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RESEARCH ARTICLE

Interspecific facilitation favors rare species establishment and reduces performance disparities among adults

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Abstract

Questions: A variety of mechanisms sustain diversity in natural communities as a result of ecological interactions between organisms. Competition has been studied extensively in the context of species maintenance, but facilitation is often conceptualized as simply reducing competition between functionally different species, which tends to decline throughout the plants' life span. Here we explore how interspecific facilitation may sustain diversity throughout the species' life by avoiding the extinction of locally rare species at juvenile stages and reducing performance disparities between neighbors of differing species at mature stages.

Methods: To do so, we measured whether rarer species relied more on facilitation than abundant ones in semiarid shrubland in southeast Spain. A mechanistic explanation of this relationship was subsequently tested by correlating rarity with the species' affinity to a particularly edaphic stressful environment. Finally, we assessed whether growing associated with neighbors in vegetation patches shaped by facilitation could balance performance disparities between species when they become adults.

Results: We show that facilitation (i) favors the rare species, which, in addition, tend to be those with low affinity to the stressful environment, and (ii) reduces the performance dissimilarities among plants growing associated within multispecific vegetation patches compared to plants growing alone.

Conclusions: These facilitative effects, beyond the reduction of competition between functionally similar species, might ensure positive and long-lasting effects of biotic interactions, implying a more critical role for facilitation in preserving biodiversity than previously thought.

KEYWORDS
diversity maintenance, facilitation, gypsum affinity, neighborhood, performance differences, rarity, stress sensitivity, stress tolerance

1 | INTRODUCTION

Interactions between organisms play a fundamental role in structuring the diversity of natural communities. Competitive interactions have largely been regarded as essential drivers of community diversity (MacArthur & Levins, 1964; Grime, 1973; Huston, 1979). However, the role of facilitation was not widely recognized until the turn of the last century, despite its potential importance in maintaining species

diversity across many different biomes (Callaway & Walker, 1997; Hacker & Gaines, 1997; Bruno et al., 2003; Michalet et al., 2006; Callaway, 2007; Brooker et al., 2008; Holmgren & Scheffer, 2010; He et al., 2013; Cavieres et al., 2014; Mcintire & Fajardo, 2014; Le Bagousse-Pinguet et al., 2014a; Soliveres et al., 2015b). Traditionally, facilitation has been viewed mainly through the lens of microenvironmental improvements that promote the establishment of sensitive species (Liancourt et al., 2005) and the subsequent adult co-occurrence of functionally distinct species that are likely to experience little interspecific competition (Cavieres & Badano, 2009; Butterfield & Briggs, 2011).

It is commonly considered that as beneficiary plants grow, the role of facilitation weakens due to competitive pressures with neighboring species (Miriti, 2006; Valiente-Banuet & Verdú, 2008). However, it is also common, especially in arid environments, that plant species co-occur as adults in vegetation patches. Therefore, in these cases, other mechanisms besides shading or water redistribution, through which nurse plants benefit the establishment of facilitated seedlings, may be operating to enhance the co-occurrence between adult plants. Some of the long-term mechanisms enhancing the co-occurrence of adult plants in vegetation patches can be related to an increase in resource availability or a more equitative use of resources, allowing the maintenance of their coexistence over time. For instance, an increase in nutrient availability due to a greater contribution of leaf litter or an enhancement of symbiotic biotic interactions, such as pollinators or mycorrhizal fungi in the shared microenvironment (Callaway, 2007; Navarro-Cano et al., 2019a, 2019b; Losapio & Schöb, 2020), can result in persistent co-occurrence among adult plants (Montesinos-Navarro et al., 2012). Moreover, there is also evidence of some mechanisms that can result in a more equal use of resources, such as nutrient transfer between adult plants cohabiting vegetation patches (Montesinos-Navarro et al., 2017). Although these mechanisms could equalize the interacting species' performance, these interactions among adult plants have received much less attention. Considering the effects of facilitation, not only on interactions between nurses and facilitated seedlings but also among adult plants, will contribute to a better understanding of the impact of facilitation at the community scale.

1.1 | Facilitation favors the establishment of rare species

Facilitation may act as a niche generator providing opportunities to establish new species that otherwise would be excluded. This process is mediated by nurse plants, which are mature plants that ameliorate their surrounding environment, favoring the establishment and survival of other plants under their canopy (Padilla & Pugnaire, 2006). This positive effect is more prominent when facilitated and nurse species differ in their ecological requirements (i.e., broad niche differences; Navarro-Cano et al., 2019a; Valiente-Banuet & Verdú, 2013), resulting in the well-documented pattern that stress-sensitive species rely more on facilitation than

stress-tolerant species. (Liancourt et al., 2005; Valiente-Banuet et al., 2006; Gross et al., 2009; Le Bagousse-Pinguet et al., 2014b; Qi et al., 2018). Species that deeply depend on facilitation can find their abundance limited by the availability of the habitat provided by their nurse plants. That might be an important factor explaining why species that rely more on facilitation are more locally rare than those that rely less on facilitation, a worldwide pattern linking facilitation and plant species coexistence (Soliveres et al., 2015a, but see Lortie et al., 2021; Lucero et al., 2021 or Vega-Álvarez et al., 2019) for particular cases in which facilitation favors abundant species.

