farlete" meteorological station, 1982–2012 period; source: Gobierno de Aragón, http://opendata.aragon.es). The landscape mainly consists of low hills (480 m.a.s.l. average) and flat-bottomed valleys, which are usually cultivated. Plant communities in gypsum hills are patchy scrublands composed predominantly of the gypsophytes *Gypsophila struthium* Loefl. ssp. *hispanica* (Willk.) G. López*, Helianthemum squamatum* (L.) Pers., *Herniaria fruticosa* L., *Ononis tridentata* L., and *Lepidium subulatum* L., and Mediterranean widespread gypsovags such as *Cistus clusii* Dunal, *Rosmarinus officinalis* L., *Helianthemum syriacum* (Jacq.) Dum. Cours., *Teucrium capitatum* L., and *Thymus vulgaris* L. (Braun-Blanquet and Bolòs, 1958).

We selected two gypsum plant communities (i.e. study sites) in the Middle Ebro Valley (Fig. A2): one to the north of the Ebro river (Site 1, "Leciñena" municipality), and one to the south of this river (Site 2, "La Lomaza de Belchite" Wildlife Reserve). These study sites are representative of gypsum plant communities within the study area regarding species composition and soil characteristics (Table A1 and Table A2; Braun-Blanquet and Bolòs, 1958; Pueyo et al., 2008, 2007). Climatic conditions differ between study sites, being Site 2 more arid than Site 1 (Table A1). At each study site, we selected an area of 6 Km^2 where we performed the vegetation surveys.

2.2. Vegetation surveys

We conducted a vegetation survey in spring 2014, concurring with the plants growing season, to determine the microsites where seedlings and adults of perennial plants preferentially are. At each study site we randomly set sixteen plots (5 × 1 m) at least 250 m distant from each other (n = 32 plots). We recorded every perennial plant occurring inside the plots, identifying them to species level and differentiating by ontogenetic stages (< 1 year-old seedlings, and adults including juveniles and reproductive individuals). We categorized plants depending on the microsite in which they were found (Fig. A3a): in open areas (OA microsite), on the edge of the canopy of adult shrubs (ES microsite) or under the canopy of adult shrubs (UC microsite). OA microsite consisted of open areas not covered by perennial plants, but occasionally occupied by biological soil crusts (i.e. lichens and mosses); ES microsite consisted of a torus placed in the outer part of the shrub canopy whose width was the 10% of the shrub radius; UC microsite consisted of the area covered by the shrub canopy minus ES microsite area. In each plot, we measured the area covered by each microsite using a grid and counting the number of 10 × 10 cm cells occupied per microsite.

We simultaneously performed an additional vegetation survey to identify key nurse species for plant establishment in these communities. We selected six dominant shrubs in the community, accounting for approximately the half of the total abundance of shrubs (Table A3). The choice of species included shrubs with contrasting sizes and life strategies, since we selected four nanophanerophytes and two large chamaephytes (at least 20 cm tall; Table A3), being three of them gypsophytes (*Gypsophila struthium*, *Ononis tridentata,* and *Helianthemum squamatum*) and three gypsovags (*Cistus clusii*, *Rosmarinus officinalis,* and *Thymus vulgaris*). All selected species occurred at both study sites except *C. clusii*; however, we included it as a target species due to its large abundance in Site 1. We randomly selected 25 individual shrubs per target species and paired adjacent open areas of equal size (Cavieres et al., 2014) placed in a random direction at least 50 cm away from any shrub to avoid the shade cast by shrubs (Table A4). We recorded richness (number of species) and abundance (number of individuals of total species) of annuals, perennial seedlings, and perennial adults occurring under the canopy of the target species and in the paired adjacent open areas. For each shrub and the adjacent open area, we determined the sampled area size by measuring the diameter of a ring matching the canopy of the shrub (n = 550 rings; 25 pairs plant-open area of each of six target species at Site 1 and 25 pairs plant-open area of each of five target species at Site 2; Fig. A3b).

We further investigated whether the roles of shrubs in structuring diversity in gypsum plant communities exceeded the area under the canopy, by analyzing the spatial distribution of plant diversity in the vicinity of all shrubs occurring in the community. We randomly arranged six paralleled 250-m linear transects at each study site. Following the line-point intercept sampling method (Goodall, 1952), we recorded all annual and perennial plant species in contact with the transect line at 20 cm intervals (n = 7506 points per study site; Fig. A3c). We analyzed plant diversity in the vicinity of shrubs with the ISAR (individual species area relationships) proposed by Wiegand et al. (2007). The $\mathrm{ISAR}_t(d)$ of a target species t is defined as the number of different species present within a distance d from all of the individuals of the target species t along the transect (Arroyo et al., 2015; Wiegand et al., 2007).

$$\mathrm{ISAR}_t(d) = \sum_{j=1}^{N} [1 - P_{tj}(0, d)]$$

where $1 - P_{tj}(0, d)$ is the probability that species j was present within a distance d of individuals of target species t. The $\mathrm{ISAR}_t(d)$ value will be the sum of the probabilities of all the species N present (Wiegand et al., 2007). The spatial resolution and thus the minimum spatial scale of the ISAR was 20 cm (equivalent to the spatial intervals in transects). We set a maximum distance *d* of 4 m (maximum spatial scale), considered an adequate detection range of plant-plant interactions in semi-arid ecosystems (Arroyo et al., 2015; Rayburn and Wiegand, 2012). In order to assess appropriate sample sizes, we computed ISAR only for shrub species having more than 20 individuals per study site.

2.3. Physical-chemical soil properties

We measured surface mechanical resistance ($kg \cdot cm^{-2}$) as a proxy of soil compaction, soil humidity (volumetric water content, %), and soil temperature (°C) to assess the potential amelioration in micro-environmental conditions under target species canopies compared to open areas. At each study site, we measured these physical soil properties under the canopy of 15 random individuals of the same target species previously selected for vegetation surveys (15 points under each of six target species at Site 1 and 15 points under each of five target species at Site 2), and at 15 random points in open areas (n = 195). We measured soil surface mechanical resistance with a force gauge equipped with a compression plate with a diameter of 2 cm (MECMESIN Basic Force Gauge 500 N). We measured soil volumetric water content (6 cm maximum depth) with a ML3 Theta-Probe soil moisture sensor (Delta-T Devices). Finally, we measured soil temperature (6 cm deep) with a T-bar digital stem thermometer (ATM Ltd ST-9265 A). We measured soil physical properties on a typical spring day with moderate temperatures (average temperature of 15 °C), three days after a rainfall event (Fig. A2).

