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LETTER

Phenotypic structure of plant facilitation networks

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Abstract

Identifying the plant traits that determine the outcome of facilitation interactions is essential to understand how communities are assembled and can be restored. Plant facilitation networks are phylogenetically structured but which traits are behind such a pattern is unknown. We sampled plant interactions in stressful ecosystems from south-eastern Spain to build seedling and adult facilitation networks. We collected 20 morphological and ecophysiological traits for 151 species involved in interactions between 879 nurse individuals benefiting 24 584 seedlings and adults. We detected a significant phenotypic signal in the seedling facilitation network that was maintained in the adult network, whereby functionally similar nurses tended to facilitate functionally similar species whose traits differ from those of their nurses. We provide empirical evidence to support a long-lasting theoretical postulate stating that facilitation networks are phenotypically structured. Trait matching through which nurse and facilitated species avoid phenotypic overlap, and consequently competition, is the main linkage rule shaping plant facilitation networks.

Keywords

Community assembly, competition, ecological networks, functional complementarity, mine tailings, phenotypic signal, plant traits.

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INTRODUCTION

Plant facilitation is an ecological interaction in which one species enhances the recruitment of another species and none of them is harmed (Stachowicz, 2001). The last three decades have witnessed a burst of observational and experimental studies aimed to unravel the mechanisms behind such interaction (Callaway, 2007; Brooker *et al.*, 2008). Most of these studies have focused on interactions established by just one (or a few) nurse species in the community (Maestre *et al.*, 2009). In 2008, plant facilitation interactions started to be considered as a complex network of multiple nurses facilitating the recruitment of many species in the community (Verdú and Valiente-Banuet, 2008). Plant facilitation networks were initially conceived as the result of the evolutionary history of plant species under the assumption that divergent evolution of traits should favour the establishment of facilitative interactions. The rationale behind this prediction is that functional traits determining the regeneration niche of plant species tend to be evolutionarily conserved and strongly different between nurses and facilitated plants (Valiente-Banuet and Verdú, 2007). While nurses have evolved traits allowing them to recruit under stressful conditions, facilitated plants are less stress tolerant (Valiente-Banuet *et al.*, 2006; Butterfield and Briggs, 2011). It is well known that the long-term success of facilitated plants is higher in stress-sensitive than in stress-tolerant plants (Navarro-Cano *et al.*, 2016), and therefore, it could be expected that nurses influence the trait values of their beneficiaries (Schöb *et al.*, 2012; García-Cervigón *et al.*, 2015). Paradoxically, more than a decade after setting the initial assumption of divergent traits favouring facilitation and despite the vast amount of literature looking at trait patterns in facilitation (Butterfield and Callaway, 2013; Le Bagousse-Pinguet et al. 2015; Liancourt and Tielbörger, 2011; Michalet *et al.*, 2011; Schöb *et al.*, 2013; Soliveres *et al.*, 2014), phenotypic distances between species have never been used to explain the structure of plant facilitation networks. Instead, phylogenetic distances – taken as a proxy of trait divergence between species – have become the common procedure to test it (Alcántara *et al.*, 2018, 2019; Marcilio-Silva et al. 2015; Valiente-Banuet and Verdú, 2008; Verdú *et al.*, 2010). Indeed, little empirical research addressing the link between traits and facilitation networks at the community level exists despite the broad consensus that predicting community and ecosystem processes from species traits is a 'Holy Grail' in ecology (Lavorel and Garnier, 2002; Funk *et al.*, 2017).

Another knowledge gap on the facilitation theory refers to the piece of the definition stating that [...] *none of them is harmed.* Studies focusing exclusively on the recruitment stage cannot discard that facilitation shifts to competition when facilitated plants grow up (Tielbörger and Kadmon, 2000). In fact, evidence exists pointing to several directions, with initial positive nurse effects on seedlings reverting to negative (Miriti, 2006), neutral (Urza *et al.*, 2019) or remaining positive (Paterno *et al.*, 2016) on adults. Phylogenetically informed facilitation networks between adult nurses and facilitated

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species have helped testing whether initial facilitation interactions persist over time (Valiente-Banuet and Verdú, 2008; Verdú *et al*., 2010). But, again, despite the rationale was that persistent interactions would be those involving the most functionally different species, phenotypically informed networks have never been used to test this hypothesis. Increasing evidence on the permanence of interactions between functionally different species exist (Navarro-Cano *et al*., 2019), and explanations have invoked not only the conventional wisdom of competition reduction but also mutual help between species (Sortibrán *et al*., 2014, 2019; Montesinos-Navarro *et al*., 2016, 2017). These new results open a research avenue to search for functional traits that could be putatively involved in the maintenance of facilitation networks with time. Here we evaluate, for the first time, the phenotypic signal of a plant facilitation network under the hypothesis that facilitation is mediated by trait differences in a phenotypically structured fashion. Phenotypic signal in plant facilitation networks may emerge under different scenarios, depending on the phenotypic distance between nurse species, between facilitated species and among nurse-facilitated species pairs (Fig. 1). Based on the knowledge explained above, we hypothesise that a positive phenotypic signal will emerge following a scenario where functionally similar nurses will tend to facilitate functionally similar species whose traits differ from those of their nurses (Fig. 1b). We also hypothesise that such a phenotypic signal will not be erased with the transition from seedling to adult networks but different traits, especially those related to competition, will have a larger contribution to the structure of the network. We first built the plant facilitation network depicting previously studied facilitative interactions occurring in abandoned mine tailings in Southern Spain (Navarro-Cano *et al*., 2018). Then, we collected information on 20 above- and below-ground phenotypic traits of the 151 species involved in facilitative interactions. Finally, we checked the existence of a phenotypic signal following the fuzzy-weighting approach developed by Bastazini *et al*. (2017) and evaluated whether the traits of nurse and their facilitated species tend to be different (Fig. 1b) or similar (Fig. 1a). To test whether the phenotypic signal of the network is eroded or amplified with time, we compared the signal of the network built with seedlings vs. that constructed with adults of facilitated plants.