1.2 | Facilitation balances species' performances among adult species

Positive interactions can change their signs and intensities over time depending on the ontogenetic states of the interacting species (Valiente-Banuet & Verdú, 2008) and indirect effects among neighboring species (Castillo et al., 2010; Schöb et al., 2013). When facilitated plants become adults, they face a new ecological context where they must deal with the cohabiting neighbors of the patch. In this context, species may endure when the net balance of competition and facilitation remains positive or neutral (Valiente-Banuet & Verdú, 2013). Plant interactions might remain positive over time by attenuating species' performance disparities. Such attenuation could be produced by reciprocal benefits between the interacting species beyond establishment. For example, some facilitative interactions are mediated by nitrogen or water transfer between interacting species (Montesinos-Navarro et al., 2016, 2017, 2019b) or the sharing of beneficial mycorrhizae (Sortibrán et al., 2019). Mechanisms that could palliate the differences in performance between co-occurring species are an equalizing force that, if maintained across time and generations, can guarantee the species' survival in a mature stage.

1.3 | Aims

The impact of facilitation on natural communities will be determined by how the two processes mentioned above interact throughout plants' lifespans. We aim to show that, under natural conditions, facilitative effects can occur at all stages of plant life, implying that facilitation plays a more significant role in species maintenance than previously thought. To that end, we examined these effects in plant communities growing in gypsum outcrops where the preponderance of positive interactions has been documented (Montesinos-Navarro et al., 2019a; Sánchez-Martín et al., 2022), favored by intense physical and chemical stresses that gypsum imposes on plant life (Escudero et al., 2015). Here, we propose that facilitation may (i) favor the establishment of rare species, which we hypothesize can also be those with low affinity to edaphically stressful soils and (ii) balance the performance disparities of the species in the community when species grow in patches promoted by facilitation.

2 | METHODS

2.1 | Study site and experimental design

We explore the role of facilitation in buffering species loss by characterizing plant communities growing on gypsum outcrops. Here, plant communities must not only deal with a lack of water and other essential macronutrients due to growing in a semi-arid climate but also with chemical and physical stresses associated with gypsum accumulations, such as Ca and S excess, and the presence of hard, even crystallized soil layers (Escudero et al., 2015). Under such stressful conditions, these communities are characterized by sparse vegetation with multispecific patches derived from the facilitative effects of nurse species (Delalandre & Montesinos-Navarro, 2018; Montesinos-Navarro et al., 2019a). These properties make the system a suitable model for studying facilitation. Specifically, we conducted the study in four localities with gypsum outcrops in the Vinalopó valley, Alicante, southeast Spain (Figure 1: 38°29′28.5″N, 0°44′18.1″W). The climate is semi-arid Mediterranean, with an average annual rainfall of 360 mm, most of which falls during seasonal pulses in spring (March–June) and autumn (September–December). We selected two contiguous (<10 m apart) sublocalities of 1 ha in each locality, one within the gypsum outcrop (stressful sublocality hereafter), and another in the surrounding less stressful limestones area (non-stressful sublocality hereafter). The four localities were no more than 20 km apart to minimize changes in climatic conditions among them. Within each locality, the non-stressful sublocalities were always contiguously located uphill from the stressful sublocalities, ensuring the potential seed dispersal from plants in the non-stressful sublocality to the stressful sublocality (Bochet, 2015). Our experimental design comprised 80 plots (150 cm × 150 cm) in each sublocality, except in one non-stressful sublocality with 79 plots. We distributed the plots randomly to wholly occupy the 1 ha sublocalities, avoiding places presenting difficult access.

We sampled the four localities between April 2019 and February 2020. Firstly, inside each plot, we quantified the number of individuals per species and estimated the species' cover by adding up the cover of all the plants per species recorded, considering the cover of recruits as negligible. Each plant cover was estimated by measuring the elliptical area of the canopy as follows:

$$\text{plant cover} = (\pi ab) \tag{1}$$

where (a) is half of the widest length of the plant canopy measured through its centre, and (b) is half the width of the canopy perpendicular to (a). We also registered whether plants lived alone (i.e., non-associated) or in a vegetation patch with other individuals of the same or other species (i.e., associated). Each patch's cover was estimated following the same procedure as described above, and the bare ground cover was obtained as the subtraction between the sampled area and the surface occupied by patches plus non-associated plants. Secondly, we identified all recruits within the plots, both in the bare ground (non-associated) and beneath other plants (associated). We considered as recruits all plants ranging from seedlings (with at least the first two leaves) to tiny plants in comparison with adults (<15% in height compared to adults), showing neither signs of reproductive structures nor lignification at the stem base. Overall,
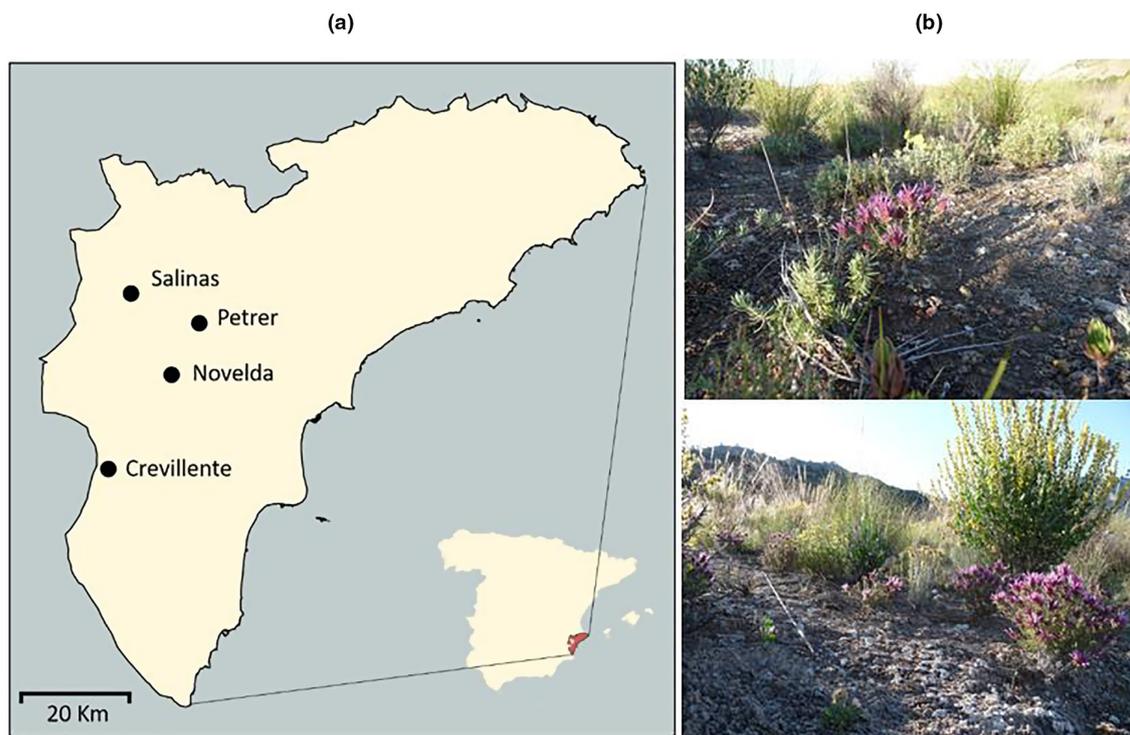
(a)   (b)

FIGURE 1 (a) Map of the study sites located throughout the the Vinalopó Valley (Alicante), southeast Spain. (b) Photographs showing the type of vegetation growing on the gypsum outcrops

we sampled 639 plots in four localities, identified 85 different species, and measured 28,566 adult plants and 20,081 recruits.

2.2 | Facilitation favors the establishment of rare species

We first tested whether the species' abundance was directly related to its degree of affinity to the edaphic stressful soil (i.e., gypsum affinity). Then, we assessed whether species with low gypsum affinity tend to rely more on facilitation. To do so, we used species' relative abundance in each gypsum stressful sublocality as a proxy for abundance and gypsum affinity index (g) as a proxy for edaphic affinity. Gypsum affinity was measured as in Sánchez-Martín et al. (2021) (Equation 2):

$$g = \frac{C_s}{C_s + C_{ns}} \quad (2)$$

where c_s is the cover (%) of a specific species in the stressful sublocality and c_{ns} is the cover (%) of the same species in the contiguous non-stressful sublocality. This metric measures which proportion of the total species cover is found in the stressful sublocality. This index was calculated with plants growing alone (i.e., excluding those growing in vegetation patches), thus avoiding the potential effects of plant–plant interactions within patches. It has been previously shown that the species' affinity in this community is positively related to harboring specific strategies to cope with harsh gypsum constraints, such as the ability of roots to penetrate hard gypsum layers and the accumulation of elements found in excess in those soils such as Ca, Mg and S (Sánchez-Martín et al., 2021). Species with g values close to 1 (high gypsum affinity) are those with the strategies mentioned above, while species with g values close to 0 (low gypsum affinity) do not show any specific response to survive in those soils (Sánchez-Martín et al., 2021).To ensure that g values were reliably estimated from a sufficient sample size, we only retained those species with at least 45 adult plants in each locality (i.e., considering both stressful and non-stressful sublocalities). Quantification of gypsum affinity was carried out for 20 different species and was based on the plant cover of 16,132 adult individuals (8504 in the stressful and 7628 in the non-stressful sublocalities).

To assess whether species with low gypsum affinity rely more on facilitation than species with high affinity, we tested a correlation between species' gypsum affinity and species' tendency to associate with other plants (i.e., facilitation or competition). We measured this tendency for those species that account for at least 0.5% of relative abundance in each stressful sublocality. Then, to ensure reliable estimations of the association tendencies, only species with at least 15 recruits in each stressful sublocality were considered. Each species' association tendency was measured according to the relative interaction intensity index (RII$_j$) described in Armas et al. (2004) (Equation 3):

$$RII_j = \frac{RD_a - RD_{na}}{RD_a + RD_{na}} \quad (3)$$

where RD$_a$ is the recruits' density of species j growing associated beneath plants of any species (i.e., number of recruits per m^2 of vegetation cover) and RD$_{na}$ is the recruit's density of the same species growing non-associated in bare ground (i.e., number of recruits per m^2 of bare ground). RII values range from −1 to 1, positive values suggesting facilitation (i.e., recruits grow preferentially associated with other plants) and negative one's competition (i.e., recruits grow preferentially in the bare ground). RII was quantified for 20 species by analyzing the recruiting patterns of 6986 recruits growing in stressful sublocalities.