In addition, we analyzed the chemical properties of the soil under the target species canopies to assess the potential enriched nutrients content compared to open areas. We collected soil samples under the canopy of five random individuals of the same target species (5 samples under each of six target species at Site 1 and 5 samples under each of five target species at Site 2) and at five random points in open areas at each study site (n = 65). We randomly collected and combined three soil cores (4 × 4 cm surface and 7.5 cm deep) per sample. Soil samples were dried and sieved over a 2 mm mesh sieve, and analyzed in the laboratory for available phosphorus (AP), total organic carbon (TOC), total carbon (TC) and total nitrogen (TN). We estimated available phosphorus extracted with Bray n°1 reagent (Bray and Kurtz, 1945) using a spectrometer (UNICAM 8625 UV/Vis Spectrometer) with the absorbance at 430 nm. We estimated total organic carbon in samples treated by a chromatic acid digestion (Heanes, 1984), using the spectrometer with the absorbance at 590 nm. Finally, we measured total carbon and total nitrogen in samples ground to a fine particle size, using a Vario MAX CN analyzer (Elementar Vario MAX CN).

2.4. Data analyses

For every recorded species and ontogenetic stage, we compared the observed frequency per microsite (OA, ES and UC microsites) to the expected frequency per microsite at each study site. We estimated the expected frequency of a species per microsite as the total observed frequency of the species (seedlings and adults separately) multiplied by the proportion of the area covered by each microsite. We performed G-tests to assess whether the observed frequencies of each perennial species (seedlings and adults separately) matched their expected frequencies per microsite at each study site.

$$G = 2\sum_{i}^{N} Oi \ln \frac{Oi}{Ei}$$

where N is the total number of observations, Oi is the observed frequency for each value i and Ei is the expected frequency for each given value i under the null hypotheses (Sokal and Rohlf, 1995).When significant differences were found among microsites ($p \leq 0.05$), we performed post-hoc pairwise G-tests to compare the observed frequencies with the expected frequencies specifically at each microsite. We analyzed differences in richness and abundance of annuals, perennial seedlings and perennial adults separately (six dependent variables in total) under target species canopies (*G. struthium*, *O. tridentata*, *H. squamatum*, *C. clusii*, *R. officinalis* and *T. vulgaris*) compared to open areas by fitting Generalized Linear Mixed Models (GLMMs). We fitted one separate GLMM per dependent variable. Target species, study site and the covariate sampled area (i.e. canopy area) were included as fixed factors and the pair plant-open area was included as random effect to control for local spatial heterogeneities. Study site should be considered as random effect in the GLMM; however, we set it as fixed factor because we only have two levels of this factor (Gelman and Hill, 2006). Poisson error distribution and log link function were assumed.

To detect whether the ISAR of a species was significantly different than expected, a confidence envelope was calculated using Monte Carlo simulations of 199 Poisson null models (Wiegand et al., 2007). Then, if a species showed the ISAR value for a given distance *d* greater than the 97.5 percentile of the confidence interval from simulations, the species presented higher species richness at that distance and it was considered a diversity accumulator. Conversely, if a species showed the ISAR value for a given distance *d* lower than the 2.5 percentile of the confidence interval from simulations, the species presented a lower species richness at that distance and it was considered a diversity repeller. When a species showed the ISAR value within the confidence envelope at a given distance *d*, it was considered neutral (Arroyo et al., 2015; Chacón-Labella et al., 2016; Perry et al., 2016; Rayburn and Wiegand, 2012; Wiegand et al., 2007). For gypsophyte and gypsovag perennial species separately, we determined the percentage of cases, out of the total of times the species occurred at both study sites, in which they acted as diversity accumulators, diversity repellers and neutrals at each distance *d* (Chacón-Labella et al., 2016; Perry et al., 2016; Wiegand et al., 2007).

Differences in physical-chemical soil properties (surface mechanical resistance, humidity, temperature, available phosphorous, total organic carbon, total carbon and total nitrogen) under target species canopies (*G. struthium*, *O. tridentata*, *H. squamatum*, *C. clusii*, *R. officinalis* and *T. vulgaris*) compared to open areas were tested with two-way ANOVAs considering target species and study site as factors.

Statistical analyses were performed in R (R Development Core Team, 2014), except ISAR analyses and Monte Carlo simulations, which were performed in MATLAB R2010b.

3. Results

3.1. Microsites where perennial plants establish

In general, at the seedling stage, gypsophytes appeared less frequently than expected in open areas (OA microsite), especially *G. struthium* and *O. tridentata* (Table 1). In contrast, seedlings of gypsophytes generally appeared more frequently than expected at the edge of adult shrubs (ES microsite). The species-by-species analysis showed that this trend was held for *H. squamatum*, *Hermiaria fruticosa* and *O. tridentata*, depending on the study site (Table 1, Table A5 and Table A.6). Seedlings of gypsophytes appeared under the canopy of shrubs (UC microsite) more frequently than expected in Site 1 and less frequently than expected in Site 2 (Table 1, Table A5 and Table A.6). As observed in seedlings, adults of gypsophytes also appeared less frequently than expected at OA microsite (*G. struthium* and *O. tridentata*, Table 1), and more frequently than expected at ES microsite (*G. struthium*, *H. squamatum*, *Lepidium subulatum* and *O. tridentata*, Table 1). Differently to seedlings, adults of gypsophytes generally appeared less frequently than expected at UC microsite in both study sites (Table 1, Table A5 and Table A.6).

Seedlings of gypsovags showed the same trend than seedlings of gypsophytes, appearing less frequently than expected at OA microsite and more frequently than expected at ES microsite. The species-by-species analysis showed that, in both microsites, this trend was held for the 30% of gypsovag species (Table 1). Seedlings of gypsovags appeared

Table 1
Summary of the results of the G-tests implemented at the two study sites to evaluate significant differences between the observed frequencies and the expected frequencies of all perennial species (seedlings and adults separately) at each microsite: in open areas (OA), at the edge of adult shrubs (ES) and under the canopy of adult shrubs (UC).