MATERIAL AND METHODS

Study sites

We performed this study in twelve mine tailings from the Cartagena-La Unión Mining District in south-eastern Spain (*Sites* in Fig. 2) whose geographical coordinates are shown in Table S1. Climate is semiarid Mediterranean (17.9°C average annual temperature, 316 mm rainfall and 762 mm evapotranspiration). These mine tailings are the product of the refining process of various metals. They were abandoned from 35 to 45 years ago. From an ecological perspective, these sites function as anthropogenic micro-deserts (tailing areas ranged from 0.4 to 9 ha) shaped by wastes that are mainly composed of quartz, gypsum, magnetite and sphalerite, with high concentrations of As, Cd, Cu, Pb, Zn, Fe and Mn among other metals (Conesa and Schulin, 2010; Navarro-Cano *et al*., 2018). These geological substrates feature very low fertility and high salinity. Still, since abandonment the tailings have been colonised by stress-tolerant species that have further allowed the patchy establishment of a community of facilitated species, as we have described elsewhere (Navarro-Cano *et al*., 2018).

Plant facilitation networks

In 2015, we sampled the plant communities in the 12-studied tailings (Table S1), including both the facilitation-driven multispecific plant patches and their surrounding open areas. Based on these data, we identified a total of 13 species acting as nurse plants that promoted seedling establishment of up to 151 beneficiary species (Navarro-Cano *et al*., 2019). Species classified as nurses were able to colonise barren soils, decrease soil abiotic stress, increase soil fertility and microbial productivity, and facilitate the recruitment of other species under their canopy (Navarro-Cano *et al*, 2018). This information, together with planting experiments beneath nurses and on the barren soil (Navarro-Cano *et al*, 2019), allowed us to know that the spatial association between species in our networks is a result of facilitation and not a consequence of shared microhabitat preferences between species. In order to build the plant facilitation network, we recorded all the beneficiary plants beneath the canopy of 879 nurse plants. A minimum of 30 randomly selected patches per nurse species was sampled in the tailings where the nurse inhabited (Table S1). In the cases where the existing patches of a nurse species was fewer than 30, all of them were sampled (Table S1). Within each patch, all beneficiary species were recorded, including seedlings (plants showing cotyledons, first leaves and soft stems) and adults. Average patch size varied depending on the identity of the nurse species, from a diameter of 18.1 ± 12.8 cm in *Limonium carthaginense* to 322.6 ± 187.2 cm in *Tamarix canariensis*. To account for the contrasted patch size, we estimated the relative abundance of each beneficiary species within the patch (number of plants$\cdot$m^{-2}).

We constructed two type of networks: (1) adult nurses facilitating seedlings of any species in the community ('seedling networks' hereafter) and (2) adult nurses facilitating adults of any species ('adult networks' hereafter). Seedling and adult facilitation networks were constructed as quantitative matrices representing the density of seedlings or adults of each plant species under each nurse species (*Facilitation matrix* F_{FN} in Figure 2). All the information on these networks can be found at Navarro-Cano *et al*. (2019) and interactive diagrams shown at https://www.uv.es/verducam/Seedlings.html and https://www.uv.es/verducam/Adults.html

Plant species traits

We constructed species trait matrices for nurses and facilitated species (T_F and T_N in Figure 2) from a database of 20 functional traits for the 151 species found in the study area (Navarro-Cano *et al*., 2019). We included two whole-organism traits (specific life form and bud height), seven above-

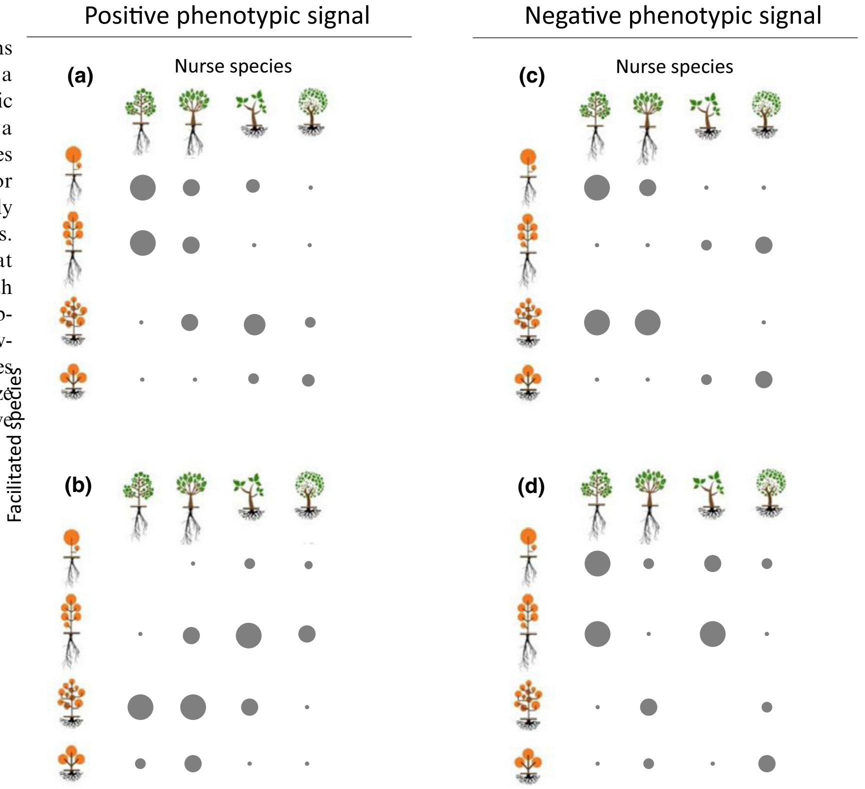

Figure 1 Facilitation networks where interactions (bubbles) between nurse and facilitated species have a positive (a and b) or negative (c and d) phenotypic signal. Positive phenotypic signals indicate a dominance of phenotypically similar species interacting with phenotypically similar species. For example, deep-rooted nurses facilitate most intensely either (a) deep-rooted or (b) shallowed-rooted species. In contrast, negative phenotypic signals indicate that phenotypically similar species tend to interact with phenotypically dissimilar species. For example, deep-rooted nurses facilitate most often deep and shallow-rooted species (c), or deep and shallow-rooted nurses facilitate deep-rooted species (d). Bubble size represents the magnitude of the facilitative interaction.