2.3 | Facilitation balances species' performances

We used relative plant cover as a performance proxy to assess whether facilitation reduces performance disparities of interacting species. Non-associated plants are less likely to remain isolated as they grow, resulting in a smaller cover than associated plants. In order to make the plant's cover range comparable between associated and non-associated individuals, in each stressful sublocality, we selected only those associated plants whose cover fell within the range defined by the non-associated plants. Moreover, we eliminated individual plants below the percentile of 1% for each species cover distribution to verify that all selected plants are unquestionably adults and that cover reflects adult performance rather than differences in the relative abundance of developmental stages (Appendix S1: Table S1). Then, to estimate differences in plant performance between species (i.e., differences in plant relative cover), we followed the following procedure: firstly, we relativized plant cover for each individual by the maximum cover of a conspecific in each sublocality to make species' cover comparable among species. This relativization preserves intraspecific cover variation, but reduces interspecific variation due to the comparison of species with different life forms. Secondly, we calculated separately for each species the median performance (i.e., median relative cover; hereafter P) of associated plants (hereafter P_a) and non-associated plants (hereafter P_{na}), including only those species with at least 10 individuals (i.e., five non-associated and five associated) (Figure 2). We used the median since it is a good population descriptor for non-normal distributed data with extreme right or left tails (Sainani, 2012). Thirdly, within each sublocality, we extracted all the possible combinations of species pairs and calculated the performance differences (PD) for each combination of species [PD(ij)], separately for non-associated [PD(ij)$_{na}$: Equation 4] and associated plants [PD(ij)$_a$: Equation 5], i and j being any specific possible pair of species (Figure 2).

$$PD(ij)_{na} = \frac{Max\left[P(i_{na}), P(j_{na})\right]}{Min\left[P(i_{na}), P(j_{na})\right]} \quad (4)$$

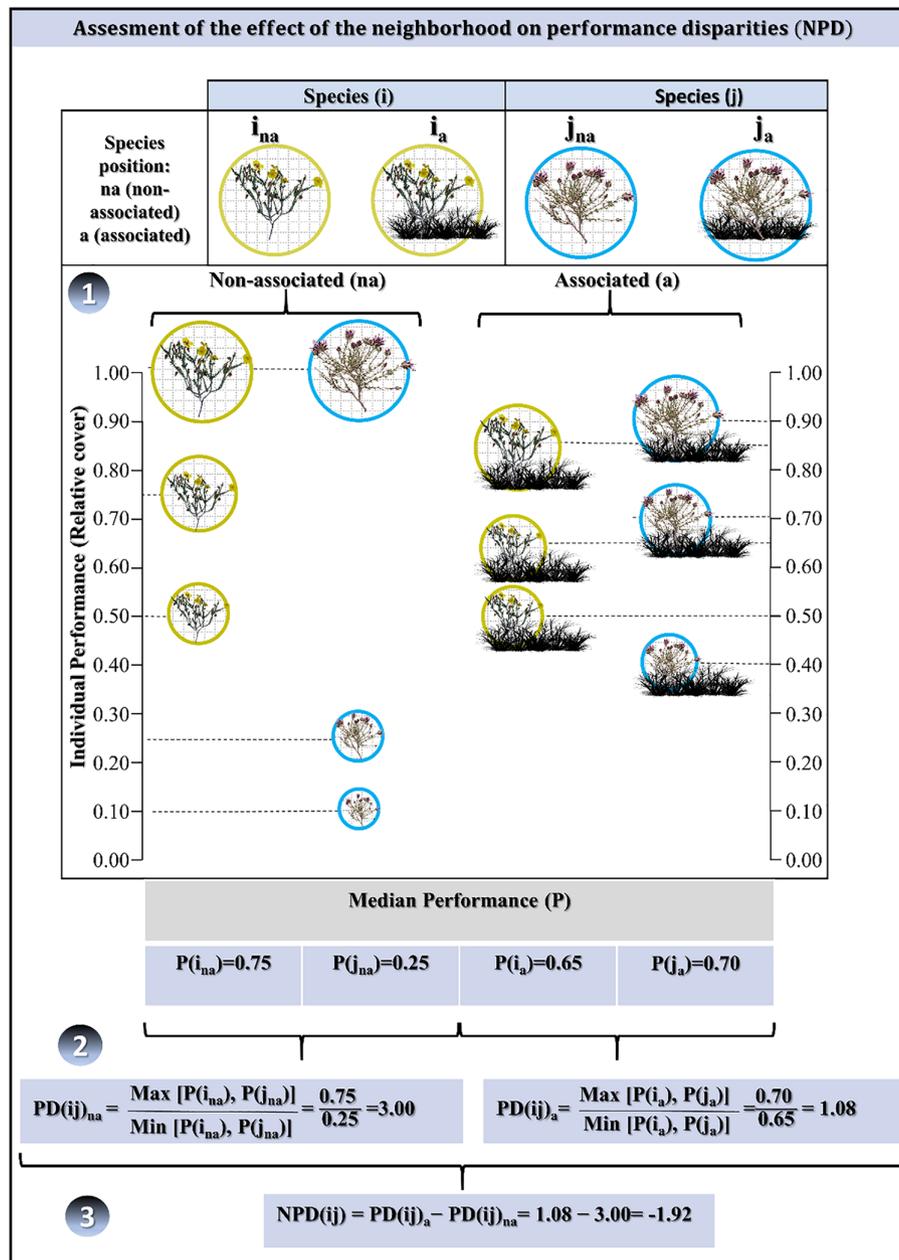$$PD(ij)_a = \frac{Max\left[P(i_a), P(j_a)\right]}{Min\left[P(i_a), P(j_a)\right]} \quad (5)$$