	Seedlings			Adults		
	OA	ES	UC	OA	ES	UC
Gypsophytes	–	+	~	–	+	–
Gypsophila struthium	–	0	+	–	+	~
Helianthemum squamatum	~	~	~	~	+	~
Herniaria fruticosa	0	~	~	~	~	~
Lepidium subulatum	0	0	0	0	+	0
Ononis tridentata	–	~	~	–	+	0
Gypsovags	–	+	~	–	+	0
Agropyron cristatum	n.a.	n.a.	n.a.	0	0	0
Brachypodium retusum	0	0	0	~	~	~
Carex halleriana	n.a.	n.a.	n.a.	0	0	0
Carduus sp.	0	0	0	0	0	0
Carlina corimbosa	n.a.	n.a.	n.a.	0	0	0
Cistus clusii	–	+	0	–	+	0
Coris monspeliensis	0	+	0	–	0	+
Dactylis glomerata	n.a.	n.a.	n.a.	0	0	0
Dorycnium pentaphyllum	0	0	0	–	+	0
Fumana ericoides	0	0	0	–	+	0
Genista scorpius	0	0	0	~	+	0
Helianthemum marifolium	–	+	+	–	+	+
Helianthemum pilosum	0	0	0	–	+	0
Helianthemum syriacum	–	+	~	–	+	–
Helichrysum stoechas	–	+	~	–	+	~
Juniperus thurifera	0	0	0	n.a.	n.a.	n.a.
Koeleria vallesiana	0	0	–	–	+	–
Linum suffruticosum	–	+	0	–	+	0
Lithodora fruticosa	0	0	0	–	0	0
Lygeum spartum	0	0	0	–	+	0
Plantago albicans	+	0	–	–	+	–
Polygala rupestris	~	0	0	–	~	~
Reseda stricta	0	0	0	0	0	0
Rosmarinus officinalis	~	~	0	–	+	~
Stipa lagascae	~	~	~	–	+	+
Teucrium capitatum	–	~	+	–	+	0
Thymelaea tinctoria	n.a.	n.a.	n.a.	0	0	0
Thymus vulgaris	–	+	~	–	+	~

Results are indicated as "+" when the observed frequencies were significantly higher than the expected frequencies wherever it is present, "-" when the observed frequencies were significantly lower than the expected frequencies wherever it is present, "0" when the observed frequencies were similar to the expected frequencies wherever it is present and "~" when the trend differed among study sites. Not available data (n.a.) are indicated when the species was not found within the plots.

at UC microsite more frequently than expected in Site 1 and as frequently as expected in Site 2 (Table 1, Table A5 and Table A.6). Gypsovags at the adult stage also appeared less frequently than expected at OA microsite (67% of the gypsovag species; Table 1) and more frequently than expected at ES microsite (59% of the gypsovag species; Table 1). Adult gypsovags generally appeared as frequently as expected at UC microsite (59% of the gypsovag species; Table 1).

3.2. Richness and abundance under the canopy of the target shrubs

Richness and abundance of annuals under shrub canopies differed significantly from open areas except for *H. squamatum* and *T. vulgaris* (Tables 2 and 3). We also found significant differences in richness and abundance of perennial seedlings under shrub canopies compared to open areas except for *H. squamatum* (Tables 2 and 3). Regarding perennial adults, richness and abundance under shrub canopies differed significantly from open areas except for *H. squamatum* concerning richness (Table 2), and except for *H. squamatum* and *T. vulgaris* concerning abundance (Table 3). In summary, target species *G. struthium*, *O. tridentata*, *C. clusii* and *R. officinalis* had significant effects compared to open areas on richness and abundance for all plant categories, having *G. struthium* and *R. officinalis* the largest and smallest effects respectively (Z scores in GLMM; Tables 2 and 3).

Richness of annuals under *G. struthium* and *O. tridentata* canopies and richness of perennial seedlings under *R. officinalis* canopy differed between study sites (Table 2), being higher in Site 2 than in Site 1 (Fig. A.5). Abundance of annuals under *G. struthium*, *O. tridentata* and *T. vulgaris* canopies, perennial seedlings under *O. tridentata*, *H. squamatum* and *T. vulgaris* canopies and perennial adults under *O. tridentata* canopy also depended on the study site (Table 3). Abundance under these target species was higher in Site 2 than in Site 1, except for annuals under *T. vulgaris* canopy (Fig. A.5).

Richness of annuals under *T. vulgaris* canopy, richness of perennial seedlings under *G. struthium* canopy, and richness of perennial adults under *G. struthium*, *O. tridentata* and *R. officinalis* canopies depended on sampled area (Table 2). Sampled area also had significant effects on abundance of annuals under shrub canopies, except for *H. squamatum* and *R. officinalis*, on abundance of perennial seedlings under *G. struthium* and *C. clusii* canopies, and on abundance of perennial adults under *G. struthium*, *O. tridentata* and *R. officinalis* canopies (Table 3). In all cases, richness and abundance were higher when sampled area under these target species was larger (Fig. A.6).

3.3. Spatial distribution of plant diversity in the vicinity of shrubs

Gypsophytes acted as diversity accumulators in up to 57% of the cases, and acted as diversity repellers in 14% of the cases at distances smaller than 100 cm (Fig. 1). All gypsophytes acted as neutrals at distances greater than 180 cm (Fig. 1). The diversity-accumulator gypsophytes were *G. struthium* and *O. tridentata* in both study sites, while *H. squamatum* acted as diversity repeller at site 2 (Fig. 2).