ground morphological traits (plant height, specific leaf area, leaf length, area, thickness, seed size and dispersal), four below-ground morphological traits (root length, depth, laterality and specific root length) and seven ecophysiological traits (metabolism, flowering phenology and span, halophytism, xerophytism, sclerophytism and resprouting ability). Whole-organism and ecophysiological traits were obtained from the literature and own local observations. Mean values of above- and below-ground morphological traits were obtained from five adult plants that were haphazardly sampled in the same mining district, fully dug up and collected, and therefore reflect the stressful environmental conditions faced by the individuals in the study site. Above- and below-ground parts of the plants were separated in the laboratory. It is obvious that adult traits cannot be responsible of the outcome of facilitated seedlings. However, the problem to score seedling traits for all the species in the network is to delimit the time along the early ontogeny when measures should be taken. Our approach assumes that adult traits are representative of seedlings. This is not unexpected as significant correspondence between traits of adults and seedlings across species has been described (Cornelissen *et al*., 2003). In any case, to check for the robustness of the results, we also calculated the phenotypic signal only with those traits that are invariant along the ontogeny (i.e. seed size, sclerophytism, metabolism, resprouting ability, specific life form, xerophytism, halophytism). The trait database containing raw data as well as their ecological meaning, following Navarro-Cano *et al*. (2019), are provided in Supplementary Material S1.

Phenotypic differences between nurse and facilitated species

We first tested the existence of significant differences between the mean values of nurse and facilitated species for all traits in the study area. Trait differences between nurse and facilitated species were tested through generalized linear models for quantitative variables with Gaussian (plant height, leaf length, area, and thickness, root length, depth and laterality, seed size) or Poisson (flowering span) distribution of errors. For categorical variables (specific life form, bud height, seed dispersal, metabolism, flowering phenology, halophytism, xerophytism, sclerophytism and resprouting ability), significant differences between nurses and facilitated species were tested through chi-square tests. Standardised residuals greater than |1.96|, which are beyond the interval that contains 95% of the population, were used to identify which trait state was significantly associated to nurses or facilitated species.

We subsequently confronted the traits of the nurses and their facilitated plants in each observed interaction to check whether they were similar (e.g. as in Figure 1a) or different (e.g. as in Figure 1b). After visually inspecting the phenotypic space covered by all the interactions between nurses and their respective facilitated plants, we compared their phenotypic distances against a null model where pairs of species were randomly associated (Navarro-Cano *et al*., 2019). If traits of nurse and their facilitated plants are different, we expect lower overlap (i.e. higher phenotypic distance) than expected by the null model. Pairwise functional distances were calculated with the Gower´s index in the *daisy* function of the cluster R package (Maechler *et al*, 2017).

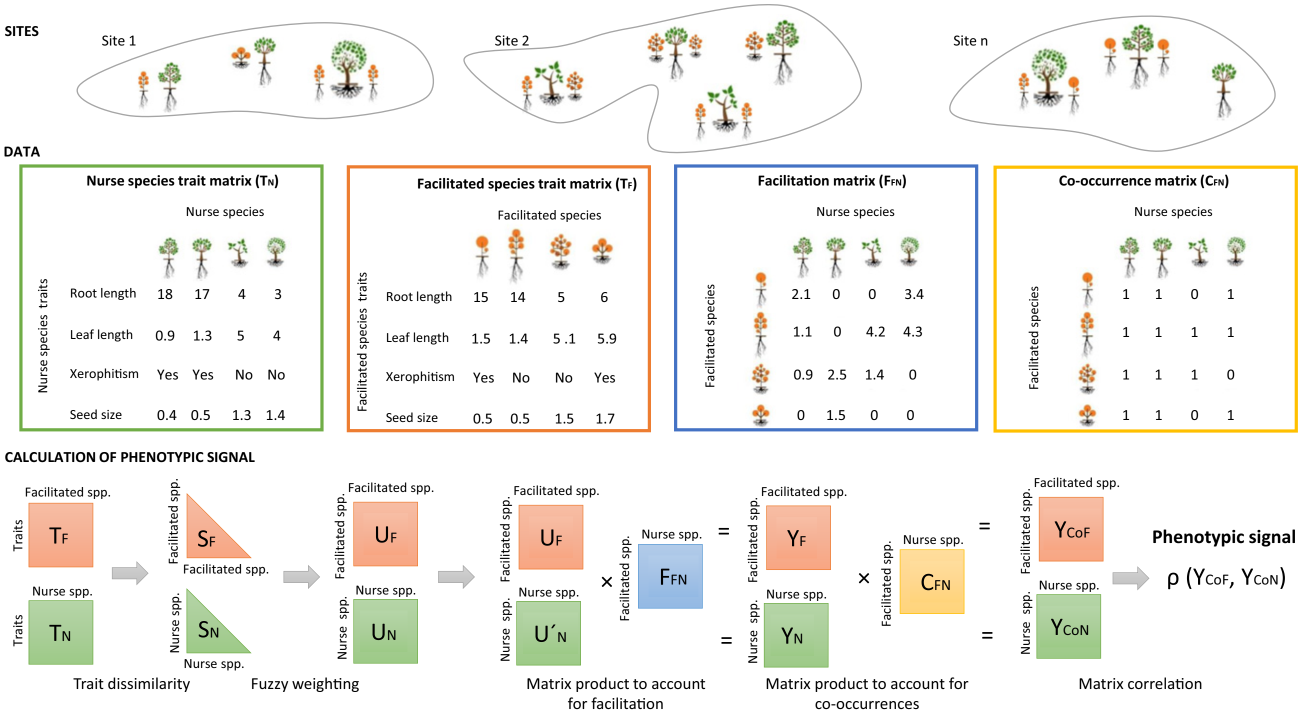

Figure 2 Analytical framework to calculate phenotypic signal for the facilitation networks, adapted from Bastazini *et al.* (2017). We used trait matrices for nurse (T_N) and facilitated species (T_F), as well as a facilitation matrix (F_{FN}) with the density of seedlings or adults of each facilitated species under each nurse species, and a co-occurrence matrix (C_{FN}) with species co-presences (not only interactions) across multiple sites. See Methods for a description of each step.