FIGURE 2 Visual scheme of the calculation of the effect of the neighborhood on performance disparities (NPD) for a specific pair of species (NPD*ij*). First (1), we select only those individuals in the range of cover defined by the plants living non-associated individually for each species (*i* and *j*) in each stressful sublocality. Then, we relativized each plant cover by the maximum cover of a conspecific in each stressful sublocality to make species with different life form comparable, which provides the values observed in the figure ranging from 1 to ca. 0. Second (2), we calculated the performance disparities between the interacting species separately for the individuals growing alone PD(*ij*)$_{na}$ and the individuals growing associated to other plants PD(*ij*)$_a$. PD is calculated as a ratio, with the species with the higher median performance in the numerator and the other species in the denominator. Finally (3), the NPD is calculated as the difference in PD between the pair when plants grow associated [PD(*ij*)$_a$] minus the same pair when plants grow non-associated [PD(*ij*)$_{na}$]. Negatives values in NPD(*ij*) suppose a reduction in performance disparities when species grow associated. We then calculated the overall NPD as the mean of all the possible interacting pairs

PD can only produce values ranging from 1 (i.e., no differences in *P* between the two species) to any positive value (the greater the value, the greater the differences in *P* between species).

We calculated the effect of the neighborhood on performance disparities (NPD) for each species pair through the differences between PD obtained with associated individuals (PD$_a$) and those that were found living non-associated (PD$_{na}$) (Equation 6; Figure 2):

$$NPD(ij) = PD(ij)_a - PD(ij)_{na} \qquad (6)$$

Finally, we calculated the overall NPD as the mean of all the paired NPD(*ij*). If the overall NPD is negative, living associated will attenuate PDs between species at the community level, a process driven by facilitation that could favor diversity. The NPD assessment

was based on the cover of 7761 adult individuals (4616 associated and 3145 non-associated) of 23 species.

2.4 | Statistical analyses

First, we evaluated the relationship between the reliance on facilitation and species' gypsum affinity and abundance. Second, we assessed if facilitation reduces performance dissimilarities at the community level, testing whether PDs between species were reduced when plants are associated.

In order to test whether facilitation promotes the survival of rare species with low gypsum affinity, we first checked whether species with low gypsum affinity are less abundant. Considering that closely related species could display more similar traits than distant relatives (Revell 2010), we applied a Bayesian phylogenetic-informed model with plant abundance in the stressful environment as the response variable, gypsum affinity (*g*) as the predictor, and locality as a random effect. Then, we tested whether facilitation (RII) was stronger in species with low gypsum affinity with another phylogenetic-informed Bayesian model. In this case, RII was the response variable, g was the predictor (fixed effect), and locality was a random effect.

We used the Markov Chain Monte Carlo Generalized Linear Mixed Model (MCMCglmm) (Hadfield, 2010) for both models. This approach allows phylogenetic corrections while using multiple replicates per species (i.e., the same species in different locations). We implemented both models with the default prior (i.e., assuming a normal posterior distribution for fixed effects and an inverse-Wishart prior for the random effects) and ran 600,000 MCMC iterations with a burn-in period of 100,000 iterations and sampled every 100 iterations, finally yielding 5000 iterations for each model. We ran both models using the "MCMCglmm" function of the R package *MCMCglmm* 2.29 (Hadfield, 2010), and we ensured model convergence through plot inspections. We also checked that autocorrelation, both in mean and variance, remained below 0.1 using the "autocorr" function of the *coda* R package (Plummer et al., 2006). Moreover, we extracted the conditional R^2 to assess how the models fit our data, including the variance explained by the whole model (fixed and random effects) using the method proposed by Nakagawa and Schielzeth (2013).

To inform both MCMC models phylogenetically, we built the phylogenetic relationship among the studied plant species with the *V.phylomaker* 0.1.0 package for R (Jin & Qian, 2019). *V.phylomaker* matches our given species list with the mega tree "GBOTB.extended.tre" that includes 74,533 species, and is the product of the combination of two previous mega trees (Zanne et al., 2014; Smith & Brown, 2018) with branch lengths indicating the chronological time (millions of years). Species that were not matched with the mega tree were added to the resulting tree following the criteria of Scenario.2, where new tips are inserted to randomly selected nodes below the genus or family level basal nodes (Qian & Jin, 2016; Jin & Qian, 2019).

Finally, to test whether facilitation balances performance disparities among associated plants in the studied communities, we compared the overall NPD against a null model, in which the position of the plants (associated vs non-associated) was randomly reshuffled 10,000 times. The reshuffling process kept our data structure regarding replicates per sublocality and species unaltered. Then we checked if our observed overall NPD was below the 95% credible interval extracted for the null model. We calculated the 95% credible interval using the method "HDI" with the function "ci" hosted in the *bayestestR* R package (Makowski et al., 2019). All analyses were carried out with the analytical software R (R Core Team, 2019).