While diversity-repeller gypsovags overcome diversity-accumulator gypsovags at short distances, being $d = 0$ (the 30% and the 10% of the gypsovags respectively), the proportion of diversity accumulators overcome diversity repellers at distances greater than 20 cm (Fig. 1). Diversity-repeller gypsovags were found at both study sites, but diversity-accumulator gypsovags were found only at Site 1 (Table A.7 and Table A.8). The 90% of the gypsovags acted as neutrals at distances greater than 40 cm (Fig. 1). Among target gypsovag species in Site 1, *C. clusii* and *R. officinalis* acted as diversity repellers at short distances, but *T. vulgaris* acted as diversity accumulator at distances between 40 and 120 cm (Fig. 2). Only the target gypsovag *T. vulgaris* was occurring in Site 2, where it acted as diversity repeller at distances smaller than 40 cm (Fig. 2).

3.4. Physical-chemical soil properties

We found significant differences between target species and open areas on all the studied physical-chemical soil properties, and these differences depended on the study site except for TOC (Tables 4 and 5). Surface mechanical resistance was lower under all target species canopies than in open areas, being this trend more evident under *O. tridentata* and *R. officinalis* canopies in Site 1 and under *G. struthium* and *R. officinalis* in Site 2 (Table 4 and Fig. 3). In general, soil humidity under target species canopies did not differ from that in open areas (Table 4). Soil temperature was lower under shrub canopies than in open areas, especially under *G. struthium*, *O. tridentata*, *C. clusii* and *R. officinalis* canopies in Site 1 (Table 4 and Fig. 3).

Regarding chemical soil properties, available phosphorus was significantly higher under *O. tridentata*, *R. officinalis* and *T. vulgaris* canopies than in open areas (Table 5 and Fig. 3). Available phosphorus was higher in Site 2 than in Site 1, especially in open areas and under *G. struthium* and *H. squamatum* canopies (Fig. 3). Total organic carbon and total carbon were higher under the canopy of most target species than in open areas (except for total carbon under *H. squamatum* and *T.*

Table 2
Summary of the GLMMs implemented to test significant effects ($p \leq 0.05$) of the target species compared to open areas, the study site, the sampled area and the interaction among these factors on richness, for annuals, perennial seedlings and perennial adults.

	Annuals (R^2 = 0.82)				Perennial seedlings (R^2 = 0.67)				Perennial adults (R^2 = 0.69)			
	Estim.	SE	Z (t)	p	Estim.	SE	Z (t)	p	Estim.	SE	Z (t)	p
G	2.97	0.52	5.76	< **0.001**	1.77	0.23	7.79	< **0.001**	2.22	0.29	7.64	< **0.001**
O	1.55	0.55	2.80	< **0.01**	1.12	0.23	4.89	< **0.001**	1.81	0.28	6.41	< **0.001**
H	1.74	0.95	1.83	0.067	0.38	0.36	1.06	0.291	0.05	0.67	0.07	0.941
C	0.97	0.38	2.56	< **0.05**	1.29	0.23	5.58	< **0.001**	1.45	0.37	3.94	< **0.001**
R	1.77	0.66	2.66	< **0.01**	0.58	0.31	1.90	**0.054**	1.41	0.39	3.62	< **0.001**
T	−0.63	0.69	−0.91	0.364	0.56	0.20	2.73	< **0.01**	1.02	0.30	3.40	< **0.001**
Site	1.21	0.31	3.87	< **0.001**	−0.68	0.15	−4.66	< **0.001**	−0.63	0.24	−2.65	< **0.01**
Site x G	−1.47	0.63	−2.33	< **0.05**	−0.54	0.32	−1.68	0.093	−0.36	0.42	−0.85	0.398
Site x O	−1.71	0.86	−1.98	< **0.05**	0.55	0.33	1.68	0.094	0.66	0.41	1.61	0.108
Site x H	−1.03	1.09	−0.95	0.342	0.52	0.55	0.94	0.348	−0.19	0.99	−0.19	0.847
Site x C	–	–	–	–	–	–	–	–	–	–	–	–
Site x R	−0.51	0.82	−0.62	0.534	1.21	0.41	2.99	< **0.01**	0.62	0.53	1.18	0.240
Site x T	1.35	0.78	1.73	0.083	0.65	0.35	1.84	0.066	0.07	0.60	0.12	0.904
Area	1.62	0.52	3.11	< **0.01**	1.51	0.19	8.14	< **0.001**	2.50	0.27	9.41	< **0.001**
Area x G	−1.06	0.89	−1.19	0.233	−1.59	0.42	−3.80	< **0.001**	−2.04	0.51	−3.97	< **0.001**
Area x O	0.13	0.99	0.13	0.893	−0.62	0.43	−1.44	0.150	−1.35	0.51	−2.64	< **0.01**
Area x H	−19.72	19.22	−1.03	0.305	4.68	6.21	0.75	0.451	6.43	11.62	0.55	0.580
Area x C	−1.14	1.72	−0.66	0.507	−1.12	0.93	−1.19	0.233	−1.35	1.47	−0.92	0.359
Area x R	−0.79	1.24	−0.64	0.525	−0.41	0.56	−0.73	0.468	−1.79	0.71	−2.51	< **0.05**
Area x T	11.86	5.47	2.17	< **0.05**	1.44	1.99	0.72	0.471	−0.37	2.95	−0.13	0.901

G = *G. struthium,* O = *O. tridentata,* H = *H. squamatum,* C = *C. clusii*, R = *R. officinalis* and T = *T. vulgaris.*

vulgaris canopies), being more evident under *G. struthium*, *C. clusii* and *R. officinalis* canopies in Site 1 (Table 5 and Fig. 3). Total nitrogen was higher under all target species canopies than in open areas, being more evident under *G. struthium*, *C. clusii* and *R. officinalis* canopies in Site 1 (Table 5 and Fig. 3).

We considered micro-environmental amelioration when surface mechanical resistance diminished, humidity increased, temperature decreased and nutrients increased under target species canopies compared to open areas. Target species that showed amelioration in more soil conditions under canopies compared to open areas were *R. officinalis* and *O. tridentata* (Fig. A.7).