Phenotypic signal of facilitation networks

The phenotypic signal of facilitation networks was calculated following Bastazini *et al.* (2017) analytical framework under the fuzzy set theory, a theory that has successfully described metacommunity assembly patterns using information on species phenotypes and co-occurrences (Pillar and Orlóci, 1991; Pillar *et al.*, 2009). The method described in Bastazini *et al.* (2017) allows to account for forbidden interactions due to non-co-occurrences. This statistical approach requires trait matrices for nurse and facilitated species (T_N and T_F, respectively, in Figure 2) as well as the facilitation matrix (F_{FN}) that records the strength of species interactions. Optionally, a co-occurrence matrix (C_{FN}) that records species co-presences (not only interactions) across multiple sites can be included. Trait matrices are first converted into distance matrices (S_F and S_N) to be subsequently transformed into fuzzy sets (U_F and U_N; Fig. 2). The product of these fuzzy set matrices with the facilitation matrix provides the interaction-weighted-by-traits matrices (Y_F and Y_N). The correlation of Y_F and Y_N (or their versions accounting for co-occurrences, Y_{COF} and Y_{CON}) is the phenotypic signal (ρ). The phenotypic signal (ρ) may take values ranging from −1 to 1. Significant positive signals indicate that phenotypically similar species tend to interact with species that are, in turn, phenotypically similar among them (Fig. 1a and b). Negative signals are indicative of phenotypically similar species interacting with species that are phenotypically dissimilar among them (Fig. 1c and d). Non-significant signals indicate that the pattern of interactions is not mediated by the traits of the species.

In our case, as sampling was performed in different tailings, we included in the analysis a binary co-occurrence matrix between nurses and facilitated species to account for the possibility of forbidden interactions (e.g. a facilitated species is not associated to a nurse species because they never coexist in the same tailing). Distance matrices including both quantitative and qualitative phenotypic traits were calculated with the Gower index as implemented in the *gowdis* function of the FD package for R (Laliberté et al. 2014). Matrix Pearson correlations were performed with Euclidean distance as a resemblance measure between trait and facilitation matrices and statistical significance estimated after 9999 permutations against a null model in which the facilitation matrix was independent from the interacting species traits as explained in Bastazini *et al.* (2017). Specifically, permutations were performed among the column vectors in one of the fuzzy weighted matrices (UF, UN). Analyses were run in the R package SYNCSA (Debastiani and Pillar, 2012) with the R script provided in Bastazini *et al.* (2017).

Transition from seedling to adult network

To test which traits are behind the transition from seedling to adult networks, we first identified those interactions surviving from seedling to adult networks, and then calculated their functional distances trait by trait and compared against the distances obtained under a null model in which pairs of species were randomly associated.

.We also tested whether the magnitude of the phenotypic signal of the seedling network statistically differs from that of the adult network. To do so, we (1) constructed different subnetworks after grouping individual tailings on the basis of their species composition as reflected by a non-metric dimensional scaling (NMDS) analysis, (2) calculated the phenotypic signal of each subnetwork, and (3) tested differences between seedling and adult network signals throughout a paired *t*-test. NMDS was performed with the help of the *metaMDS* command in the vegan package for R (Oksanen et al. 2019).

RESULTS

Phenotypic differences between nurse and facilitated species

When nurses and facilitated species were analysed separately, they showed contrasted phenotypes in half of the traits examined (Table 1). Nurses tended to be tall perennial mesophanerophytes with long leaves and large roots, CAM/C4 metabolism and ability to resprout. In contrast, facilitated species tended to be short annuals or hemicryptophytes with short leaves, small roots and C3 metabolism. Other traits associated to phenology, sclerophytism, xerophytism, halophytism, seed size and seed dispersal did not differ between nurses and facilitated species (Table 1).

When the phenotype of nurses was confronted with that of their respective facilitated species for each pairwise interaction, the phenotypic space where facilitation interactions occur is not randomly filled for most of the traits (Figure 3). The predominance of points above the diagonal of plant height (85%), root length (87%), root depth (83%) and root laterality (88%) plots in Figure 3 indicates that facilitation interactions are mainly established between nurses that are taller and have longer, deeper and wider root systems than their facilitated species. The reverse situation with nurses that are shorter and have swallower roots than their facilitated species also occurs, but less often (points below the diagonal in Fig. 3). Regarding leaf traits, nurses tended to establish more facilitation interactions with species that have higher SLA (75%) and SRL (91%) although the reverse situation also occurred.

Seven traits (specific life form, photosynthetic metabolism, root length, depth and laterality, sclerophytism and halophytism) showed significant segregation between nurses and their respective facilitated species, whereas only three traits (leaf length, xerophytism and seed dispersal) were significantly overlapped (Table 2). Integrating all the traits in the analyses, the phenotypes of nurses and their respective facilitated plants were significantly more segregated than expected by chance (Table 2).

Seedling facilitation network

When nurses and facilitated species were analysed into a network context, including not only realised interactions but also non-realised interactions and forbidden links, we detected a positive and significant phenotypic signal. The signal was similar considering all traits ($\rho = 0.69$; $P < 0.0001$) or only those that are invariant along the ontogeny ($\rho = 0.70$; $P < 0.0001$). To check the relative contribution of individual traits to the

Table 1 Descriptive statistics of traits associated to nurse and facilitated species in the study area