3 | RESULTS

Our results indicate that plant communities on gypsum outcrops were strongly shaped by facilitation since all the studied species benefited from the facilitation (i.e., for all species RII > 0). These species represent the target community well since they include 93.18% of the adult plants and 91.23% of the community recruits. Besides, these species vary in their relative abundance (from 1% to 20%) and are gradually distributed along the gypsum affinity gradient (Figure 3).

The evaluation of the effect of neighborhood on performance differences (NPD) is based on 23 species that represent well the target community, as their coverages account for 88.60% of total cover in the stressful sublocalities. The plants growing associated were grouped in 2513 patches with an average of 2.96 ± 1.62 species per patch and a maximum of 13 species in a unique patch. In addition, there was considerable variation in the difference between plant size associated vs non-associated across species, with some species showing up to 67% reduction of plant size when growing associated, while others increased their size up to 77% (mean $\pm$ SD = 17.03 ± 35.67). These differences across species regarding the influence of the neighborhood on their size provide the arena to observe compensatory effects potentially resulting in a reduction of species' dissimilarities in size (i.e., performance dissimilarities).

3.1 | Facilitation favors the establishment of rare species

Our results show a significant relationship between species' abundance and gypsum affinity (*g*), with abundant species showing a greater gypsum affinity [model a, *g* post mean effect = 0.142, 95% confidence interval (CI) = (0.075, 0.215), R^2 = 0.2001]. At the same time, species with low gypsum affinity, and therefore rare species, show higher facilitation strength [model b, *g* post mean effect = −0.257, 95% CI = (−0.386, −0.146), R^2 = 0.479; Figure 4]. These relationships were significant after accounting for the species' phylogenetic relationships (Appendix S1: Figure S1) and locality effects in both models: (a) phylogeny post mean effect = 0.002, CI 95% (0, 0.006), locality post mean effect < 0.001, CI 95% (0, <0.001); (b) phylogeny post mean effect < 0.001, CI 95% (0, <0.001), locality post mean effect = 0.043, CI 95% (0, 0.115).
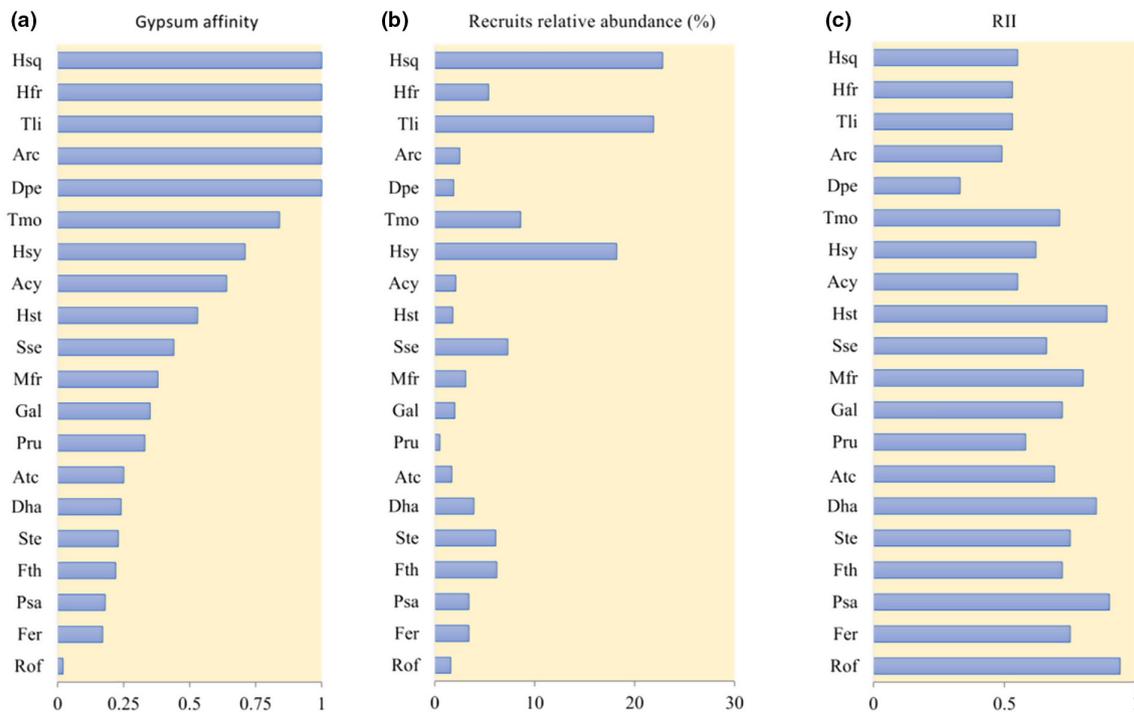
FIGURE 3 Characteristics of the examined species: (a) gypsum affinity (g), (b) relative abundance of recruits, (c) relative interaction intensity index (RII) showing the degree of facilitation, as all RII values are greater than 0. Check Table S2 for detailed numbers and variation across localities. Species codes: Acy, *Anthyllis cytisoides*; Arc, *Artemisia campestris*; Atc, *Atractylis cancellata*; Dha, *Diplotaxis harra*; Dpe, *Dorycnium pentaphyllum*; Fer, *Fumana ericoides*; Fth, *Fumana thymifolia*; Gal, *Globularia alypum*; Hfr, *Herniaria fruticosa*; Hsq, *Helianthemum squamatum*; Hst, *Helichrysum stoechas*; Hsy, *Helianthemum syriacum*; Mfr, *Matthiola fruticulosa*; Pru, *Phagnalon rupestre*; Psa, *Phagnalon saxatile*; Rof, *Rosmarinus officinalis*; Sse, *Sedum sediforme*; Ste, *Stipa tenacissima*; Tli, *Teucrium libanitis*; Tmo, *Thymus moroderi*