4. Discussion

Our results highlight the relevance of being spatially associated to other plants at establishment stage in gypsum plant communities, underlining the role of some key nurse species in structuring plant diversity in their local vicinity by facilitating the establishment of other species. Following other studies, we inferred biotic interactions from spatial patterns of plants in the community (Arroyo et al., 2015; Cavieres et al., 2006; Saiz and Alados, 2012; Soliveres and Maestre, 2014). It is challenging to infer biotic interactions at the community level based on observational data. The reason is that plant spatial patterns are the result of biotic interactions acting together with other biotic and abiotic factors, as seed dispersal patterns or environmental heterogeneity (Ramón et al., 2018; Escudero et al., 2005). However,

Table 3
Summary of the GLMMs implemented to test significant effects ($p \leq 0.05$) of the target species compared to open areas, the study site, the sampled area and the interaction among these factors on abundance, for annuals, perennial seedlings and perennial adults.

	Annuals (R^2 = 0.95)				Perennial seedlings (R^2 = 0.95)				Perennial adults (R^2 = 0.89)			
	Estim.	SE	Z (t)	p	Estim.	SE	Z (t)	p	Estim.	SE	Z (t)	p
G	7.81	0.74	10.55	< **0.001**	2.41	0.14	17.74	< **0.001**	2.31	0.21	11.25	< **0.001**
O	4.04	0.56	7.27	< **0.001**	0.99	0.12	8.31	< **0.001**	1.66	0.21	7.78	< **0.001**
H	1.26	1.04	1.21	0.226	0.09	0.33	0.28	0.776	0.74	0.55	1.34	0.180
C	2.55	0.18	14.20	< **0.001**	2.37	0.24	9.93	< **0.001**	1.74	0.38	4.54	< **0.001**
R	2.00	0.66	3.03	< **0.01**	1.59	0.31	5.17	< **0.001**	2.60	0.39	6.74	< **0.001**
T	−0.92	0.76	−1.22	0.222	0.61	0.21	2.85	< **0.01**	0.56	0.36	1.59	0.113
Site	3.10	0.46	6.73	< **0.001**	−1.63	0.20	−8.07	< **0.001**	−1.21	0.25	−4.82	< **0.001**
Site x G	−5.44	0.75	−7.22	< **0.001**	−0.26	0.27	−0.99	0.321	0.10	0.40	0.25	0.800
Site x O	−1.91	0.64	−3.00	< **0.01**	0.61	0.24	2.56	< **0.05**	0.85	0.54	2.16	< **0.05**
Site x H	−1.35	1.13	−1.19	0.233	1.54	0.60	2.58	< **0.01**	−0.35	0.90	−0.39	0.693
Site x C	–	–	–	–	–	–	–	–	–	–	–	–
Site x R	0.28	0.72	0.39	0.699	0.03	0.40	0.08	0.934	−1.03	0.54	−1.90	0.058
Site x T	2.74	0.82	3.36	< **0.001**	1.03	0.41	2.54	< **0.05**	0.56	0.68	0.83	0.408
Area	3.24	0.77	4.22	< **0.001**	1.33	0.30	9.79	< **0.001**	3.82	0.33	11.49	< **0.001**
Area x G	−6.49	1.02	−6.36	< **0.001**	−2.46	0.23	−10.86	< **0.001**	−1.94	0.34	−5.71	< **0.001**
Area x O	−2.40	0.81	−2.25	< **0.05**	−0.19	0.20	−0.95	0.340	−1.82	0.34	−5.27	< **0.001**
Area x H	−10.38	22.53	−0.46	0.645	10.99	5.87	5.87	0.061	−5.44	9.50	−0.57	0.567
Area x C	−4.40	0.66	−6.67	< **0.001**	−4.31	0.85	−5.09	< **0.001**	−1.81	1.51	−1.19	0.233
Area x R	1.73	1.26	1.38	0.169	−0.75	0.85	−1.37	0.170	−3.01	0.68	−4.40	< **0.001**
Area x T	28.91	7.40	3.91	< **0.001**	0.97	0.55	0.41	0.686	−0.80	4.20	−0.19	0.849

G = *G. struthium,* O = *O. tridentata,* H = *H. squamatum,* C = *C. clusii*, R = *R. officinalis* and T = *T. vulgaris.*

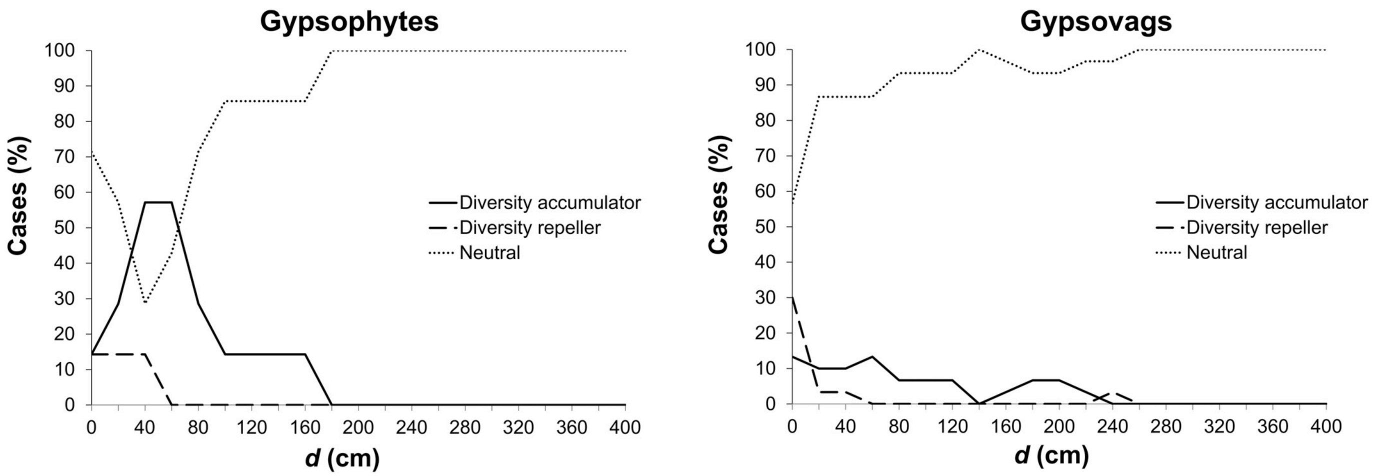

Fig. 1. Percentage of cases (out of the total of times they are present at both study sites altogether) in which gypsophyte and gypsovag perennial species acted as diversity repellers, neutrals, and accumulators, at different distances d from the target individuals ($d_{\max} = 400$ cm). Detail of the behavior of each species in Supplementary material (Table A.5 and Table A.6).