Trait	Nurse	Facilitated	Statistical test
Specific life form (num. species)			
Annual	0^-	70^+	$\chi^2 = 9.1$; $P = 0.002$
Perennial	13^+	77^-	
Bud height (num. species)			
Chamaephyte	5	28	$\chi^2 = 17.1$; $P = 0.001$
Geophyte	1	5	
Hemicryptophyte	2^-	95^+	
Mesophanerophyte	3^+	5^-	
Nanophanerophyte	2	14	
Plant height (cm)	56.3 ± 7.5^a	27.2 ± 2.6^b	$t = 3.2$; $P = 0.001$
Flowering phenology (num. species)			
Autumn	0	7	$\chi^2 = 2.04$; $P = 0.56$
Spring	7	95	
Summer	3	18	
Winter	3	27	
Flowering span (months)	4.8 ± 0.9^a	4.3 ± 0.4^a	$t = 0.7$; $P = 0.45$
Leaf length (mm)	58.1 ± 22.1^a	31.3 ± 3.1^b	$t = 2.2$; $P = 0.03$
Leaf area (mm^2)	160 ± 54^a	478 ± 174^a	$t = -0.5$; $P = 0.58$
Leaf thickness (mm)	0.43 ± 0.06^a	0.37 ± 0.03^a	$t = 0.6$; $P = 0.52$
Seed size (mm)	3.20 ± 0.83^a	2.40 ± 0.14^a	$t = 1.5$; $P = 0.14$
Metabolism (num. species)			
C3	10^-	141^+	$\chi^2 = 4.93$; $P = 0.02$
C4/CAM	3^+	6^-	
Root length (cm)	62.0 ± 13.9^a	19.8 ± 1.4^b	$t = 3.7$; $P = 3\times10^{-10}$
Root depth (cm)	21.3 ± 2.9^a	11.3 ± 0.7^b	$t = 4.0$; $P = 9\times10^{-5}$
Root laterality (cm)	64.4 ± 17.3^a	13.6 ± 1.2^b	$t = 7.9$; $P = 3\times10^{-13}$
Specific leaf area	5.97 ± 0.8^a	13.05 ± 0.69^b	$t = -2.9$; $P = 0.003$
Specific root length	4.59 ± 1.45^a	146.1 ± 23.4^b	$t = -4.6$; $P = 6\times10^{-6}$
Sclerophytism (num. species)			
No	11	132	$\chi^2 = 0.01$; $P = 0.91$
Yes	2	15	
Halophytism (num. species)			
No	9	130	$\chi^2 = 2.3$; $P = 0.12$
Yes	4	17	
Xerophytism (num. species)			
No	2	37	$\chi^2 = 0.2$; $P = 0.65$
Yes	11	110	
Resprouting ability (num. species)			
No	3^-	96^+	$\chi^2 = 7.3$; $P = 0.006$
Yes	10^+	51^-	
Seed dispersal (num. species)			
Short distance (< 1 m)	1	43	$\chi^2 = 3.2$; $P = 0.19$
Medium distance (1–10 m)	9	69	
Long distance (> 10 m)	3	35	

For quantitative traits, means and standard errors of each trait are provided and statistical differences between nurses and facilitated species are denoted by different letters in the superscripts following generalized linear models with Gaussian or Poisson distribution of errors. For qualitative traits, the number of species in each category is shown and statistical differences are assessed through chi-square tests. Positive and negative superscripts indicate the category with more or less species than expected by chance.

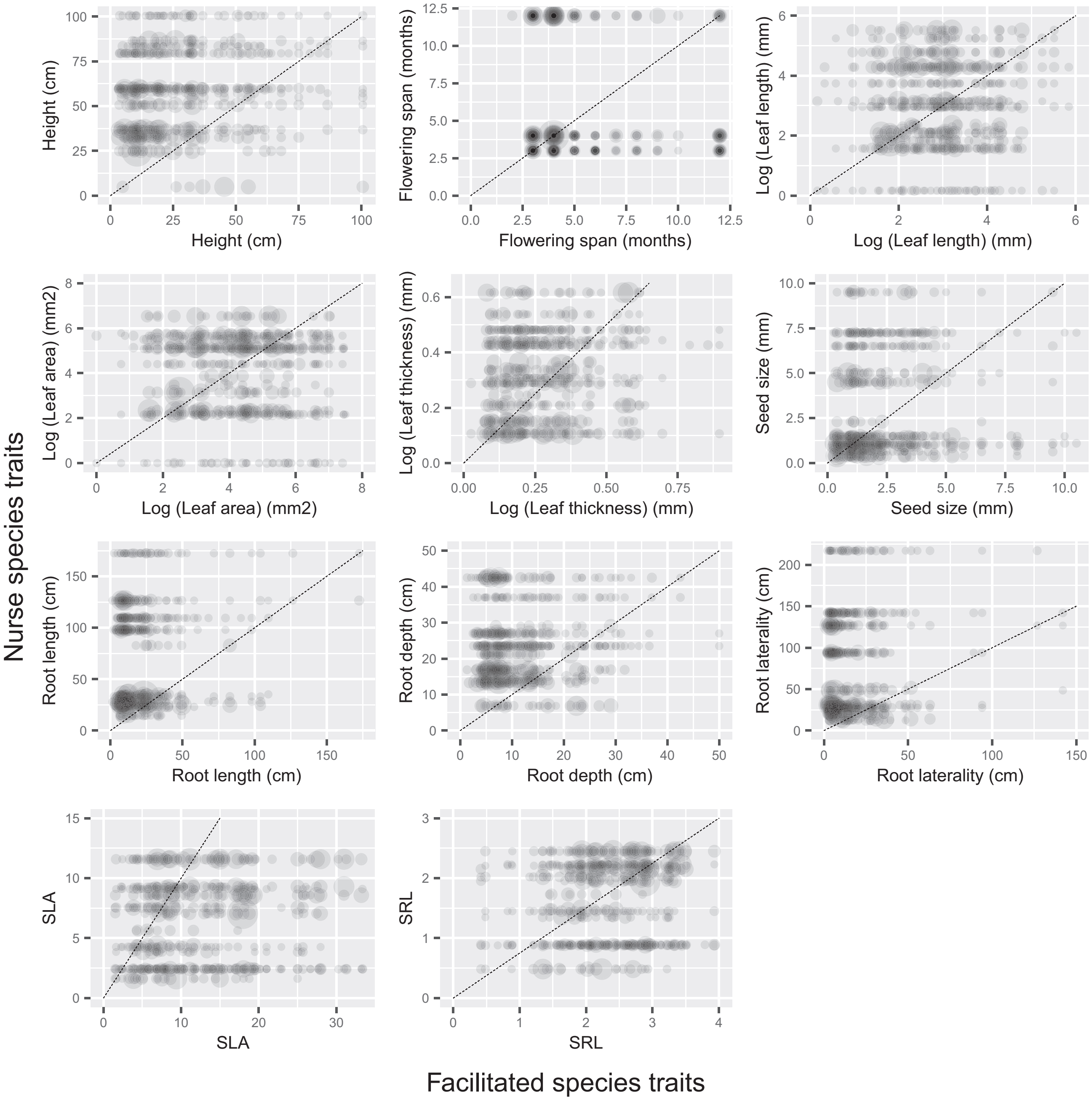

Figure 3 Representation of the continuous trait values of nurses (y-axes) and their facilitated (x-axis) plant species. Dot size is proportional to the facilitation strength. Points above (below) the dotted line indicate interactions where nurse have larger (smaller) trait values than their facilitated species.

phenotypic signal of the seedling network, we rerun the analyses contrasting trait by trait as shown in the left panel of Figure 4. Most of the phenotypic signals were positive (see color and key histogram in Figure 4) with values ranging from ρ=−0.17 to ρ = 0.91. The traits structuring more strongly the network of facilitation interactions (i.e. darker cells in the heatmap of Figure 4) included, for nurses, a cluster of leaf traits and plant height. For facilitated species, it involved a cluster of many traits related to plant height, leaves, roots and seed size.

