

RESEARCH ARTICLE

Homogeneous microenvironmental conditions under nurses promote facilitation

Ricardo Sánchez-Martín¹  | Alicia Montesinos-Navarro¹  | Helga Ochoterena² | Irene Pisanty³ | Mariana Rodríguez-Sánchez^{2,3} | Miguel Verdú¹  | Hilda Flores-Olvera²

¹Centro de Investigaciones Sobre Desertificación (CIDE, CSIC-UV-GV), Valencia, Spain

²Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico

³Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico

Correspondence

Ricardo Sánchez-Martín
Email: ricardosm92@gmail.com

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Abstract

1. Biotic interactions are highly affected by species traits and micro-environmental variability. Research on facilitation has primarily focused on how nurse species alleviate abiotic stress for beneficiary species, while the impact of the micro-environmental variability generated by nurse plants in shaping facilitation outcomes is poorly understood. This study has two objectives: (i) To evaluate which traits define beneficiary species and (ii) to evaluate whether nurse and non-nurse species differ in their ability to reduce abiotic stress and its variability under their canopy.
2. We sampled recruits in two arid and stressful environments to assess (i) which species accumulate more juveniles beneath their canopy controlling for their coverage (nurse vs. non-nurse species) and (ii) which species benefited from facilitation by determining whether they tend to recruit more beneath other species or on the bare ground (beneficiary/non-beneficiary). First, we compared how nurse and non-nurse species modify the physical and chemical microenvironments underneath their canopy, both in terms of magnitude and variation. Second, we compared root growth, water retention and nutrient accumulation in juvenile plants of beneficiary and non-beneficiary species.
3. We found that facilitation is enhanced by species that provide a more homogeneous microenvironment rather than an intense reduction of microenvironmental stress under their canopy. In addition, the juveniles of beneficiary species invest more in root development, accumulate Ca and S in their shoot tissues, and show a higher water content than non-beneficiary species.
4. Our findings indicate that the homogeneity of microenvironments plays a crucial role in facilitative interactions, and the juveniles of beneficiary species show a less conservative strategy, investing more in resource acquisition than juveniles of non-beneficiary species.

KEYWORDS

beneficiary species, Cuatrociénegas, gypsum soils, homogeneity, microhabitats variability, nurse species, plant facilitation, traits

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1 | INTRODUCTION

In nature, many plant species face challenges in establishing due to harsh abiotic conditions. Nonetheless, these species can still thrive within a community by benefiting from the microhabitat enhancements produced by neighbouring species. This process, known as facilitation, hinges on the support provided by nurse species—mature plants that ameliorate their immediate surroundings, benefiting the establishment and survival of other species sheltered beneath their canopy, known as beneficiary species (Bronstein, 2009; Brooker et al., 2008; Bruno et al., 2003; McIntire & Fajardo, 2014; Padilla & Pugnaire, 2006).

Facilitative interactions help preserve diversity in plant communities by providing a myriad of different microhabitats that can relax environmental filters for stress-sensitive species that find new windows of opportunity to survive in unsuitable environments (Brooker et al., 2008; Bruno et al., 2003). Facilitative interactions are ubiquitous in many natural systems, especially in stressful environments, from alpine (Chen et al., 2015) and polar areas (Cavieres et al., 2018) to deserts (Macek et al., 2018; Verdú & Valiente-Banuet, 2008), but also in milder environments such as forests (Gómez-Aparicio et al., 2004), grasslands (Rebollo et al., 2002), and even in the case of crops (Brooker et al., 2021).

Biological interactions, such as facilitation, depend on a delicate balance between the organisms involved and the environment in which they occur (Poisot et al., 2015). First, they depend on the establishing individuals and their capacity to cope with the abiotic and biotic environment. In that sense, plant traits offer a mechanistic link between abiotic conditions and the likelihood of species survival (Losapio & Schöb, 2017). Second, the traits of adult species will also play a crucial role in determining how they modify their environment and whether these modifications enable them to act as nurses (Gross et al., 2008; Navarro-Cano et al., 2021; Schöb et al., 2012, 2017). In this sense, those traits that allow abiotic stress reduction have been considered crucial for facilitation. For instance, we can find examples of facilitation beneath the shelter of nurse species that reduce the impact of extreme temperatures (Sotomayor & Drezner, 2019), protect against herbivores (Baraza et al., 2006) or increase water availability or nutrient concentrations beneath the nurse plant (Gómez-Aparicio et al., 2004).

However, the same plant traits that promote abiotic stress reduction can also influence microhabitat variability beneath the nurse plants, an aspect that has received less attention. This variability in the microenvironmental conditions may affect the quality of nurses and, consequently, the outcome of facilitation. Nurse-induced microhabitat heterogeneity can have opposing effects on facilitation outputs depending on how it affects the potential beneficiaries. Large heterogeneity in the stress reduction effect can promote facilitation by diversifying the conditions from which more species can benefit (López-Pintor et al., 2006) or reduce it if the generated conditions do not meet facilitated species' requirements (Anthelme et al., 2014).

This study aims to better understand the properties that make a plant suitable for harbouring beneficiary species (i.e. acting as a nurse). Specifically, we aim to understand how the variability in the habitats generated by nurse species contributes to their nursing

capacities by contrasting them with the well-known role of abiotic stress reduction. Furthermore, focusing on the beneficiary species, we assessed whether there are differences in the functional traits of species benefiting from facilitation compared to those that do not. To do so, we first determined which species act as nurse plants and which species benefit from facilitation in two plant communities growing under high abiotic pressure in a harsh edaphic environment within a desertic zone. Then, to understand the type of microenvironments that favour the establishment of beneficiary plants, we evaluated how nurse species modify their abiotic environment both in magnitude (i.e. the strength of the effect caused by nurses to abiotic variables) and variability (i.e. the degree of heterogeneity in the same abiotic variables beneath the nurse). Finally, we investigated functional differences in juvenile individuals belonging to beneficiary and non-beneficiary species, focusing on traits related to growth and water and nutrient acquisition strategies.