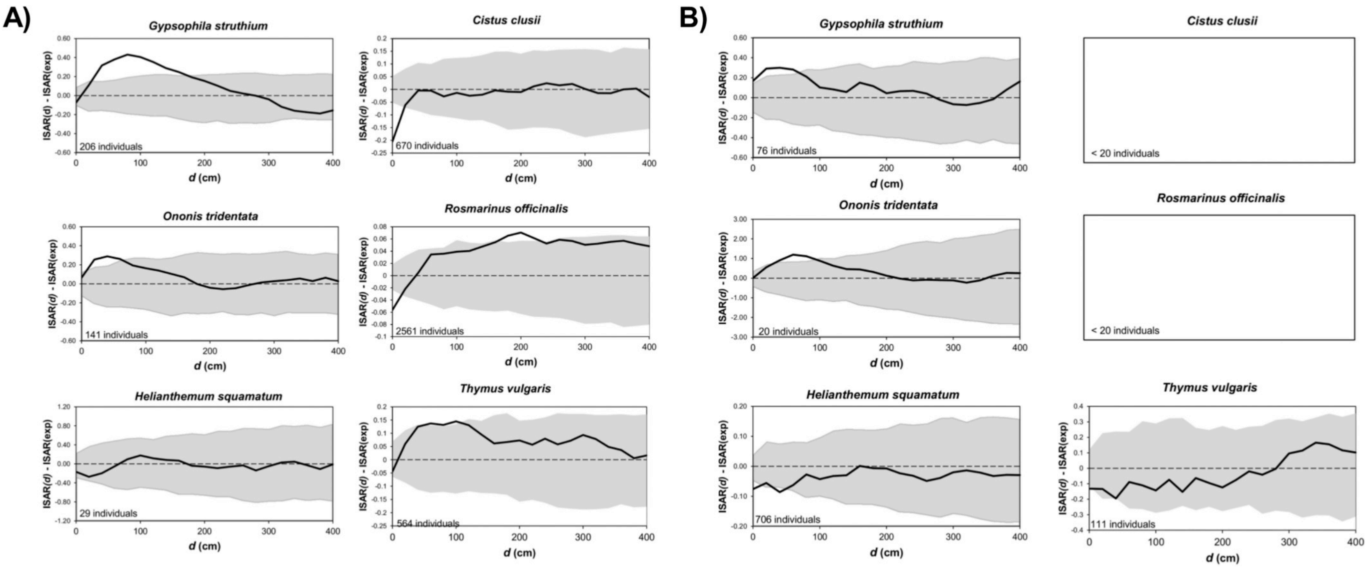

Fig. 2. ISAR curves of target shrubs with more than 20 individuals in Site 1 (A) and Site 2 (B). When ISAR curve is represented above the confidence envelope (grey shaded), the species act as diversity accumulator, when it is represented below the confidence envelope, the species act as diversity repeller and when it is represented within the confidence envelope, the species act as neutral.

Table 4

Summary of the ANOVAs implemented to test significant effects ($p \leq 0.05$) of the target species compared to open areas, the study site, and the interactions between these factors on surface mechanical resistance, soil humidity and soil temperature.

	Surface mechanical resistance ($R^2 = 0.52$)				Soil humidity ($R^2 = 0.46$)				Soil temperature ($R^2 = 0.55$)			
	Estim.	SE	t	p	Estim.	SE	t	p	Estim.	SE	t	p
G	−1.85	0.42	−4.40	< **0.001**	−0.23	0.90	−0.25	0.802	−5.23	0.74	−7.11	< **0.001**
O	−2.60	0.42	−6.19	< **0.001**	−0.94	0.90	−1.04	0.299	−6.07	0.74	−8.25	< **0.001**
H	−1.20	0.50	−2.38	< **0.05**	0.22	1.08	0.21	0.837	−1.74	0.88	−1.97	< **0.05**
C	−2.30	0.42	−5.48	< **0.001**	−0.21	0.90	−0.24	0.813	−4.08	0.74	−5.55	< **0.001**
R	−2.81	0.42	−6.69	< **0.001**	−1.79	0.90	−1.98	< **0.05**	−5.29	0.74	−7.19	< **0.001**
T	−2.38	0.42	−5.67	< **0.001**	1.51	0.90	1.67	0.096	−2.87	0.74	−3.90	< **0.001**
Site	1.59	0.43	3.72	< **0.001**	−2.81	0.81	−3.45	< **0.001**	−7.20	0.64	−11.23	< **0.001**
Site x G	−1.30	0.60	−1.50	< **0.05**	−2.93	1.21	−2.41	< **0.05**	5.72	0.98	5.86	< **0.001**
Site x O	−0.34	0.60	−0.56	0.575	−2.01	1.21	−1.66	0.099	6.45	0.98	6.61	< **0.001**
Site x H	−0.99	0.67	−1.50	0.136	−1.99	1.36	−1.47	0.144	2.69	1.10	2.45	< **0.05**
Site x C	–	–	–	–	–	–	–	–	–	–	–	–
Site x R	−0.55	0.56	−0.98	0.328	1.95	1.13	1.73	0.085	4.81	0.90	5.32	< **0.001**
Site x T	0.62	0.60	1.04	0.299	−2.57	1.21	−2.11	< **0.05**	4.04	0.98	4.14	< **0.001**

G = *G. struthium,* O = *O. tridentata,* H = *H. squamatum,* C = *C. clusii*, R = *R. officinalis* and T = *T. vulgaris.*

Table 5
Summary of the ANOVAs implemented to test significant effects ($p \leq 0.05$) of the target species compared to open areas, the study site, and the interactions between these factors on chemical soil properties.