Adult facilitation network

The adult facilitation network also showed a significant phenotypic signal ($\rho = 0.63$; $P < 0.0001$). For individual pairs of traits, most of the phenotypic signals were positive and ranged from ρ= −0.35 to ρ = 0.90. The nurse traits that best explained the pattern of facilitation adult interactions were, in addition to plant height and leaf traits, root depth and seed size (right panel in Figure 2). For facilitated plants, a myriad of traits related to height, leaves, roots and seed size were

Table 2 Comparison of observed trait distances between nurses and facilitated species (TDobs) against the mean distances (and standard deviations) obtained by a null model randomly associating pairs of species in the community (Mean TD null and sd TDnull)

Trait	TDobs	Mean TDnull	sd TD null	*P*-value
Specific life form	0.413	0.369	0.015	0.996
Bud height	0.768	0.749	0.014	0.880
Plant height	0.129	0.125	0.003	0.903
Flowering phenology	0.630	0.610	0.016	0.885
Flowering span	0.265	0.268	0.011	0.405
Leaf length	0.135	0.173	0.006	0.000
Leaf area	0.012	0.017	0.002	0.049
Leaf thickness	0.082	0.083	0.003	0.429
Seed size	0.249	0.253	0.007	0.293
Metabolism	0.349	0.285	0.015	0.999
Root length	0.323	0.265	0.008	0.999
Root depth	0.285	0.259	0.006	0.999
Root laterality	0.306	0.240	0.008	0.999
Specific leaf area	0.155	0.152	0.005	0.684
Specific root length	0.066	0.067	0.004	0.465
Sclerophytism	0.266	0.229	0.013	0.998
Halophytism	0.432	0.379	0.015	0.997
Xerophytism	0.237	0.311	0.014	0.000
Resprouting ability	0.597	0.563	0.016	0.972
Seed dispersal	0.534	0.568	0.015	0.013
All traits	0.312	0.292	0.003	0.999

Null model was run 999 times and therefore *P*-value > 0.975 indicates TDobs higher than expected by chance (i.e. trait segregation; dark grey rows), whereas *P*-value < 0.025 is indicative of TDobs lower than expected by chance (trait overlap; light grey rows).

relevant traits leaving a phenotypic signal in the network (right panel in Figure 2).

Transition from seedling to adult network

In the transition from seedling to adult networks, 80% of the 399 initial facilitation interactions survived to the adult stage. These surviving interactions were those involving nurses and facilitated species that differ in traits like photosynthetic metabolism, sclerophytism and root laterality more than expected by chance (Table S2). At the same time, surviving interactions occurred between species of similar leaf length, xerophytism, SLA and SRL (Table S2).

To check whether these changes in the traits explaining the transition of the interactions from seedling to adult networks resulted in an overall shift in the magnitude, we statistically compared their phenotypic signals after constructing subnetworks for groups of tailings with similar species composition (see non-metric multidimensional analysis in Figure S1). The magnitude of the seedling and adult subnetworks (Table S3) were not statistically different (paired *t*-test = 0.93; d.f.=3; *P* = 0.41).

DISCUSSION

We show, for the first time, that plant facilitation networks are structured following a significant phenotypic pattern. This pattern emerges because functionally similar species tend to recruit under functionally similar nurses, as in Fig. 1b. Furthermore, such phenotypic structure of the network is not eroded with time, when facilitated seedlings become adults.

A significant phenotypic signal in an interaction network results when interactions are not produced at random but mediated by the traits of both benefactors and beneficiaries (Bastazini *et al*., 2017). Previous phenotypic characterisations of nurses and facilitated species in different biomes have shown that both groups differ in their traits. Butterfield and Briggs (2011) found that facilitated species from North American deserts have larger seeds, are taller and invest more in roots than nurses. In Mediterranean-type ecosystems, Valiente-Banuet *et al.* (2006) showed that facilitated plants are animal-dispersed, evergreen, long-rooted, resprouter species with large leaves while nurses have the opposite trait states. Here we show that functional differences also exist between nurses and facilitated plants in extremely stressful mine tailings but in a different direction: nurses tend to have CAM/C4 metabolism, ability to resprout and are taller, have longer leaves and larger roots than facilitated species. It becomes clear that universal syndromes of nurse and facilitated plants do not exist and are strongly dependent on the environmental context (Butterfield and Callaway, 2013).

Facilitation is a species-specific interaction and therefore a suitable nurse for some species can be a strong competitor for others (Callaway, 2007). Consequently, the structure of our networks is the final outcome of a balance between competition and facilitation that requires further information than a simple categorisation of nurses and facilitated plants. To understand the outcome of the facilitation interactions, we should go beyond the characterisation of phenotypes of nurses and facilitated species separately and, instead, confront how these phenotypes match each other. Previous studies support this expectation, showing that differences in the effect traits of three nurse species significantly explain the differences in response traits of their facilitated plants (Schöb *et al*., 2017). Trait matching has been shown to drive other positive interactions, like pollination, and can be mediated by trait complementarity and/or exploitation barriers (Santamaría and Rodríguez-Gironés, 2007). Trait complementarity occurs when the trait value of one species fits the trait value of its interacting species (i.e. long-proboscis pollinator interacts with long-corolla plants while short proboscis pollinator interacts with short-corolla plants). In this case, trait values of both partners tend to overlap. In contrast, exploitation barriers, defined as traits that hamper access to the interaction, occur when a trait limits the interaction to those species whose traits are below a barrier value (i.e., long-corolla plants impede the interaction to short-proboscis pollinators) (Santamaría and Rodríguez-Gironés, 2007). In this case, trait values of both partners are not expected to overlap. Our results suggest that trait matching via exploitation barriers is the most relevant linkage rule explaining our facilitation network because trait values of nurses and facilitated plants tend to segregate rather than overlap. For example, in Figure 3, it can be appreciated that root depth is acting as a barrier trait with deep-rooted nurses impeding deep-rooted species to access its facilitative effect. However, the barrier is not impregnable as we found also cases of root-shallowed nurses facilitating deep-rooted species. Overall, the final result is translated into a significant