2 | METHODS

2.1 | Study site

We conducted the study in two sites within the gypsum flats of the Cuatrociénegas protected area in the Chihuahuan desert, Coahuila, México (Figure 1a,b). Fieldwork was conducted with permission from the directorate of the Cuatrociénegas flora and fauna protection area, ensuring compliance with environmental regulations. Plant communities are characterised by sparse vegetation, generally grouped in multispecific patches mainly composed of camephytes and shrubs (Rodríguez-Sánchez et al., 2022). These communities develop in an arid environment with an average annual rainfall of 211 mm, most of which falls along the summer (June–September). The average yearly temperature is 21.9°C, with the coldest month being January at 12.9°C and the hottest being July at 28.8°C. Throughout the year, the region experiences strong temperature fluctuations ranging between 0°C and 50°C (Montiel-González et al., 2018). Besides the arid conditions, plants face critical physical and chemical edaphic limitations due to extremely high concentrations of gypsum in the soils ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$; Rodríguez-Sánchez et al., 2022). In this type of environment, Ca and S excess have been proven to interfere with the acquisition of other macronutrients and to become toxic for plants (Duvigneaud & Denaeyer-de Smet, 1966; Guerrero-Campo et al., 1999; Romão & Escudero, 2005; Ruiz et al., 2003).

In order to ensure that our data represent the soil heterogeneity present in this environment, we included two study sites with a contrasted physical structure of gypsum outcrops. In one of the sites, the gypsum is hard and presents crystallised layers displaying low porosity and high particle aggregation (Figure 1c), thus limiting root development (Bridges & Burnham, 1980; Escudero et al., 2015; Guerrero Campo et al., 1999). In the other site, the gypsum soils are sandy and unstable, moving with the wind to the point of establishing embryonic gypsum dunes.

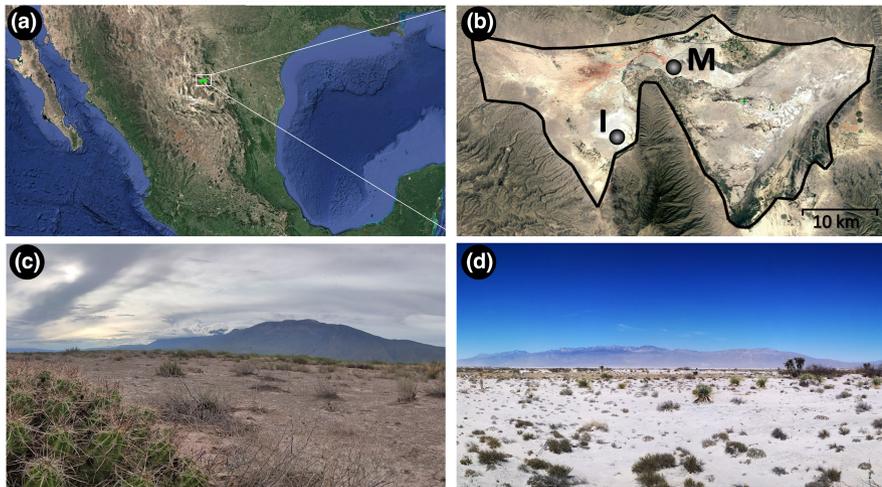


FIGURE 1 Study site location and description. (a) Map showing the location of Cuatrociénegas, Coahuila, Mexico (white box). (b) Location of the sampling zones in the Cuatrociénegas protected area (I: Interdunes locality, M; Mezquites locality). The bottom panels represent the two environments sampled, being (c) the Mezquites locality, distinguished by consolidated soils, while (d) depicts the Interdunes locality, characterised by sandier soils. Both localities are approximately 12 km apart.

2.2 | Community sampling

We conducted a field campaign in March 2020. The sampling design comprised a total of 36 (300×300cm) plots. We randomly distributed half of the plots on the consolidated environment (hereafter called Mezquites, Figure 1c) and the other half on the unstable environment (hereafter called Interdunes, Figure 1d).

We followed the same sampling process described in Sánchez-Martín et al. (2022) and Sánchez-Martín, Verdú, et al. (2023). First, within each plot, we identified all adult plants and measured the maximum and minimum diameter to approximate each plant cover using the ellipse equation:

$$\text{cover} = (\pi ab)$$

Where (a) is the semi-major diameter and (b) is the semi-minor diameter. When the adult plants grew in associations (i.e. cooccurring in vegetation patches), we also estimated the cover of these patches using the same formula. Then, we calculated the bare ground cover by subtracting the surface occupied by patches and non-associated plants from the sampled area.

We also identified all recruits within the plots and whether they were located on the bare ground or under an adult plant, identifying the species of the adult plant. When recruits inhabited patches with multiple species, we assigned the recruit to the nearest adult plant whose canopy covered it (Alcántara et al., 2019). We considered as recruits all plants ranging from seedlings (with at least the first two leaves) to tiny plants (<15% in height compared to adults), showing neither signs of reproductive structures nor evident lignification at the stem base (Alcántara et al., 2019; Sánchez-Martín et al., 2022; Sánchez-Martín, Verdú, et al., 2023).

2.3 | Recognizing beneficiary species

To recognise beneficiary species, we analysed the recruitment pattern of its juveniles to test whether the distribution of recruits tends to be spatially more associated with plants than with bare ground. We used juveniles because the recruitment rate (i.e. the density of

recruits of a species) can be considered a proxy of the performance of that population, and therefore differences in performance across microenvironments (i.e. associated with plants or in the bare ground) is a sign of the presence (or absence) of facilitative interactions (Sánchez-Martín, Verdú, et al., 2023). However, other non-direct facilitative effects, such as seed dispersal, cannot be discarded with our approach and may also contribute to the observed spatial patterning (Verdu & Garcia-Fayos, 1996).

We estimated the dependence on facilitation for each species at each site by comparing the density of recruits growing under plants to that on bare ground. For this assessment, we employed a modification of the Relative Interaction Intensity Index (RII) defined in Armas et al. (2004).

$$\text{RII_beneficiaries} = \frac{\text{RDv} - \text{RD}_{\text{bg}}}{\text{RDv} + \text{RD}_{\text{bg}}}$$

where RDv is the density of recruits of a species growing under the canopy of any species of the community (i.e. number of recruits per m² of vegetation) and RD_{bg} is the density of recruits of the same species established on bare ground (i.e. number of recruits per m² of bare ground). RII values vary between -1 and 1. Positive values suggest facilitation since recruits tend to grow preferentially in association with other plants, while negative values suggest competition, meaning that recruits tend to grow preferentially in bare ground.

Then, we assessed the significance of each observed RII by comparing it to a null model that randomly reshuffles 1000 times the number of recruits of each species into vegetation or bare ground based on the relative cover of each microenvironment. This provided us with 1000 weighted recruits' random distribution. Finally, species with observed RIIs above 97.5% of the RIIs null model distribution were considered beneficiaries of facilitation. The rest of them were considered non-beneficiary species.