	AP ($R^2 = 0.94$)				TOC ($R^2 = 0.65$)				TC ($R^2 = 0.61$)				TN ($R^2 = 0.59$)			
	Estim.	SE	t	p	Estim.	SE	t	p	Estim.	SE	t	p	Estim.	SE	t	p
G	−4.60	6.65	−0.69	0.492	2.53	0.52	4.90	< **0.001**	5.20	1.22	4.27	< **0.001**	0.28	0.06	4.36	< **0.001**
O	43.36	6.65	6.52	< **0.001**	1.36	0.52	2.64	< **0.05**	2.06	1.22	1.69	**0.097**	0.15	0.06	2.38	< **0.05**
H	−8.75	6.65	−1.32	0.194	1.33	0.52	2.58	< **0.05**	1.99	1.22	1.63	0.109	0.13	0.06	1.99	**0.05**
C	5.17	6.65	0.78	0.440	2.98	0.52	5.79	< **0.001**	5.96	1.22	4.89	< **0.001**	0.32	0.06	4.97	< **0.001**
R	60.64	6.65	9.12	< **0.001**	3.35	0.52	6.50	< **0.001**	7.21	1.22	5.92	< **0.001**	0.37	0.06	5.83	< **0.001**
T	61.52	6.65	9.25	< **0.001**	1.57	0.52	3.05	< **0.01**	2.09	1.22	1.72	0.092	0.13	0.06	2.11	< **0.05**
Site	67.93	6.65	10.22	< **0.001**	−0.24	0.52	−0.47	0.638	−0.36	1.22	−0.29	0.772	−0.01	0.06	−0.15	0.880
Site x G	9.03	9.41	0.96	0.341	−0.59	0.73	−0.81	0.421	−0.76	1.72	−0.44	0.662	−0.03	0.09	−0.35	0.726
Site x O	−25.10	9.41	−2.67	< **0.05**	0.38	0.73	0.52	0.604	1.28	1.72	0.74	0.461	0.06	0.09	0.64	0.526
Site x H	17.45	9.41	1.86	0.069	0.36	0.73	0.49	0.625	1.86	1.72	1.08	0.287	0.07	0.09	0.75	0.455
Site x C	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Site x R	−32.08	9.41	−3.41	< **0.01**	−1.52	0.73	−2.09	< **0.05**	−3.64	1.72	−2.11	< **0.05**	−0.22	0.09	−2.45	< **0.05**
Site x T	−44.75	9.41	−4.76	< **0.001**	−0.73	0.73	−1.00	0.320	−0.77	1.72	−0.45	0.658	−0.04	0.09	−0.46	0.648

G = *G. struthium,* O = *O. tridentata,* H = *H. squamatum,* C = *C. clusii*, R = *R. officinalis*, T = *T. vulgaris,* AP = available phosphorus, TOC = total organic carbon, TC = total carbon and TN = total nitrogen.

when species aggregate in space more often than expected by chance, it can be considered that these species benefit from aggregation, assuming positive biotic interactions among them (Saiz and Alados, 2012).

It is well known that facilitative interactions are crucial for seedling establishment, particularly in stressful environments (Soliveres and Maestre, 2014) where harsh conditions hamper plant establishment (Escudero et al., 2015). In arid and semi-arid environments, most seedlings are not able to survive in open areas, as they are often subjected to potentially lethal temperatures and intense dryness (Flores and Jurado, 2003). Our data showed that seedlings mainly established in microsites associated to adult shrubs more often than expected by chance. We expected that the establishment of gypsovags would be facilitated to a greater extent than gypsophytes, which might be able to establish in open areas because of their ability to tolerate the harsh conditions inherent to gypsum environments (Escudero et al., 1999, 2015; Palacio et al., 2014; Romão and Escudero, 2005). Contrary to our expectations, gypsophytes were also found close to adult shrubs at frequencies higher than expected. These observations further reinforce the importance of facilitation for plant establishment in semi-arid gypsum plant communities, regardless of plant life strategies.

Although proximity to nurse plants may enhance seedling establishment, the positive effects may vary in intensity depending on the relative nurse-facilitated plant position (Reisman-Berman, 2007). Shade provided by shrubs can create favorable microsites for plant establishment (Callaway, 2007), however limits light availability, which may decrease understory plant performance (Valladares and Pearcy, 2002). Furthermore, facilitated plants development may be at risk due to competition with nurse plants for water or nutrients (Coomes and Grubb, 2000). The results of this study suggest that the most favorable microsite for plant establishment is at the edge of the canopy of adult shrubs, where most gypsophytes and gypsovags were found at frequencies higher than expected. At this microsite, the likely positive effects of nurse shading overcome competition for water, nutrients and light (Reisman-Berman, 2007). The competitive response of a species may be inverse to its ability to tolerate stress (Liancourt et al., 2005; Maestre et al., 2009). In general, gypsophytes (stress tolerant) appeared at microsites directly under adult shrubs canopies at frequencies lower than expected, suggesting competitive exclusion by nurse plants. However, some gypsovags also seem to avoid this microsite, indicating that these less tolerant plants may be excluded by competition as well.