3.2 | Facilitation balances species' performances

Performance disparities were lower between plants growing associated than those growing non-associated with other plants, as indicated by the negative effect of the neighborhood on performance disparities (NPD = −1.012). The observed overall NPD was lower than 99.21% of the overall NPDs obtained with randomized data under the null model (Appendix S1: Figure S2). In addition, the negative NPD was consistent for the majority of the species in the community (Figure 5). Thus, when we independently considered the averaged NPDs across all the pairwise interactions in which each species is involved, 17 of the 23 species presented overall negative values, representing 97.46% of total relative abundance in the community.

4 | DISCUSSION

Our findings show two critical aspects of facilitation than can buffer species loss. First, we show that facilitation favors the establishment of rare species with low affinity for the substrate. Second, when plants become adults, we show that facilitation reduces performance dissimilarities between the community

species. These observations could have implications for species maintenance.

4.1 | Facilitation favors the establishment of rare species

Our results indicate that rare species tend to show low gypsum affinity, and facilitation is stronger for these species. These findings suggest that facilitation could maintain higher species richness than expected on the bare ground by preventing the local extinction of these low-abundant species. Some studies have shown that facilitation favors rare species (Soliveres et al., 2015a; Calatayud et al., 2020), while others have provided empirical evidence that facilitation is more determinant for those species living out of their ecological optimum (Liancourt et al., 2005; Gross et al., 2009; Le Bagousse-Pinguet et al., 2014b; Qi et al., 2018). Our results help bring together these two visions, showing that rarity and environmental fitting can be related. Species with low edaphic affinity may show limited abundance as they live out of their ecological optimum. These species differ from those with high gypsum affinity in the functional traits determining their responses to overcome environmental constraints (Sánchez-Martín et al., 2021).
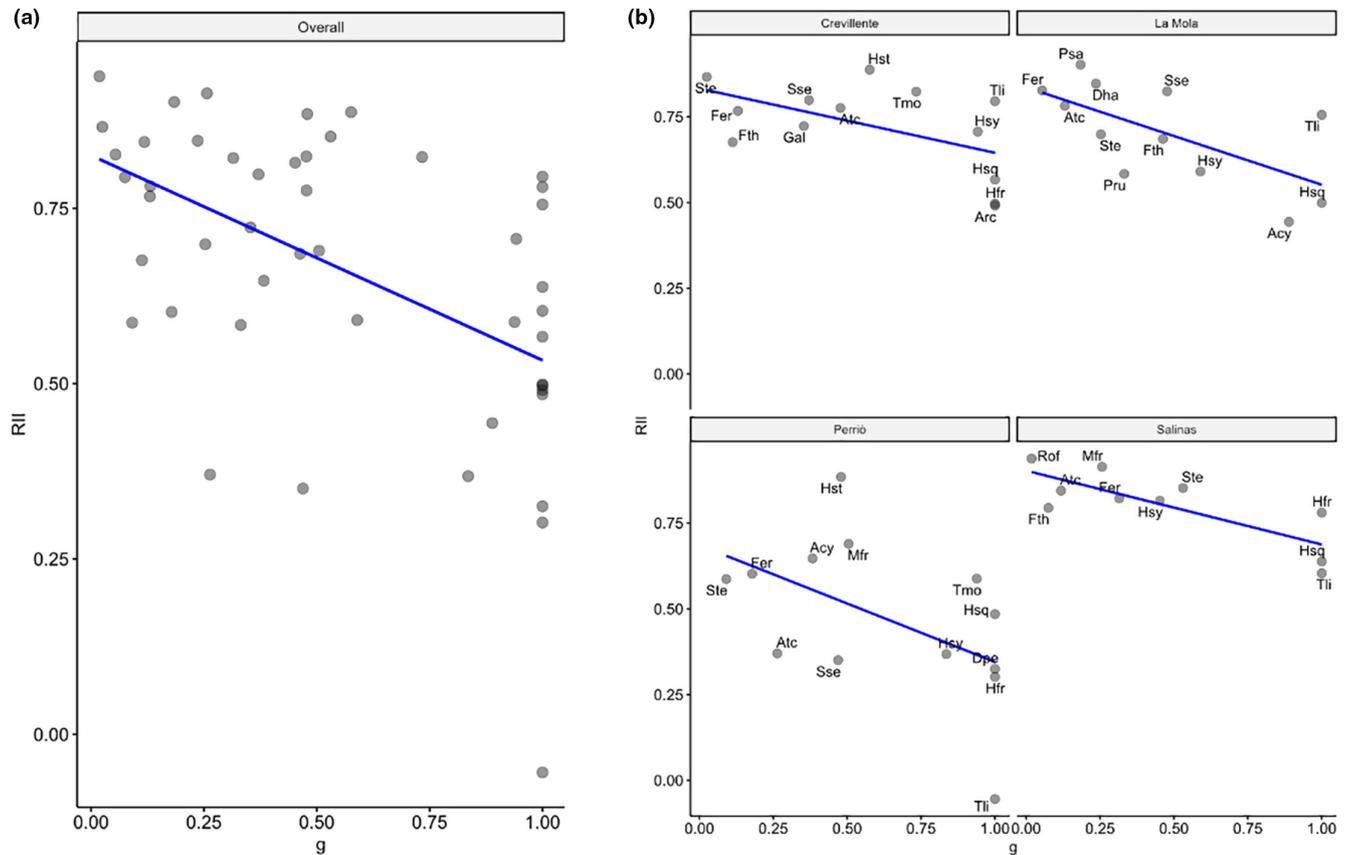
FIGURE 4 (a) Overall correlation between plant–plant interaction strength (RII) and gypsum affinity index (_g_), showing a negative correlation between facilitation and species' gypsum affinity, pooling data from all the localities together. (b) Correlation between RII and _g_ for each locality showing that the overall pattern found in (a) is consistent across localities. Species codes as in Figure 3
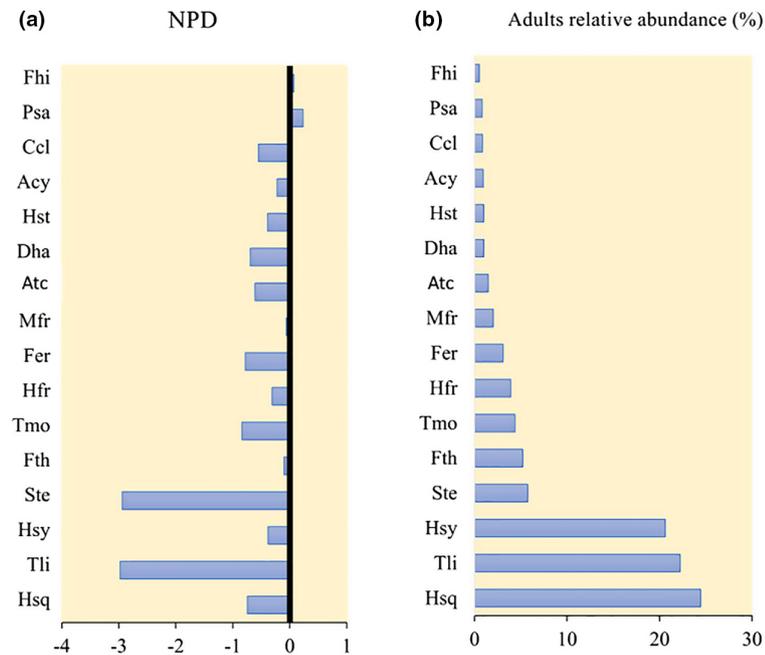
4.2 | Facilitation balances species' performances among adult species