2.4 | Recognizing nurse species

We assessed the nursing capacity of each species by accounting for the number of recruited individuals under it, regardless of the

identity of the recruiting species. As the study focuses on inter-specific facilitation, we did not consider juveniles recruiting under the canopy of a conspecific. For each nurse species, we assessed whether they harboured a higher density of recruited plants under their canopies than the recruits' density on the bare ground, using a modification of the above-explained RII index:

$$\text{RII}_{\text{nurses}} = \frac{R_n - R_{bg}}{R_n + R_{bg}}$$

Here, R_n is the density of recruits, regardless of their species, growing under the canopy of each species in the community (excluding recruitment under conspecifics), and R_{bg} is the density of recruits growing on bare ground. Positive RII values suggest that the nurse species positively influences the recruitment of other species. Conversely, negative RII values suggest that recruits avoid that particular species and preferentially recruit on bare soil instead.

Then, as done with beneficiary species, we evaluated each observed $\text{RII}_{\text{nurse}}$ by comparing it to a null model. In this model, recruits are randomly assigned to adult species based on their relative cover in the community, including the bare ground cover as another species. This random assignment is repeated 1000 times. Plants with observed $\text{RII}_{\text{nurse}}$ values above the 97.5th percentile of the null model were categorised as nurse species, while the rest were classified as non-nurse species.

2.5 | Species selection

After identifying all nurse/non-nurse species in the study system, we focused on every nurse species that fulfilled a set of criteria related to a consistent presence in the community over time, relative abundance and consistent role as nurse versus non-nurse species across sites to ensure that the process studied are consistent across contrasted environments. Then, we selected the same number of non-nurse species that fulfilled the same criteria to balance the design. This resulted in the selection of more than 78% (8 out of 11 species) of the species recorded as adults in the study system (Figure S1).

For the selection of beneficiary and non-beneficiary species, we employed criteria similar to those used for nurse/non-nurse species selection based on a consistent presence in the community over time, the availability of a minimum number of juvenile individuals growing on bare ground, and consistent role as beneficiary versus non-beneficiary species across sites. The final selection included more than 70% of the species recorded as juveniles in the study system (5 out of 7 species; Figure S2).

2.6 | Nursing effects

We tested for differences in how nurse and non-nurse species modify the abiotic microenvironment under their canopy, both in

magnitude and variation. In order to avoid the potential effects of neighbours on the abiotic variables, we focused on 10 isolated adult individuals of each of the selected species. For every individual, we carried out a paired sampling design (Figure S3), measuring abiotic conditions under the plant and in the immediate surroundings (<1 m away from the canopy border). We considered both physical and chemical properties, as they provide primary constraining elements within these arid gypsum communities (Escudero et al., 2015). Specifically, we recorded three physical variables (soil temperature, soil water content [SWC], and amount of photosynthetic active radiation [PAR]), as well as four chemical variables (soil pH, Electrical conductivity [EC], and N and C concentrations).

Sampling was conducted at the end of summer (September 2022). Using a pairwise sampling approach, we contrasted points situated within the plant with paired points located on the nearby bare ground (within less than 1 m). This comparison allowed us to account for the potential influence of the plant's canopy on a very short temporal scale, enabling us to isolate variations independent of the natural fluctuations in light and temperature that occur throughout the day. Moreover, to ensure a comprehensive understanding of the canopy's impact on the environment, we strategically distributed each in/out pair of points along a circumferential path around the target plant to catch the effects of different orientations. Each abiotic variable was sampled three times, except for PAR, a parameter particularly susceptible to even subtle shifts in plant canopy structure. Consequently, we incorporated five data points to account for this parameter's inherent variability.

We measured temperatures at the surface and underground (7 cm below the surface) levels. The surface temperatures were measured with an infrared thermometer laser KETOKET® (KT550D), while the underground temperatures were measured with a k-type temperature probe of 7 cm length from the same model. We quantified the irradiance of PAR ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) using a PAR quantum sensor (SKP200, ELE International). We also quantified the SWC. For this, we collected approximately 20 g of three soil samples under each plant and three from the surrounding bare ground, weighing them immediately. Once in the laboratory, the fresh samples were dried in an oven at 50°C for 21 days, when we confirmed that the weight remained stable. We quantified the SWC as follows:

$$\text{SWC} = \frac{\text{Soil fresh (g)} - \text{Soil dry (g)}}{\text{Soil fresh (g)}} \times 100$$

After water gravimetric measurements, the three soil samples for each plant and each microenvironment (in/out the effect of the canopy) were homogenised in two composite samples per plant, sieved to 2 mm, and analysed in the Ionomics Service of CEBAS-CSIC (Murcia, Spain). Soil pH and EC were measured in an aqueous extract (1: 5, w/v), employing a conductance meter and a pH meter (GLP 31 and GLP 21, Crison Instruments, Hach Lange Spain). The N and C concentrations were measured by elemental analyser/continuous flow isotope ratio mass spectrometry

(ANCA/SL elemental analyser coupled with a Finnigan MAT Delta PlusXL IRMS).

2.7 | Magnitude and variation of abiotic stress reduction

For each abiotic physical and chemical property (i.e. surface temperature, deep temperature, PAR irradiation, SWC, pH, electric conductivity and C/N concentrations), we calculated the change beneath plants (Δ) as follows:

$$\Delta X = \frac{X_{\text{in}} - X_{\text{out}}}{X_{\text{out}}}$$

where X is any physical and chemical variable, X_{in} the value for the variable obtained under the plant canopy and X_{out} the value for the same variable in the bare ground closest to the paired inner point. The higher the value of ΔX , the bigger the difference in that variable between the underplant and the bare ground measurements. Negative values imply a reduction, while positive values imply an increase of that variable beneath the plant compared to the bare ground. Then, for each variable, we calculated the average and coefficient of variation (CV) of the 3 paired samples ΔX s (5 in the case of PAR) measured for each plant (i.e. ΔX and $CV(\Delta X)$, respectively). We also calculated the coefficient of variation of the points beneath each plant to estimate the variability beneath each plant's canopy ($CV(X)$). That was not done for chemical variables since we only have one composite sample per position (in/out) that does not provide variability.

Therefore, we obtained the average change for surface temperature (Δ_{TSUR}), underground temperature (Δ_{TDEEP}), soil water content (Δ_{SWC}), photosynthetically active radiation (Δ_{PAR}), C concentration (Δ_{C}), N concentration (Δ_{N}), pH (Δ_{pH}) and electric conductivity (Δ_{EC}). Furthermore, for the physical measures, we also quantified the coefficient of variation of the Δ variables: $CV\Delta_{\text{TSUR}}$, $CV\Delta_{\text{TDEEP}}$, $CV\Delta_{\text{SWC}}$, $CV\Delta_{\text{PAR}}$, and the coefficient of variation underneath each plant CV_{TSUR} , CV_{TDEEP} , CV_{SWC} , CV_{PAR} .