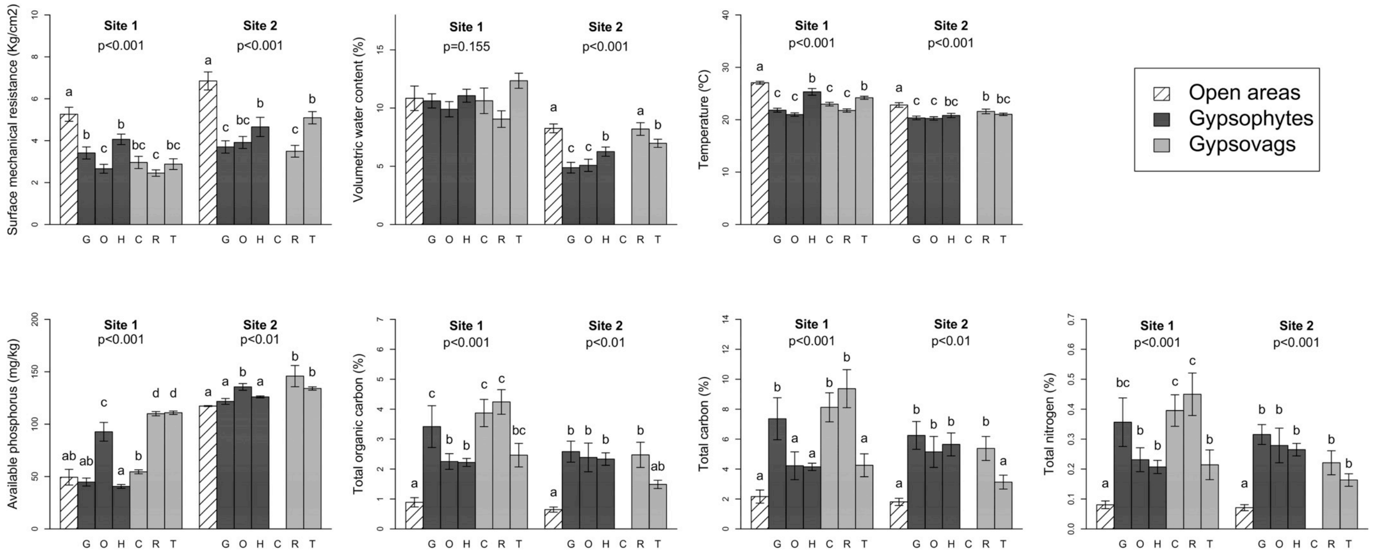

Fig. 3. Barplots representing mean values of the physical-chemical soil properties (surface mechanical resistance, humidity, temperature, available phosphorus, total organic carbon, total carbon and total nitrogen) in open areas and under the canopy of the target species (G = *G. struthium*, O = *O. tridentata*, H = *H. squamatum*, C = *C. clusii*, R = *R. officinalis*, and T = *T. vulgaris*) at each study site. Different letters indicate significant differences among target species after pairwise Tukey's post-hoc tests when $p \leq 0.05$ in ANOVAs fitted per study site.

Generally, shrubs are considered to have a positive role in plant communities (Gómez-Aparicio et al., 2005). To a lesser or a greater extent, most studied shrub species harbored more richness and abundance than open areas. The target species whose understories harbored the highest richness and abundance were the gypsophytes *G. struthium* and *O. tridentata* (especially for perennials). Other studies support the role of *G. struthium* and *O. tridentata* as nurse species in gypsum plant communities (Navarro-Cano et al., 2014, 2016). In the case of *O. tridentata*, it belongs to the family *Fabaceae*, which holds the highest number of nurse species recorded in arid and semi-arid environments (Flores and Jurado, 2003), likely due to N fixation in N-limited ecosystems (Sprent and Gehlot, 2010). Indeed, our results showed that the species harboring the highest richness and abundance also have enhanced physical-chemical soil conditions under canopy compared to open areas (*e.g.,* total nitrogen; Fig. A. 18 and Fig. A.19). Nevertheless, we are aware that observational data provided are not sufficient to detect the abiotic factors driving facilitation, but further investigation is needed.

Gypsovags also harbored more richness and abundance of plants under canopies than open areas, but to a lesser extent than gypsophytes. For example, the gypsovag *R. officinalis* showed a weaker effect on richness and abundance than other shrubs with similar physiognomy, such as the gypsophytes *G. struthium* and *O. tridentata*. Some of the most abundant gypsovag shrubs that are present in gypsum plant communities of the Middle Ebro Valley have demonstrated allelopathic activity (i.e. *R. officinalis* and *T. vulgaris;* Vokou et al., 1993; Thompson et al., 2003). Allelopathy could be a mechanism of less adapted plants (*e.g.*, gypsovags) to avoid competition for scarce resources and succeed in gypsum plant communities. Nevertheless, this idea would need to be tested in other gypsum areas to ascertain whether this phenomenon is either species-specific or relies on life strategies.

Plant interactions play an important role in structuring plant communities in arid and semi-arid environments (Saiz et al., 2014; Arroyo et al., 2015; Chacón-Labella et al., 2016; Perry et al., 2016). The presence of key nurse species in the community is reflected in the accumulation of plant species forming species-rich areas (Soliveres et al., 2011), whereas the presence of highly competitive or allelopathic plants is reflected in a decrease of plant diversity in the local vicinity (Arroyo et al., 2015). We found two dominant nurse species in gypsum plant communities of the Middle Ebro Valley (the gypsophytes *G. struthium* and *O. tridentata*), which had an important role in plant spatial structure by accumulating plants in the local vicinity. Similar findings were obtained by Saiz et al. (2014) in the same gypsum plant communities following different methodologies. On the other hand, our study showed that 30% of gypsovags acted as diversity repellers at short distances, especially the most abundant gypsovag shrubs in these communities (i.e. *C. clusii* and *R. officinalis*). However, in line with the findings of Perry et al. (2016), only a few species acted as either accumulators or repellers in our study site compared to neutrals.

We found that plant spatial associations differed between study sites. Aridity conditions differ between study sites, showing Site 2 higher aridity, and consequently providing more stressful conditions for plant establishment. Taking our findings together, we found greater nurse effects and greater diversity accumulation in the local vicinity of gypsophytes in the least arid site (Site 1), and greater diversity repulsion by gypsovags in the most arid site (Site 2). These findings suggest a shift in biotic interaction outcomes from facilitative net effect towards interference along with stress increment, as reported by numerous studies (Maestre et al., 2009; Saiz et al., 2014; Soliveres and Maestre, 2014). Nevertheless, this result must be taken with caution, as only two study sites along an aridity gradient were considered (Maestre et al., 2006).

In conclusion, this observational study at community level revealed that in such stressful environments most plants were spatially associated to adult shrubs and therefore required being facilitated to become established. The survey of species richness and abundance under the canopy of the most abundant shrubs reported that plant establishment and survival were facilitated mostly by adult gypsophytes, especially by *G. struthium* and *O. tridentata*. Facilitation mediated by gypsophytes led to species enrichment in their vicinities, thus structuring plant diversity in species-rich areas around gypsophytes. Therefore, our study confirmed that gypsophytes play key roles in the spatial patterning of plant establishment in gypsum plant communities of the Middle Ebro Valley. Further research should test the observed patterns of plant establishment and the role of substrate-specialists in different gypsum plant communities to verify the generalization of our findings. Besides, testing our hypotheses by controlled experiments would help unravel the underlying mechanisms driving the observed patterns.

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Conflicts of interest

The authors declare that they have no competing interests.

Research involving human participants and/or animals

The authors declare that the research did not involve human participants nor animals.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2018.09.003.

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