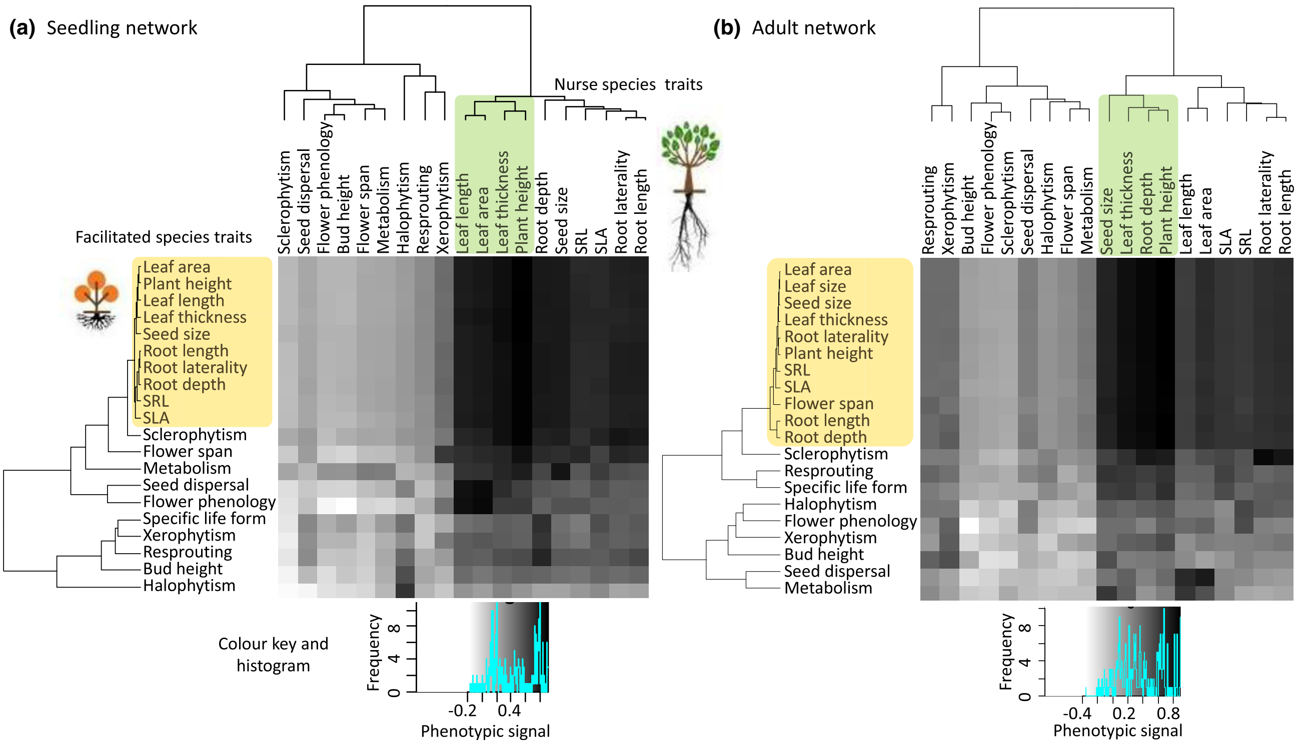

Figure 4 Heatmap showing the phenotypic signal of the facilitation network of interactions estimated with all pairs of facilitated and nurse traits for (a) seedlings and (b) adults of facilitated species. Phenotypic signal is proportional to cell darkness, as shown in the color key and histogram plots. Dendrograms group traits producing similar phenotypic signals across nurses (on columns) or across facilitated species (on rows). Shaded traits are those that best explained the phenotypic signal of the facilitation network.

phenotypic signal, indicating that nurses with similar phenotypes tend to facilitate species which are also similar in their phenotypes while being phenotypically distant from their benefactors. This result agrees with the experimental evidence provided in the same study system by Navarro-Cano *et al.* (2019) who found that the probability of germination of seeds from 10 species sown under 5 different nurses increased with the trait distance between the nurse and the facilitated species. Altogether, these results validate the premise and support the prediction made by previous studies using phylogenetic as a proxy of phenotypic distances between nurses and facilitated plants (Alcántara *et al.*, 2018, 2019; Marcilio-Silva et al. 2015; Valiente-Banuet and Verdú, 2008; Verdú *et al.*, 2010).

The significant phenotypic signal of our facilitation network reflects the combined effects of a suite of 20 functional traits in both nurses and facilitated species. To open the black box of this multivariate approach and identify the most relevant traits, we have recalculated the phenotypic signal in the network by using individual traits of nurses and facilitated species, as discussed below. This Cartesian reductionism is probably not the best way to understand the mechanisms underlying plant interactions but combining reductionistic and holistic approaches can be synergistic (Fang and Casadevall, 2011). The same methodology can be easily applied to delimitate the suite of traits that maximises the phenotypic signal of the facilitation network, and thus detect the combination of traits integrated at the whole-plant level that define recruitment strategies.

The network of facilitation interactions between nurses and seedlings is expected to display a phenotypic signal if (1) nurse species with similar traits provide similar microhabitats and (2) seedlings of species resembling in their traits require similar microhabitats to recruit (Verdú *et al.*, 2010). In our study system, we found that the most relevant nurse traits to explain the phenotypic structure of seedling facilitation networks were leaf traits and plant height. Both plant height and leaf characteristics can be important traits related to light interception and therefore shade provisioning, a key feature related to the first stages of facilitation (Callaway, 2007). On the other side of the interaction, the relevant traits for facilitated seedlings included a long list including plant height, seed size, root and leaf traits. All these traits correspond to the main components of the LHS (Leaf-Height-Seed) axes that define functional strategies in plants (Westoby, 1998) but adding a below-ground dimension and suggesting the phenotypic complexity that underlies facilitation networks. The below-ground dimension – the root traits of facilitated species – is directly related to seedling establishment and survival (Aschehoug and Callaway, 2014). Similarly, seed size is a direct and critical trait for establishment and survival (Harper *et al.*, 1970) and, as expected, we found it as one of the relevant traits of facilitated seedlings explaining the phenotypic signal of our facilitation network.