2.8 | Recruits functional traits related to facilitation

We examined possible differences in functional traits of juvenile plants of beneficiary and non-beneficiary species growing isolated on bare soil. We selected isolated individuals to reduce the influence of neighbouring plants, which could mask the juvenile response to the abiotic environment. Then, we selected a set of traits potentially affecting juveniles' survival in oligotrophic, gypsum-enriched arid areas. Specifically, we assessed traits related to water acquisition, root:shoot investment, and strategies for coping with excess Ca and S in gypsum soils. (see Table 1 for a detailed list). To assess differences between beneficiary and non-beneficiary species in these traits, we collected 10 recruiting individuals from the selected beneficiary and non-beneficiary species. The specimens were extracted from the soil in the field with a careful effort to extract the entire root without damaging it. The length of the aerial and subterranean parts of the plants was measured in the field, as well as the diameter of the root neck. Afterward, the plant materials were stored in airtight bags with a moistened substrate to bring the plant material to its maximum turgor, and the above- and below-ground parts were weighed separately once they were fully hydrated. Afterward, once in the laboratory, samples were processed using a conventional plant press to fully extract the moisture, which was kept in a desiccant oven for 10 days at 50°C. Once the materials were fully desiccated, the above and belowground biomass was determined again. With these data, we calculated the functional traits related to water acquisition and root: shoot investment enlisted in Table 1. Finally, keeping above- and below-ground samples always separated, we milled them to a fine powder and analysed them in the Ionomics Service of CEBAS-CSIC (Murcia, Spain). Ca and S concentrations were measured using inductively coupled plasma optical emission spectrometry (ICP-OES, ThermoElemental Iris Intrepid II XDL, Franklin, MA, USA) after microwave-assisted digestion with $\text{HNO}_3:\text{H}_2\text{O}_2$ (4:1, v:v).

TABLE 1 List of traits assessed for recruiting individuals. *The wet weight refers to the weight of the plant at its maximum turgor pressure to achieve a standardised measurement.

Traits	Abbreviation and formula	Function
The proportion of growth allocated in roots (below-ground length)	$BGL = \frac{\text{root length}}{\text{stem length}}$	The bigger the value, the more the individual invests in root growth. Dependent on plant architecture
The proportion of biomass allocated in roots (below-ground biomass)	$BGB = \frac{\text{dry root biomass}}{\text{dry aerial biomass}}$	The bigger the value, the more the individual invests in root production. Independent of plant architecture
Plant water content in roots	$WCR = \frac{\text{wet root biomass} - \text{dry root biomass}}{\text{wet root biomass}}$	The bigger the value, the more water content storage in roots
Plant water content	$WC = \frac{\text{wet plant biomass} - \text{dry plant biomass}}{\text{wet plant biomass}}$	The bigger the value, the more water content is stored in the whole plant
Root neck diameter	$R\emptyset = \text{Diameter of root neck in mm}$	The bigger the value, the slower the plant development (Sun et al., 2021)
Root elongation	$RE = \frac{R\emptyset}{\text{dry root biomass}}$	Small values show plants that invest more in their exploratory function, while high values suggest a greater investment in attachment

2.9 | Replication statement

Table 2 shows a replication statement depicting the scale of inference for each of the analyses, the scale at which the factor of interest is applied and the number of replicates for each scale.

2.10 | Statistical analyses

We first examined how the presence of a canopy impacted the measured physical and chemical attributes in the understory compared to bare ground. To do this, we conducted *t*-tests over each one of the environmental change measured attributes (Δ_{TSUR} , Δ_{TDEEP} , Δ_{SWC} , Δ_{PAR} , Δ_{C} , Δ_{N} , Δ_{pH} , Δ_{EC}). Then, we tested whether nurse and non-nurse species differed in their ability to modify the microenvironmental conditions considering the mean and the coefficient of variation of these variables. We also tested whether species that benefit from facilitation differed in their functional traits from those that do not require facilitation. To do so, in both cases, we combined two multivariate analyses to account for the possible covariability between variables. First, we conducted a permutational multivariate analysis of variance (PERMANOVA) to assess significant differences between groups (i.e. nurse vs. non-nurse species and beneficiary vs. non-beneficiary species, respectively). We performed the PERMANOVA employing the “adonis” function hosted in *vegan*/2.5.7 R package, which allows multivariate analyses that do not assume multivariate normality nor covariance homogeneity (Anderson, 2017). Second, we conducted a canonical discrimination analysis (CDA). CDA generates discriminant functions that maximise the separation between predefined groups. Since a discriminant function is a weighted linear combination of the measured predictor variables, the weights (called discriminant coefficients) can be used to define the contribution (i.e. importance) of each predictor variable to the observed discrimination between groups (Cruz-Castillo et al., 1994). CDA was performed employing the R function “candisc” hosted in *Candisc*/0.8.6 R package (Friendly & Fox, 2017). For the nurse vs. non-nurse comparison, we used the 16 abiotic measured metrics (Δ_{SWC} , Δ_{PAR} , Δ_{TSUR} , Δ_{TDEEP} , Δ_{N} , Δ_{C} , Δ_{pH} , Δ_{EC} , $\text{CVA}_{\Delta_{\text{SWC}}}$, $\text{CVA}_{\Delta_{\text{PAR}}}$, $\text{CVA}_{\Delta_{\text{TSUR}}}$, $\text{CVA}_{\Delta_{\text{TDEEP}}}$, $\text{CV}_{\Delta_{\text{SWC}}}$, $\text{CV}_{\Delta_{\text{PAR}}}$, $\text{CV}_{\Delta_{\text{TSUR}}}$, $\text{CV}_{\Delta_{\text{TDEEP}}}$) as dependent variables. The role (nurse/non-nurse) was treated as a nested factor with species, as each species was assigned to one of the roles. Locality was also included as a predictor (i.e. ~Role/SP + Locality). Table S1 demonstrates the consistency of results under different model structures. Similarly, for the beneficiary versus non-beneficiary comparison, we used the six functional traits (Table 1) and the Ca and S concentrations below and above ground as dependent variables. The species' role (beneficiary/non-beneficiary) with species as a nested factor, and locality were employed as predictors (i.e. ~Role/SP + Locality). Table S1 demonstrates the consistency of results under different model structures. We also conducted univariate analyses for the above-mentioned variables

to see if the patterns raised by the multivariate models remain with univariate analyses.

3 | RESULTS

3.1 | Nurses

In the Mezquites locality, 8 out of 22 species provided significant nursing effects (Table S2). These species represent 76.90% of the plant cover in Mezquites (Figure 2). In contrast, only 2 out of 18 species showed nursing effects in the Interdunes locality, representing only 14.99% of the plant cover (Table S2; Figure 3).