We show that co-occurring adult species growing in interspecific vegetation patches reduce performance disparities compared to their isolated adult conspecifics. Although our approach does not allow us to identify the precise mechanisms that balance species' sizes, the observed effect must be directly or indirectly mediated by facilitative effects between the neighboring plants. Among the potential underlying mechanisms at work could be those related to nutrient and water transfer (Montesinos-Navarro et al., 2016, 2017, 2019b), or the sharing of beneficial mycorrhizae (Sortibrán et al., 2019), among others. Moreover, the observed reduction in NPD is consistent when we independently considered the averaged NPDs across all the pairwise interactions, which implies that the facilitation role in reducing performance disparities is not derived from the effect of particular species but something general to the community. Our findings highlight that facilitative effects may endure throughout the species' life. Despite the potential implications of our findings, further research is needed to understand what specific processes or mechanisms underpin our observational data to comprehend how facilitation shapes the diversity of natural communities.

We show that facilitation not only plays an essential role in allowing the establishment of rare species, but it also balances

species' performances at the adult stage. That balance in performance can guarantee the interactant's survival by complex mechanisms beyond abiotic amelioration that reduces the likelihood of the species' exclusion. Indeed, both processes may have additive effects, boosting the role of facilitation in preserving diversity. It is tempting to make an analogy between these two processes and the two major forces for species' coexistence (Chesson, 2000): on the one hand, the promotion of rare, stress-sensitive species could be assimilated with stabilizing niche differences that limit species' dominance when species become common while avoiding the extinction of rare ones; on the other hand, the reduction of disparities in performance could be viewed as equalizing mechanisms reducing fitness differences between species. Our findings suggest that the role of facilitation in species coexistence is more intricate and substantial than previously thought. Combining multiple facilitation mechanisms may result in emerging effects that favor diversity maintenance in communities driven by facilitative effects through the whole lifespan of the species. These findings have implications for species conservation. The demonstrated influence of facilitation in shaping the assembly of natural communities prompts a greater understanding of the interplay of processes that determine the realization of these interactions and how these may be affected by environmental changes.

FIGURE 5 (a) Average effect of the neighborhood on performance disparities (NPD) for each species and (b) their relative abundance (%). The results show consistency regarding the effect of the neighborhood on reducing performance disparities. Only species with a relative abundance greater than 0.5% are displayed. Species codes as in Figure 3

DATA AVAILABILITY STATEMENT

Data and R code needed to reproduce the manuscript's results are available in Zenodo at: https://doi.org/10.5281/zenodo.7774656

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SUPPORTING INFORMATION

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

Appendix S1. Supporting figures and tables.