Even after facilitated seedlings have grown up, the majority of the initial facilitation interactions are maintained over time (80%). By comparing this figure with the 53% occurring in

Mexican desert communities strongly shaped by facilitation (Valiente-Banuet and Verdú, 2008), it becomes evident that facilitation is also crucial for adults to survive in our stressful mine tailings. Tracking the changes of interactions with the ontogeny of facilitated plants revealed a complex phenotypic landscape. More specifically, nurse and facilitated species resembling in leaf size, xerophytism, SLA and SRL and/or differing in photosynthetic metabolism, sclerophytism and root depth, constituted the pairs of species with higher probability to maintain their association until adult stages. A combination of conflicting forces, like habitat filtering limiting trait variability, and competition release promoting trait disparity, may explain this amalgam of traits underlying the fate of the facilitation interactions with time (Soliveres *et al.*, 2012). Despite all these changes in the transition from seedling to adults, the phenotypic signal of the interaction network was not eroded and maintained a similar magnitude. However, different traits, especially in nurses, were responsible of the structure of the network. Seed size and root length are traits that together with height and leaf traits become relevant for nurses to interact with their facilitated adult plants. Seed size cannot be considered as a trait directly linked to the nurse effect but it is correlated with a large number of ecophysiological traits indirectly related to it, such as plant longevity, growth rate, seed number or mycorrhizal infection (Leishman *et al.*, 2000). Root depth is also a crucial nurse trait in the adult network suggesting that below-ground competition becomes important between adult nurse and facilitated species. This result agrees with phylogenetic network analyses indicating that at this adult stage, nurses are no longer indifferent to the identity of their associated species because competition may alter the outcome of the interaction (Verdú *et al.*, 2010).

A signal left by competition is the reduction of trait overlap. For example, modelling approaches have detected that competition between roots of different depths is half that of roots of similar length (Rubio *et al.*, 2001). Indeed, our results shown in Table 2 indicate that facilitation traits of nurses and facilitated plants tend to segregate rather than to overlap, suggesting that competitive release is structuring the network. Not only trait segregation was more prevalent than overlap (7 vs. 3 traits) but, more importantly, the multidimensional phenotypes of nurses and their facilitated plants were significantly more different than expected by chance. Trait differences may result not only in reduced competition but also in increased benefits derived from complementarity (i.e. hydraulic lift from deep to shallow-rooted species; Zou *et al.*, 2005), ultimately promoting facilitation (Montesinos-Navarro *et al.*, 2017). Different linkage rules might be simultaneously shaping the structure of plant facilitation networks given the fact that plant interactions may result in synergic or antagonistic effects depending on the factor considered (Tirado *et al.*, 2015). The identification of relevant traits for each particular ecological process will allow us to understand how plant facilitation networks are assembled.

Caution is needed to infer casual ecological mechanisms based on correlations obtained in observational studies like those aimed to characterise complex ecological networks. Although experiments involving all the species in the complex network are logistically unfeasible, the observed patterns can be properly tested in a subset of species. The correlative patterns we show in our facilitation network are greatly supported by the reanalysis, trait by trait, of the germination experiment described in Navarro-Cano *et al.* (2019). The emergence success of the seeds experimentally sown under nurses significantly increased with the trait distance between the target and the nurse species in terms of seed size, specific leaf area, specific root length and seed dispersal (Table S4).

To guide the identification of relevant traits for future studies, we highlight here several methodological outcomes emerged from our analysis. The most evident issue is that continuous variables have greater explanatory power than categorical variables. Thus, future studies would benefit from more accurate measures of variables that are usually categorised in classes. For example, photosynthetic metabolism has been recognised as a relevant trait for facilitation (Yu & D´Odorico 2015) but categorical classes like CAM/C4/C3 could be better quantified given that the same species may vary its nocturnal rates of CO_2 fixation depending on the environment and its ontogenetic stage (Winter *et al.*, 2015). Quantitative measures of the relevant traits for facilitation are especially important in situations where subtle differences in phenotypes cascade into drastic microhabitat differences for facilitated seedlings (Cavieres *et al.*, 2008; Hupp *et al.*, 2017). To properly capture not only the continuous nature of the measured variable but also its variation with time and space, intraspecific trait variability should be included in the study of plant facilitation networks (Poisot *et al.*, 2015). For example, some studies have shown that a single nurse species may have different phenotypes that have very contrasting effects on their facilitated plants (Michalet *et al.*, 2011; Jiang *et al.*, 2018; Pistón *et al.*, 2018). To capture the intraspecific temporal variation of traits is especially problematic for seedlings, which have fast growing rates and it is hard to determine when to measure them (Butterfield and Briggs, 2011). Assigning adult traits to seedlings is not an optimal solution, but our results indicate its ability to predict the network of interactions. Caution is needed with this approach and other sources of trait variability, such as environmental or geographical, should be captured by measuring adult traits *in situ* to reflect the actual conditions under which individuals are growing.

In conclusion, we demonstrate that a trait-based approach may successfully explain the complexity of plant interactions. The identification of traits behind the interaction patterns established between nurse and facilitated plants will allow us not only to understand how biodiversity is shaped but also to apply such a knowledge to ecological restoration. This field is recently including trait-based facilitation approaches in order to promote plant–soil feedbacks and restore not only species but also ecosystem functions (Montoya *et al.*, 2012; Navarro-Cano *et al.*, 2018).

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AUTHORSHIP

All the authors conceived the study. JANC and MG collected the field data. MV and JANC conducted the statistical analyses and wrote the first draft. All authors provided critical reviews before giving approval for submission of the final version.

DATA ACCESSIBILITY STATEMENT

Data on plant species traits are provided as Supplementary Material and will be archived in Dryad. Network figures, including detailed data or every link are deposited in https://www.uv.es/verducam/Seedlings.html and in https://www.uv.es/verducam/Adults.html

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SUPPORTING INFORMATION

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

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