For further assessment and following the criteria established in the species selection section, only four species passed the filters (Figure S1) for proven nursing effects and seven did not show nursing effects. The nurse species were: *Allenrolfea occidentalis*, *Drymaria coahuilana*, *Grussonia grahamii* and *Isocoma coronopifolia*. As non-nurse species, we chose four out of the seven available to maintain a balance in the number of species selected by locality (Figure S1). The four selected non-nurse species were *Atriplex proso-pidium*, *Cylindropuntia leptocaulis*, *Euphorbia ser-pifolia* and *Fouquieria splendens*.

Overall, the presence of the canopy of the studied plant species, regardless of whether they are nurse or non-nurse species, had a significant effect on the physical and chemical properties measured in the soil, showing more water, N and C content, and less temperature, light and pH underneath the canopy compared with the nearby bare ground (Table 3). Moreover, we found a statistically significant difference between nurses and non-nurse species in how they modified their abiotic environment (Permanova: *F* statistic = 2.513, *p*-value 0.001; see Table S1 for full report). The structure coefficients of the CDA (squared canonical correlation 0.320, eigenvalue 0.471, likelihood ratio test 0.680) revealed the relative contribution of each abiotic variable to the differentiation between nurse and non-nurse species (Figure 3). The structure coefficients related to heterogeneity (CV variables) were more important than those associated with magnitude (Δ variables). Higher values in the heterogeneity metrics are related to non-nurse species in five out of eight heterogeneity variables. The variables, ranked by relative importance, for being a non-nurse species were $\text{CVA}_{\Delta_{\text{SWC}}}=0.393$, $\text{CV}_{\Delta_{\text{TSUR}}}=0.353$, $\text{CVA}_{\Delta_{\text{TSUR}}}=0.342$, $\Delta_{\text{pH}}=0.308$, $\text{CV}_{\Delta_{\text{PAR}}}=0.294$, $\Delta_{\text{EC}}=0.229$, $\text{CV}_{\Delta_{\text{TDEEP}}}=0.185$, $\Delta_{\text{TSUR}}=0.105$, $\Delta_{\text{TDEEP}}=0.007$ (Figure 3, structure panel, arrows pointing upward). Conversely, the factors contributing the most to nursing effects were: $\Delta_{\text{PAR}}=-0.570$, $\text{CVA}_{\Delta_{\text{PAR}}}=-0.436$, $\Delta_{\text{C}}=-0.295$, $\Delta_{\text{SWC}}=-0.269$, $\text{CVA}_{\Delta_{\text{TDEEP}}}=-0.172$, $\Delta_{\text{N}}=-0.090$, $\text{CV}_{\Delta_{\text{SWC}}}=-0.025$ (Figure 3, structure panel, arrows pointing downward). Although univariate models do not control potential co-variation with the other variables included in multivariate analyses, our results were consistent with multivariate patterns when assessed on a variable-by-variable basis through univariate linear models (Table 4).

TABLE 2 Replication statement.

Analysis	Scale of inference	The scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Facilitation requirements and nursing effects	Species	Recruitment niche of all the species identified in the 36 plots (bare ground vs. other species)	1070 plant-plant interactions
T-test determining the effect of canopy over environmental parameters	Vegetation versus bareground	8 environmental parameters	240 paired points per parameter except for light (400)
Nurse/non-nurse comparison	Species	4 nurses versus 4 non-nurses	16 variables of 10 individuals per species. Variation metrics derived from 3,5 paired points within each species for physical variables
Beneficiary/non-beneficiary comparison	Species	2 beneficiary/3 non-beneficiary species	10 traits of 10 individuals per species

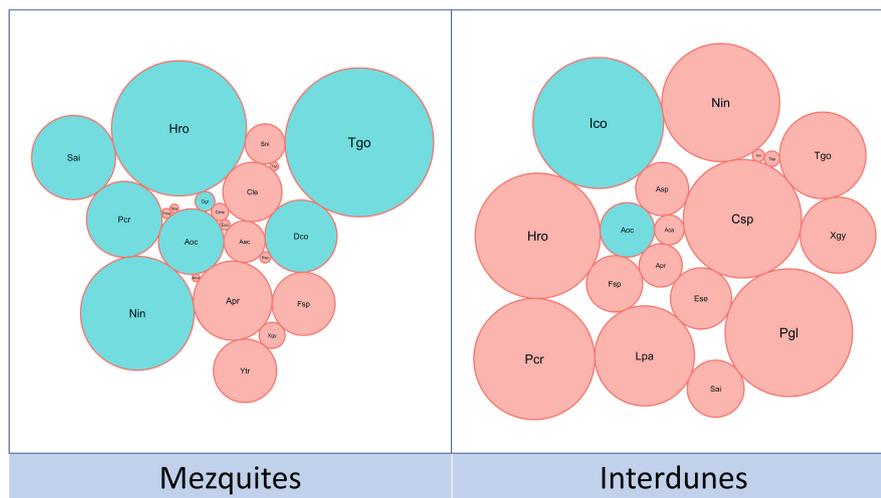


FIGURE 2 The circle plot represents each study area's species richness and cover. Each circle represents a single species with size proportional to each species' relative cover. The blue circles represent the species in which the nurse's role was detected, while the red circles represent those that were not. Statistical tests to determine the nurse/non-nurse role are available in Table S2. Codes for each species are listed in Table S3.

3.2 | Recruits

Concerning the establishment requirements, we identified that nine out of 15 species benefited from facilitation in the Mezquites locality. In contrast, only three out of nine species benefited from facilitation in the Interdunes locality (Table S4). Overall, 80.59% of the total number of recruiting individuals belonged to species that were benefiting from facilitation in Mezquites and 12.01% in interdunes.

Then, for further research, according to the criteria outlined in the selection species section, we selected two species that benefit from facilitation (*Allionia incarnata* and *Xanthisma gypsophillum*) and three that do not benefit from facilitation (*Fouquieria splendens*, *Petalonyx crenatus* and *Prosopis glandulosa*).

The beneficiary species significantly differed in their traits from the non-beneficiary ones (Permanova: F statistic=12.601, p -value=0.001, see Table S1 for full report). According to the CDA (squared canonical correlation 0.695, eigenvalue 2.278, likelihood ratio test 0.305), beneficiary species tend to accumulate more water and minerals in tissues and invest more in root development. The beneficiary species were characterised by high levels of the

following variables: Ca and S concentration in above-ground biomass ($Ca_{above}=0.867$ and $S_{above}=0.854$), plant water content ($WC=0.657$), diameter of the root neck ($R\emptyset=0.406$), water storage in roots ($WCR=0.339$), proportion of biomass and height in roots ($BGB=0.263$, $BGL=0.258$), Ca concentration in below-ground biomass ($Ca_{below}=0.070$) and root elongation ($RE=0.021$; Figure 4, structure panel, arrows pointing upward). In contrast, non-beneficiary species accumulate more S than beneficiary species in root biomass ($S_{below}=-0.129$) (Figure 4, structure panel, arrows pointing downward). These results remain qualitatively the same when variables are assessed separately in univariate linear models (Table 5).

4 | DISCUSSION

We found that the distinction between nurse and non-nurse species lies not so much in the magnitude of their effect on the amelioration of environmental stress, but rather in the fact that the former provide a less variable microenvironment. Also, we identify that in these stressful edaphic environments, species benefiting

FIGURE 3 Canonical discriminant analysis (CDA). Left panel: Boxplot of canonical scores. The canonical axis generated maximises the differences between nurses and non-nurses species. Right panel: Vector diagram showing the magnitudes of the structure coefficients (variables) of CDA. The arrow's length is proportional to the variable's relative contribution to the nurse/non-nurse segregation. Therefore, long blue arrows represent the variables contributing the most to being a nurse species, while long red arrows depict those variables displaying high values for non-nurse species.

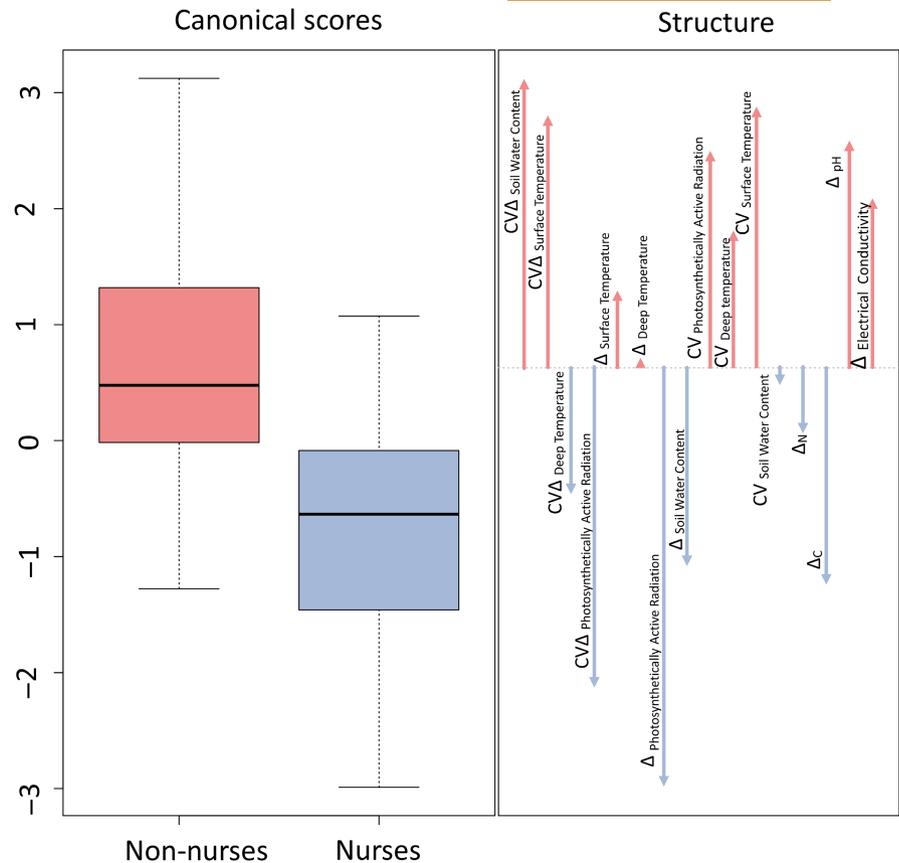


TABLE 3 Results of the t-test comparing whether ΔX variables are significantly different from 0. Negative significant values of ΔX depict a reduction in a particular variable X below the canopy of the plant in comparison with the bare ground. In contrast, positive values suggest the opposite, that is an increase in a particular variable X below the canopy of the plant in comparison with the bare ground.

Variables	Mean	t	p-value
Δ_{SWC}	1.802	2.681	0.009
Δ_{PAR}	-0.441	-16.103	<0.001
Δ_{TSUR}	-0.149	-10.142	<0.001
Δ_{TDEEP}	-0.039	-8.194	<0.001
Δ_{N}	0.648	5.419	<0.001
Δ_{C}	0.606	6.715	<0.001
Δ_{pH}	-0.003	-1.691	0.095
Δ_{EC}	0.0229	0.788	0.433

from facilitation invest more in root development, Ca and S accumulations and water content than species that do not benefit from facilitation.

4.1 | The environment beneath the nurse species

Our results show that nurse species are characterised by producing a low PAR reduction, but photosynthetic radiation is not

usually limited in deserts. Juvenile plants growing beneath the canopy of adult plants receive a reduced amount of solar irradiance, which can lead to harmful effects related to other limiting factors. For example, the shading effects do not lessen stomatal conductance proportionally to PAR, resulting in lower water use efficiency for plants beneath the shrubs in deserts (Forseth et al., 2001). Moreover, nurse species also show a low variability in micro-environmental variables related to water and temperature compared to non-nurse species. It is probable that the observed variation in microenvironmental conditions under each plant is a result of both canopy heterogeneity (spatial variability) and daily fluctuations (temporal variability), which were captured through sampling at different times of day and in different cardinal directions from the nurses' plants. Less variable environments may provide stable biotic refuge for species evading the harsh effects of growing on bare soil. For instance, plants protected by neighbouring vegetation experience fewer abiotic fluctuations in arid regions than species growing directly on the exposed bare ground (Ghazian et al., 2020; Sotomayor & Drezner, 2019). These effects have also been observed in other systems, such as alpine environments, where cushion species provide a more stable environment than tussock species, resulting in more significant nursing effects for the former (Anthelme et al., 2014).

In contrast, the magnitude of abiotic differences in the other measured variables, excluding light, has a less critical effect on differentiating nurses from non-nurse species. For example, although SWC is higher beneath a plant than in the bare ground (Table 3), we found

Variable	Role		F-value	P-value
	Nurse	Non-nurse		
Δ_{SWC}	2.708 ± 0.966	0.968 ± 0.927	1.34	0.252
Δ_{PAR}	-0.363 ± 0.038	-0.512 ± 0.036	23.029	<0.001
Δ_{TSUR}	-0.157 ± 0.021	-0.142 ± 0.020	2.466	0.032
Δ_{TDEEP}	-0.039 ± 0.007	-0.040 ± 0.007	1.002	0.431
Δ_{N}	0.703 ± 0.174	0.599 ± 0.166	0.806	0.569
Δ_{C}	0.739 ± 0.129	0.483 ± 0.124	3.622	0.004
Δ_{pH}	-0.007 ± 0.003	-0.001 ± 0.003	1.4965	0.193
Δ_{EC}	-0.010 ± 0.042	0.005 ± 0.0040	2.072	0.069
$\text{CV}\Delta_{\text{SWC}}$	1.903 ± 0.577	3.440 ± 0.554	4.135	0.001
$\text{CV}\Delta_{\text{PAR}}$	1.570 ± 0.362	0.492 ± 0.348	3.286	0.007
$\text{CV}\Delta_{\text{TSUR}}$	0.807 ± 0.466	1.881 ± 0.447	4.479	0.462
$\text{CV}\Delta_{\text{TDEEP}}$	2.228 ± 2.711	2.551 ± 1.877	1.271	0.283
CV_{SWC}	0.357 ± 0.043	0.350 ± 0.041	0.911	0.492
CV_{PAR}	0.454 ± 0.057	0.566 ± 0.054	4.946	<0.001
CV_{TSUR}	0.104 ± 0.015	0.142 ± 0.014	2.093	0.066
CV_{TDEEP}	0.029 ± 0.005	0.037 ± 0.005	1.883	0.097

TABLE 4 Results of univariate linear models for each of the variables included in Permanova and canonical discriminant analysis, testing for differences between nurse and non-nurse species. Nurses and non-nurses columns display the estimates \pm standard errors of the univariate models. The F-value and p-value are the results of the ANOVA comparing both groups. Structure of the univariates models (Variable ~ Role/ SP + Locality).

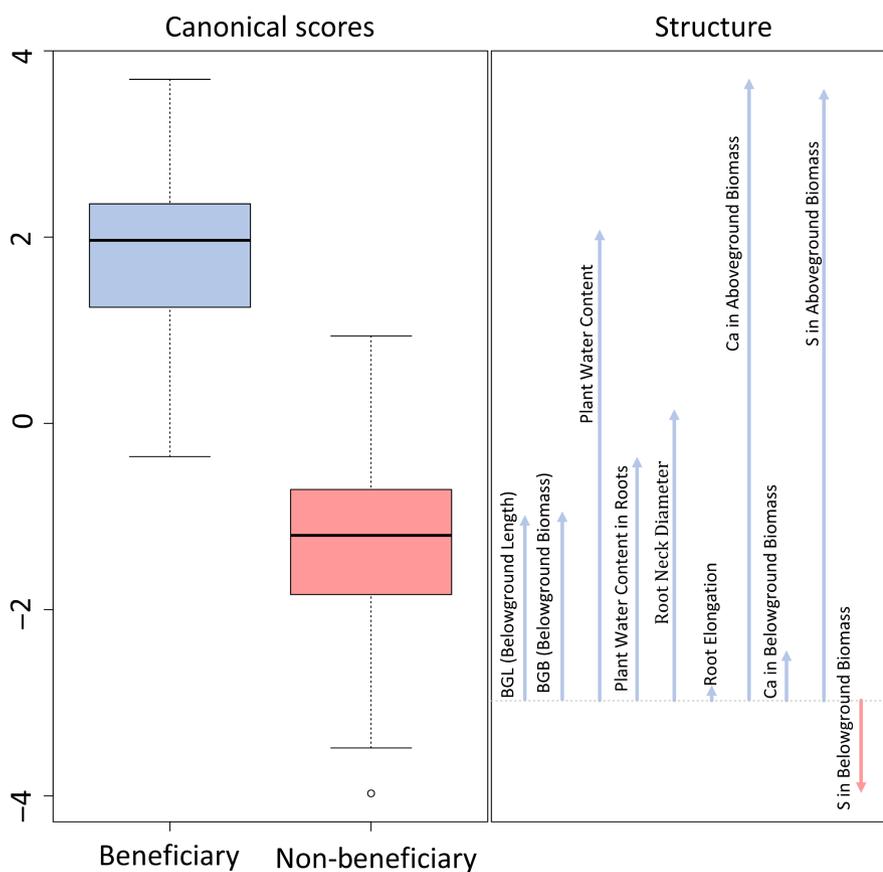


FIGURE 4 Canonical discriminant analysis (CDA). Left panel: Boxplot of canonical scores. The canonical axis maximises the differences between species requiring facilitation (beneficiary) and species not requiring it (non-beneficiary). Right panel: Vector diagram showing the magnitudes of the structure coefficients (traits) of CDA. The arrow's size is proportional to each trait's relative contribution to facilitation demand segregation. Therefore, large blue arrows represent the traits of species that require facilitation. Here, non-beneficiary species display lower values of the traits being studied. Names and meanings of the variables are available in Table 1.

no difference between nurse and non-nurse species concerning this variable (Table 4). Instead, nurse and non-nurse species differ in the variation of the microenvironmental conditions underneath their canopies. Nurses provide a stable SWC, while non-nurse species show higher micro-heterogeneity, which could jeopardise juvenile

development. Similarly, while nurse and non-nurse plants had a similar effect on the overall soil temperature reduction, we found sharp differences in temperature variability, with nurse species showing a lower variability in temperature reduction than non-nurse species. A reduced variation in water availability and temperature appears

TABLE 5 Results of univariate models for each of the variables included in Permanova and canonical discriminant analysis, testing for differences between beneficiary and non-beneficiary species. See each the full name of each variable in Table 1. Beneficiary and Non-Beneficiary columns display the estimates \pm standard errors of the univariate models. The *F*-value and *p*-value are the results of the ANOVA comparing both groups. Structure of the univariate models (Variable ~ Role/ SP + Locality).

Variable	Role		<i>F</i> -value	<i>p</i> -value
	Beneficiary	Non-beneficiary		
BGL	0.711 \pm 0.028	0.653 \pm 0.023	2.929	0.093
BGB	0.399 \pm 0.031	0.334 \pm 0.025	5.11	0.028
WCR	0.631 \pm 0.020	0.574 \pm 0.017	13.507	<0.001
WC	0.686 \pm 0.020	0.560 \pm 0.017	45.431	<0.001
RØ	12.399 \pm 1.649	6.816 \pm 1.347	10.245	0.002
RE	170.290 \pm 61.070	160.150 \pm 49.870	0.02	0.889
Ca_above	4.424 \pm 0.255	1.912 \pm 0.208	74.516	<0.001
Ca_below	2.075 \pm 0.261	1.932 \pm 0.213	0.2308	0.632
S_above	1.647 \pm 0.116	0.541 \pm 0.095	53.606	<0.001
S_below	0.686 \pm 0.187	0.877 \pm 0.153	0.941	0.337

to be crucial for plant life in extreme, variable, and unpredictable environments, as those investigated in this study.

Regarding the soil's chemical properties, nurse species accumulate more organic matter under their canopy than non-nurse species. This is evidenced by higher concentrations of C and N, and a lower pH under nurse species, which may help enhance the growth and development of juveniles found in these environments (Navarro-Cano et al., 2019). Moreover, the concentration of dissolved salts in the soil regulates plant water uptake. When the concentration of salts is high, the capacity of plants to absorb water may decrease due to ion competition in the soil solution (Marschner, 2012). Therefore, the observed reduction in EC under nurse species could suggest that juveniles recruited there have easier access to water than juveniles recruited on the bare ground.

4.2 | The functional traits of beneficiary species

We observed that the two species benefiting from facilitation in our system have traits related to water storage in plant tissues and a strong investment in roots. The most benefited species from facilitation are those growing outside their optimal habitats, thus obtaining benefits by growing associated with other plants while avoiding interspecific competition with their nurse species, a balance highly dependent on the abiotic environment (Qi et al., 2018; Sánchez-Martín, Verdú, et al., 2023).

We found that the two species benefiting from facilitation invest more in root production than the three species that do not depend on it. This seems a general pattern in nature, as it has been observed by other studies (Butterfield & Briggs, 2011; Valiente-Banuet et al., 2006). Developing deep root systems is a common strategy to survive in arid environments since it allows the recruited species to reach deeper and more stable water reservoirs (Ryel et al., 2008). However, investing in deep roots can be limited in hard, aggregated soils with crystallised layers that make root development difficult (Bridges & Burnham, 1980; Escudero et al., 2015; Moore et al., 2014; Valentine et al., 2012), and could explain, at least in part, why facilitation is more prevalent in the harsh soil community (i.e. mezquites), while facilitation is weaker in interdune areas (i.e. interdunes) where root penetration is not constrained (Valentine et al., 2012).

Concerning plant water storage capacity, we identified that the two-beneficiary species accumulate more water in their tissues than the three non-beneficiary species. In arid environments, plants reduce their relative water storage, sacrificing growth for survival (Šimová et al., 2017; Zhou et al., 2019). Species that do not follow this strategy can subsist by benefiting from the environmental enhancements provided by the nurses. In fact, it is widely assumed that plants with greater succulence usually require facilitation, while woody plants act as nurses (Miquelajauregui & Valverde, 2010; Romo-Campos et al., 2013; Valiente-Banuet et al., 2006; Weidlich et al., 2021). However, beneficiary species share the available resources under the canopy of the nurse plant with other beneficiary species (O'Brien et al., 2021; Schöb et al., 2013). Therefore, the presence of a water reservoir may work as a safeguard that can diminish potential competition with other beneficiary species and even with the nurse species when drought situations are aggravated. In addition, the higher water content could indicate higher water demand by these species. In this sense, it has been shown that Tertiary species, relicts of a wetter era, survive under the improved conditions provided by Quaternary nurse species, more adapted to current xeric conditions in many habitats worldwide (Valiente-Banuet et al., 2006).

Our two-beneficiary species also accumulate more Ca and S, especially in above-ground biomass, than our three non-beneficiary species. This could be related to a water acquisition strategy since the accumulation of ions could be a mechanism to adjust the species' osmotic potential, allowing them to take up water from ions-rich soils (Chen & Jiang, 2010). However, it could also be a simple passive mechanism derived from water acquisition from these soils, leading to the accumulation of Ca and S in plant tissues (Marschner, 2012) as a consequence of inhabiting an environment enriched in these elements (Escudero et al., 2015).

4.3 | Future avenues

The results presented above give rise to a series of inquiries that require further research. Assessing the impact of the variability of the microenvironmental conditions on plant–plant interactions may

contribute to a better understanding of which traits define species as nurses. This is essential for the physical parameters exhibiting substantial daily fluctuations.

The observed spatial micro-heterogeneity beneath plants is likely to be influenced by both daily oscillations of the environmental conditions and the structural characteristics of the canopies that can temperate this variation. Therefore, tall plants cast a moving shadow throughout the day that amplifies the spatial micro-heterogeneity, while plant species with canopies closer to the ground are more likely to produce consistent shadows.

From the perspective of the beneficiary species, it would be interesting to expand this beneficiary species knowledge to other plant species and ecosystems and evaluate how the functional traits of the beneficiary species change depending on their environmental context, that is how the traits of these plants vary when growing isolated in bare soil compared to their species growing associated with a nurse.

5 | CONCLUSIONS

Our study indicates that the quality of nurse plants in this system is primarily associated with creating stable microenvironmental conditions under their canopy rather than with the extent to which they reduce abiotic stress. Moreover, beneficiary species invest more in root development and accumulate more water, calcium and sulphur in their tissues than species not benefited by facilitation.

AUTHOR CONTRIBUTIONS

All authors contributed to the experimental design and data collection. Ricardo Sánchez-Martín led data analyses and wrote the first draft of the manuscript. All authors discussed the results' implications, contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare. Alicia Montesinos-Navarro is an Associate Editor of *Functional Ecology* but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Repository: <https://doi.org/10.5281/zenodo.10227731> (Sánchez-Martín, Montesinos Navarro, et al., 2023).

ORCID

Ricardo Sánchez-Martín  <https://orcid.org/0000-0001-5272-3276>

Alicia Montesinos-Navarro  <https://orcid.org/0000-0003-4656-0321>

Miguel Verdú  <https://orcid.org/0000-0002-9778-7692>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Selection criteria for nurse and non-nurse species: red rows represent available non-nurse species, whereas blue rows represent available nurse species.

Figure S2. Selection criteria for beneficiary and non-beneficiary species: red rows represent available non-beneficiary species, whereas blue rows represent available beneficiary species.

Figure S3. Scheme of the experimental design showing the pairwise measured variables (i.e. underplant and bare soil).

Table S1. PERMANOVA results for comparing nurse/non-nurse species and beneficiary/non-beneficiary species using different structures for predictor variables.

Table S2. This table provides all the information required to detect nursing effect beneath the canopy of different species by site (RII_{sig} positive).

Table S3. Code of the species studied.

Table S4. This table provides all the information required to detect the presence of facilitative effects for each species of recruits (RII_{sig} positive).

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